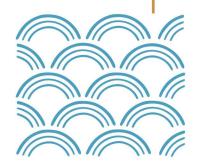
# THE FOSSIL WEEK

# **ABSTRACT BOOK**



# 5™ INTERNATIONAL PALAEONTOLOGICAL CONGRESS



From July 9th to 13th, 2018 France









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Dear Colleagues

Welcome to the Fossil Week!

After Sydney (Australia) in 2002, Beijing (China) in 2006, London (United Kingdom) in 2010 and Mendoza (Argentina) in 2014, we have the honour to organize the IPC5 in France and in Paris.

France is often considered to be the birthplace of palaeontology (not only by the French!), with Georges Cuvier as the founding father of the discipline. The large number of important fossil localities that were easily accessible to the first natural scientists was of great importance for the early development of palaeontology.

The Count of Buffon, Steward of the King's Garden and encyclopaedic naturalist of the 18th century, influenced greatly Georges Cuvier, who is widely considered to be the founder of palaeontology. Indeed, Georges Cuvier developed palaeontology into a scientific field; the term "palaeontology" was used for the first time by Henri-Marie Ducrotay de Blainville, his successor in the Museum. As for Jean-Baptiste Lamarck, founder of invertebrate palaeontology, he laid the foundations of biostratigraphy and of palaeoclimatology. The first Chair of Palaeontology in the National Museum of Natural History was created for Alcide d'Orbigny.

We have deliberately chosen to hold the Congress in the 5th arrondissement which is one of the oldest neighbourhoods in Paris. Perhaps it will be less convenient than a big congress centre but we expect that you will enjoy the undeniable charm of our capital and particularly of the surroundings of the Congress area.

Thank you for joining us to enjoy the Fossil Week!

Sylvie Crasquin General chair





#### ORGANIZING COMMITTEE



The organizing structure is the CR2P (<u>Centre of Research on Palaeobiodiversity and Palaeoenvironments</u>). This laboratory is composed of lecturers and professors from the <u>MNHN</u> (<u>National Museum of Natural History</u>) and the <u>Sorbonne University</u> and of researchers from the <u>CNRS (National Scientific Research Center</u>). Altogether, the CR2P includes 41 tenured scientists, 27 postdocs and PhD students, and 27 engineers, technicians and administrative staff. This makes it one of the largest research laboratories in the world exclusively devoted to Palaeontology. The French Geological Society (SGF) will support the congress organization.

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# **PLENARY LECTURES**

Marion Bamford // Diversity of Gondwanan fossil woods from southern Africa and palaeoclimate implications
Anjali Goswami // Assessing the macroevolutionary consequences of phenotypic integration with dense phenomic data from living and extinct tetrapods
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Diego Pol // Major evolutionary steps in the history of gigantic dinosaurs: new evidence from the Southern Hemisphere



#### Diversity of Gondwanan fossil woods from southern Africa and palaeoclimate implications

Marion Bamford\*†

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In southern African the Karoo Basin is well known for its vertebrate fossil record and the Carboniferous to Jurassic biostratigraphic based on the fauna. There is, however, a good record of fossil plants and woods, of the Glossopteris and Dicroidium floras. A large collection of Permian and Early Triassic silicified woods from South Africa, Zimbabwe, Namibia, Botswana, Mozambique and Zambia is housed in the Evolutionary Studies Institute. By far the most common genus of secondary xylem woods is Agathoxylon with at least two species, A. africanum and A. karooensis. This genus has the typical araucarian alternate bordered pitting on the tracheid walls and has been called Dadoxylon and Araucarioxylon in the past. Other genera include Australoxylon with clusters of pits on the tracheid walls, and Prototaxoxylon with spiral thickenings on the tracheids, from the early Permian. Podocarpoxylon with abietinian tracheid pitting and Rhexoxylon with lobes of xylem separated by parenchyma, each with only a few species, have been collected from Triassic strata. In the Late Carboniferous and early Permian there are a few woods with piths preserved such as Megaporoxylon which were collected many years ago. This apparent lack of diversity in the woody plants is investigated and compared with the much higher diversity of leaf and pollen fossils. Preliminary work on growth rings is of limited use in palaeoenvironmental interpretations. Upper Cretaceous woods from onshore and offshore deposits are still predominantly gymnospermous but outcrops are not abundant. These woods are mostly podocarpaceous but members of the Euphorbiaceae and Monimiaceae occur on the south coast (Pondoland). The few Cenozoic records comprise and increasing diversity of angiospermous woods but do not reflect the huge floral diversity indicated by the pollen and the modern vegetation. In contrast with the Karoo Basin fossil record the Cretaceous and Cenozoic periods are poorly represented. The "African Erosion Surface", long recognised by geologists but with no consensus on its timing, is probably to be blamed for the poor fossil record of the Cenozoic.



<sup>\*</sup> Speaker

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# Assessing the macroevolutionary consequences of phenotypic integration with dense phenomic data from living and extinct tetrapods

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Phenotypic integration is a pervasive characteristic of organisms. Interactions among morphological traits, termed phenotypic integration, can be readily identified through quan-titative analysis of geometric morphometric data from living and extinct organisms. These interactions have been hypothesized to reflect genetic, developmental, and functional rela-tionships and to be a fundamental influence on morphological evolution on small to large time scales. Simulations using covariance matrices derived from landmark data for diverse vertebrate taxa confirm that trait integration can influence the trajectory and magnitude of response to selection. At a macroevolutionary scale, high phenotypic integration produces both more and less disparate organisms, and most often the latter, than would be expected under unconstrained evolution, thereby increasing morphological range, but also homoplasy and convergence. However, this effect may not translate simply to evolutionary rates. Here, I will discuss the macroevolutionary consequences of phenotypic integration for cranial evolution through deep time in tetrapods. While most large-scale studies of phenotypic integration and morphological evolution utilise relatively limited descriptors of morphology, such as lengths or a small set of homologous landmarks, surface sliding semilandmark analysis allows for detailed quantification of complex 3D shapes, even across highly disparate taxa. We conducted the largest analysis to date of morphological evolution across diverse tetrapod clades using a dense dataset of landmarks and sliding semi-landmarks spanning the entire cranium and nearly 300 million years of evolution. Crania are highly modular, but this pattern varies across tetrapods. Modules also have disparate magnitudes of trait integration, which reflect developmental complexity in some, but not all clades. Tempo and mode are similarly highly variable, with some modules, such as the basicranium of birds, showing early bursts of shape evolution, while other regions, such as the rostrum, show sustained change throughout clade evolution. Leveraging this high density morphometric data, we further demonstrate that variation is unequally distributed across the cranium and that distinct patterns of variation characterize different tetrapod clades.



<sup>&</sup>lt;sup>\*</sup> Speaker

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# Proterozoic-Phanerozoic state change in the blobal biosphere

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The familiar world of the Phanerozoic Eon characterizes only the last 14% of recorded Earth history. Proterozoic rocks record a distinct state of the Earth surface system, separated from the modern biosphere by temporally overlapping geochemical, tectonic, climatic and biological events. Multiple lines of evidence support the hypothesis that late Neoproterozoic biological transition occurred in the context of oxygen increase, although causation, quantification and timing remain uncertain. Data and models increasingly point to phosphorous as a key player in both the long term maintenance of the Proterozoic biosphere and its transformation to a distinct Phanerozoic steady state. In a low oxygen Proterozoic world, the kinetics of iron oxidation would have limited erosional fluxes of P to the oceans, and chemistry in ferruginous oceans would have expanded sinks for P, while limitations in oxidant availability would have restricted organic remineralization. The result would have been oceans with low rates of (mostly cyanobacterial) primary production. As Proterozoic sinks for P were oxygen dependent, any increase in pO2 would increase P availability and, hence, rates of primary production and O<sub>2</sub> generation: P and O<sub>2</sub> form a positive feedback loop that would facilitate long term state change. It has long been appreciated that oxygen should influence animal evolution for physiological reasons, but the P perspective suggests that rising pO2 would have played another, ecological role. Increasing primary production should increase the resource base for organisms atop food chains. Ecological models also suggest that as primary production increased, larger eukaryotic phytoplankton would have gained ecological importance, further enhancing the transfer of energy to highertrophic levels. Thus, oxygen may have facilitated animal radiation for both physiological and ecological reasons, with the diversification of carnivores further influencing animal ecology and evolution. Evidence that anoxic subsurface waters persisted well into the Paleozoic Era is consistent with narratives of late Neoproterozoic state change, as O<sub>2</sub> levels needed to support large predatory animals or achieve a new steady state with regard to P are much lower than those required to fully oxygenate the oceans. Although the timing and, therefore, drivers of eon-bounding state change remain contentious, both global glaciation and late Neoproterozoic orogenesis may have played key roles.

Speaker

# Digging up the Ediacaran: evidence for the early onset of intense animal activity from western Mongolia

Tatsuo Oji\*

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There are excellent exposures of Cryogenian to early Cambrian rocks in the Govi-Altai and Zavkhan provinces of western Mongolia. Bedded muddy limestone of the Zuun-Arts Formation in Bayan Gol valley in southern Altai Province preserves abundant trace fossils of deep, U-shaped burrows assignable to the ichnogenus Arenicolites. The horizons with Arenicolites are dated to the uppermost Ediacaran, based on a combination of carbon isotope chemostratigraphy and its correlation to other sections such as in China and Morocco, and the local first occurrence datum of the base-Cambrian index trace fossil Treptichnus pedum. There are many flat-pebble conglomerates associated with these Arenicolites. However, Arenicolites presumably lived on a relatively deep slope, rather than in a shallow shelf environment because of common slump beds near the horizons, suggesting that the flat-pebble conglomerates were also made by slump. Presence of deep burrowing in the late Neoproterozoic Mongolian succession suggests that the "Cambrian agronomic revolution" has commenced earlier, at least locally in tropical settings near the palaeo-equator. The existence of U-shaped burrows, presumably made by bilaterians, also suggests complex animal behavior such as predation and predator-avoidance in the burrows, a view that diverges from that of the "Garden of Ediacara".

Speaker

# Major evolutionary steps in the history of gigantic dinosaurs: new evidence from the Southern Hemisphere

Diego Pol\*†

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Sauropodomorpha is one of the three major lineages of dinosaurs and first radiated in the Late Triassic, becoming the dominant megaherbivores of most terrestrial ecosystems during the Mesozoic. During this period of time the group achieved major evolutionary transforma-tions, including the acquisition of the largest body sizes in the history of land animals, their complete adaptation of herbivory, and the development of a distinctive body plan. Recent discoveries suggest the presence of punctuated phases of major evolutionary change in the history of the group during the Mesozoic. In particular, the fossil record from the Southern Hemisphere has provided key specimens that shed light to some of these events. Here I summarize information coming from recent discoveries from the southern continents with particular emphasis on those coming from South America. Soon after their appearance in the Late Triassic sauropodomorphs radiated during the Norian into various basal lineages recorded in disparate regions of Pangea. This radiation involved the first steps in the acquisition of the sauropodomorph body plan including a decrease of the relative skull size and the appearance of the first dinosaurs with quadrupedal stance and large body weights. New evidence from the Late Triassic of Argentina indicate sauropodomorphs achieved body sizes similar to those of the derived sauropods that are fully quadrupedal but retained a plesiomorphic postcranial anatomy. The Early Jurassic is highlighted as a second key stage in the evolution of the group, marked by the acquisition of the body plan characteristic of true sauropods (including elongation of the neck, highly pneumatic axial skeleton, graviportalism) that will be overall maintained until the end Cretaceous. The southern fossil record (Africa, South America, Antarctica, India) provides key data to date the radiation and dominance of true sauropods in the Toarcian, prior to what is recorded in the Europe and Asia. Subsequent evidence of sauropodomorph evolution in the Southern Hemisphere is dominated by the di-versification of diverse neosauropod lineages in the Late Jurassic and Early Cretaceous, with the notable appearance of titanosaur sauropods by the late Early Cretaceous. This clade was the most diverse and successful lineage of neosauropod dinosaurs and achieved worldwide distribution. Their initial radiation includes the origin of various lineages including a clade of giant titanosaurs in the Albian of Patagonia.



<sup>\*</sup> Speaker

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#### Ambers and resins, past and future

Leyla Seyfullah\*

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Amber (fossil plant resin) is rightly famed for the preservation of organisms (often in life position) that it contains. Our understanding, however, of why plants produced the resin is limited currently. There are several suggestions, but not many have been tested. Chemical analyses of amber have previously mainly focused on attempts to link a fossil resin deposit to its original source plant, and these have had a certain amount of success. More recently, the potential value of amber as a medium for preserving ecological or environmental signals of the original resin is seen as contentious and developing area. This includes attempts to relate potential biomarkers preserved in amber as signals that might be linked to insect attack or climate that caused the original resin outpouring.

To try to understand what affects resin chemistry, the first step has been to demonstrate the variability within naturally occurring resins and amber. In modern resins carbon isotopes are highly variable, even the height on the tree at which the resin was sampled has an effect. The variability of carbon isotopes within fossil resins is illustrated using the Carnian (late Triassic) Dolomites amber, and Cretaceous ambers as specific examples. The Cretaceous examples mean that extreme care is needed in using amber as a proxy for palaeoatmospheric reconstructions. Building on this basis, I have been testing for biomarker signals that might occur in resins, and what they may indicate about the environment surrounding the resin-producing plant at the time of resin exudation. To tackle this, experimentally produced araucarian resins from both *Agathis australis* and *Wollemia nobilis* have been produced and analysed. These results and the next steps will be highlighted.



Speaker

#### **Cretaceous Burmese amber biota**

#### Bo Wang\*

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Burmese amber (amber from northern Myanmar) contains the most diverse biota of all Cretaceous amber. During the last 100 years, Burmese amber has received worldwide scientific interest; more than 300 families of arthropods plus diverse plants and vertebrates have been reported. Burmese amber has been known for nearly 2000 years, and it has been traded with China since Han Dynasty times (202 B.C. to 220 A.D). The first reported animal inclusions in Burmese amber were presented between 1917 and 1922 by Dr. Cockerell. The renaissance in Burmese amber research started at the very end of 20th century and the investigations on inclusions of Burmese amber are now in full bloom. Recently, amber and its inclusions have been thoroughly investigated, with international collaborations that have resulted in prolific papers and reports published on the identification and description of numerous fossil inclusions. We have reinvestigated this biota based on new, abundant fossils and got some new and surprising discoveries. We found a number of arthropod groups that are rare or extremely rare in amber, e.g. crabs (Brachyura), camel spiders (Solifugae), whip-scorpions (Thelyphonida), and onychophorans (Onychophora). Insects are the most common group in Burmese amber and show a remarkable mixture of basal and derived forms. They document a particularly active time in the evolution of life on land, the Cretaceous terrestrial revolution. Flowering plants were flourishing and diversifying, the insects that fed on the flowers were also flourishing and diversifying, and the predators that fed on the insects (spiders, lizards, mammals, and birds) were flourishing and diversifying. The stories of plants, insects and other invertebrates, and predator interactions documented in Burmese amber offer an unprecedented view into the co-evolution of insects and plants, the evolution of pollination, adaptations to various types of food and habitats, and the formation of recent ecosystems and biotas. Although the list of exciting discoveries is long, only about 20% of the inclusions have been formally described from Burmese amber. Therefore the Burmese amber biota requires much more extensive and detailed taxonomic investigation.

<sup>°</sup> Speaker

#### New mordellid-like beetles from Upper-Cretaceous Burmese amber and their ecological implications

Tong Bao\*<sup>+ 1</sup>, Katarzyna Walczynska <sup>2</sup>, Jes Rust <sup>1</sup>, Bo Wang<sup>3</sup>

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A new family of tenebrionid beetle (Coleoptera: Polyphaga: Tenebrionoidea) is described based on two genera from Burmese amber (lower Cenomanian, ca. 99 Ma). The new family is undoubtedly attributed to Tenebrionoidea by the retractile wedge-shaped body and tarsal formula 5-5-4. It shares some similarities with Mordellidae such as, a convex head and hind legs that are well-developed. However, it is more closely related to the Jurassic Wuhua beetle because of the absence of pygidium and other micro structures like the claw formula. Furthermore, Wuhua is supposed to be the basic taxon of the new family.

Based on the morphological characters of the flower feeding extant Mordellidae, Ripiphoridae, and of the pollen feeding Tenebrionoidea, the morphology of the new Cretaceous tenebrionid beetle family suggests a similar pollen feeding strategy. The evolutionary and phylogenetic relationship between Mordellidae, Ripiphoridae and the new family are discussed. The fossil records of Ripiphoridae from the Middle Jurassic share a similar body plan, which may indicate their success of occupying an ecological niche from the Jurassic. However, Mordellidae and the new family show obvious morphological changes during the Cretaceous probably due to the rise of angiosperms. Compared to Jurassic Praemordellidae and setae system on their ventral and dorsal body surfaces, which alludes to that their locomotion evolved from simple crawl to jump-fly and their diet preference evolved from surface nutrition (fungi, moose, lichen, etc.) to herbaceous flowers. Mordellidae possess the elongated pygidium, well-developed hind leg, C-shape curved body and expanded maxillary palp, which provide more efficient jumping and feeding ability.



<sup>\*</sup> Speaker

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#### Myrmicine ant (Hymenoptera: Formicidae) diversity in Miocene amber of Zhangpu, China

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The middle Miocene (Langhian) Fotan Group of Zhangpu County (Fujian Province, SE China) is known to contain a rich paleoflora including leaves and fruits of dipterocarp trees, reflecting a northern expansion of tropical dipterocarp forest ecosystems until South Fujian during the mid-Miocene Climatic Optimum. Recently, the presence of amber of dipterocarp origin has also been documented. Investigations of Zhangpu amber has revealed a plethora of arthropod inclusions, among which a remarkable ant fauna comprising more than 1 000 individuals (workers and gynes) from 9 subfamilies, all belonging to extinct species of still living genera. Myrmicinae is by far the most abundant subfamily (65% of the total ants; *ca* 650 ind.), followed by Dolichoderinae (9%), Ponerinae (8%), and Formicinae (6%). Myrmicines comprise at least 20 species in 16 genera, among which *Carebara* and *Pheidole* are largely dominant (21% and 19%, respectively). *Lophomyrmex, Crematogaster,* and *Tetramorium* are also well represented (*ca* 5% each), and several occurrences are the first fossil records of extant genera (e.g., *Cardiocondyla, Gauromyrmex, Meranoplus, Myrmicaria, Proatta*). The ant paleocommunity of Zhangpu amber is mostly similar to the present-day fauna that is found in tropical rainforests from SE Asia and eastern Australia, particularly the dipterocarp forests of Borneo, Philippines or Malaysia. Overall, our findings highlight a closely related geographical distribution of some Australasian ant genera and dipterocarp forest ecosystems.



Speaker

### Molecular composition of fossil and extant dammar resins: insights into molecular taphonomy of plant terpenoids

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The composition of sesquiterpenoids and triterpenoids in the solvent extract of extant, Miocene and Eocene resins has been determined and compared to investigate the diagenetic fate of these terpenoids. Eocene resins were collected from Tadkeswar lignite mine, Cambay Basin, western India. The Miocene resins were sourced from Assam Basin, Mizoram, NE India. Significant changes in the sesquiterpenoid composition of the fossilised Eocene resin compared to the modern resin were evident, whereas the triterpenoid products reflected only minor differences. The presence of dammarane compounds (e.g., hydroxydammarenone and 20,24epoxy-25-hydroxydammaran-3-one) in the total extract of the ambers clearly suggests that the fossil resins were produced by angiosperm tree family Dipterocarpaceae. The major sesquiterpenoids in the extant dammar resin are the volatile compounds,  $\alpha$ copaene,  $\beta$ -bourbonene,  $\beta$ elemene,  $\beta$ -caryophyllene, germacrene D, germacrene B and spathulenol. In contrast, the major sesquiterpenoids in the fossilised resins were C15 cadalene-based compounds such as dihydro-arcurcumene,  $\alpha$ -muurolene, calamenene, 5,6,7,8tetrahydrocadalene and cadalene. Interestingly, volatile bioterpenoids are preserved in Miocene ambers. These compounds are used to play active role in forest ecology, especially in plant-animal interactions. The survival of these unaltered bioterpenoids can be attributed to the existence of extraordinary taphonomic conditions conducive to the preservation of volatile biomolecules through deep time. In general, the triterpenoid assemblages in both fossil and extant resins were very similar with abundant  $\beta$  and  $\alpha$ -amyrin in the studied resins. We have also investigated the molecular signature of partially and severely altered Eocene ambers from Tadkeswar lignite mine and compare their triterpenoid distribution. Several aromatized and unsaturated triterpenoids are exclusively detected in the altered ambers. Amyrin-derived A-ring monoaromatic triterpenoids are highly abundant in the total extracts of both partially and severely altered ambers whereas tetra-aromatic and des-Atriterpenoids are identified in severely oxidized ambers. An A-ring contracted triterpenoid (i.e. A-neooleana(ursa)-3(5),2-diene), indicator of dehydration reaction, is detected in all studied altered ambers. These aromatic compounds are mainly produced by microbial alterations.



Speaker

# The lowermost Eocene Oise amber: new data, new methods

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Oise amber, also called Paris amber, has been discovered in Lowermost Eocene (Ypresian, 53-55Ma) lignitic sands of Oise Department in the early 90's. A large amount of this highly fossiliferous amber is now housed in the collection of the Muséum National d'Histoire Naturelle in Paris (MNHN). More than 24,000 inclusions have already been identified, and investigations are still in progress on the remaining raw amber from recent collecting campaigns carried out with the support of the Lafarge company, operating fossiliferous sand pits. Oise amber is highly valuable for insect studies, being among the first fossiliferous deposits from the post K-Pg boundary, together with the Earliest Eocene amber deposits from Canada, China, and India. Its great palaeodiversity allows to trace the oldest known representatives of many modern insect families. Coleoptera (with 45 families), Diptera, Hymenoptera, and Hemiptera are the dominant orders in number of specimens and diversity. A recent overview of the arachnid specimens has revealed more than 350 spiders (2% of total inclusions) in at least 26 families among which several new ones, an unexpected palaeodiversity. This arthropod palaeobiocoenosis confirms a biogeographical proximity with Baltic amber deposits, nevertheless with a rather marked tropical tendency, confirmed by a complete comparative study of Aranae palaeocommunity and by several insect taxa. To complement the observations, cutting-edge analytical tools such as flurorescence microscopy, laser confocal microscopy, OCT and CT scan tomography are used for the description of inclusions and syninclusions, and to better address the taphonomic aspects. A citizen science program is underway with the SAGA association (geologist amators associated to MNHN), which helps to sort inclusions, and additional field work is planned with volunteers from this association to increase the sampling.

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Speaker

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#### Cretaceous dragonflies (Insecta: Odonata) preserved in amber

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Odonatans (dragonflies and damselflies; dragonflies in the broad sense) are rare as amber inclusions, but quite diverse in mid-Cretaceous Burmese amber (circa 100 million years old) with 27 species in 22 genera representing 13 families: this is the most abundant dragonfly assemblage so far discovered as amber inclusions.

In the past two years, over 20 new species have been found by the authors after examining over 300 odonatans (from over a quarter of a million amber inclusions).

Most of the species have now been published and here we provide a brief review; more new species will be described in the future, especially rare ones. They were collected in the Hukawng Valley of Kachin Province, Myanmar and the age of Burmese amber is considered to be Early Cenomanian.

The amber containing the dragonflies is normally yellow or red and transparent. Photographs were taken using a Zeiss Stereo Discovery V16 microscope system and Zen software. All the specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS).

Three suborders of crown Odonata have been recorded, including the damselfly (zygopteran) families or superfamilies Platycnemididae, Platystictidae, Perilestidae, Hemiphlebiidae, Coenagrionoidea, Pseudostigmatoidea, Mesomegaloprepidae and Dysagrionidae, plus the dragonfly (anisopteran) families Lindeniidae, Gomphaeschnidae and Burmaeshnidae, and the damseldragonfly (anisozygopteran) family Burmaphlebiidae.

All these taxa are based on the adult stage, but there are still many immature insect inclusions (nymphs/larvae) which need to be studied. The inclusions, especially true damselflies (zygopterans), were entrapped in a resinous, coniferous woodland amidst the burgeoning angiospermous flowering plants along the north-eastern fringe of the Tethyan ocean. The inclusion of so many large insects in amber is unusual. They can help us evaluate the origin, evolution, and palaeobiogeography of the modern families of Odonata. Questions remain, however, such as what the forest palaeoecology was really like. The occurrence of aquatic immature stages is of palaeoenvironmental significance.



Speaker

#### Hidden secrets of Mimarachnidae planthoppers (Hemiptera: Fulgoromorpha)

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The Hemiptera is one of the "Big Five" insect orders presenting the highest taxic diversity and morpho-ecological disparity. Planthoppers (Fulgoromorpha) is one of the hemipteran suborders displaying enormous diversity, with 30 extant and extinct families currently recognized and with fossil record reaching the Permian. Until now, the extinct family Mimarachnidae Shcherbakov, 2007 was known exclusively from compression/impression fossils in sedimentary deposits of Buryatia (Russia), Japan and Spain (some not formally described taxa come from Mongolia and probably also from Brazil), which restrict the family distribution to the middle to high latitudes probably with the seasonal alteration (Szwedo and Ansorge 2015). Recently, Shcherbakov (2017) reported the first representative of this group from Burmese amber, representing the record from a tropical palaeoequatorial region, and indicating that this family can also live in the tropical forest, with a worldwide distribution. Here, we report the more representatives of the family preserved as inclusions in the mid-Cretaceous Burmese amber. Surprisingly, the taxonomic and morphological disparity of these fossils exceed far beyond the richness of fossils already known. Several eco-morphologial traits present among modern planthoppers are to be observed also among representatives of Mimarachnidae from Burmese amber. Also taxonomic diversity of these fossils preserved as inclusions allow us to erect a number on new taxa of specific, generic and higher levels. Mimarachnidae seems to be an endemic family for the Cretaceous period, but its disparity is comparable to modern planthoppers leading to the questions of tempo and mode of eco-evolutionary adaptations on one hand, and reasons for rapid origination and extinction of this group on the other. Also relationships of the Mimarachnidae within the Fulgoromorpha clade are not fully elaborated, and recent discoveries contest the already proposed relationships of Mimarachnidae with Cixiidae-like lineage of the Fulgoromorpha. The recent discoveries of particular Mimarachnidae with peculiar venation, hardly comparable with modern planthoppers put a set of new questions and possibility of new explanations of the Fulgoromorpha phylogeny and relationships. Inclusions in amber also allow for the detailed study of genital elements of both females and males of Mimarachnidae. It seems these structures only hardly match to the model presented by modern planthoppers.



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# Ectoparasites of arthropods in amber forest – the case of terrestrial Parasitengona mites

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Terrestrial Parasitengona constitute an ecologically distinguished group within prostigmatid mites (Arachnida, Actinotrichida), and encompass over 5 000 nominal species. Representatives of this world-wide distributed group are highly diversified, both with respect to biology and morphology, and inhabit a wide range of habitats. They are characterised by a complex life cycle involving alternation of active (larvae, deutonymphs and adults) and inactive (prelarvae, protonymphs and tritonymphs) instars. Larvae of Calyptostomatoidea, Erythraeoidea and Trombidioidea (excl. Trombiculidae), heteromorphic in relation to postlarval instars, are ectoparasites of arthropods and, considering the extant fauna, can be found on representatives of almost all insect and arachnid orders, although the most numerous associations involve dipteran, hemipteran and orthopteran hosts.

In search for hosts the larvae penetrate litter and lower vegetation layers. However, due to the relatively high mobility of hosts, the larvae which, contrary to predatory, edaphic postlarval forms, are considered the main dispersal instar via their hosts, are significantly more often embedded in amber. The knowledge of host-parasite associations between parasitengone larvae preserved together with their hosts in the fossil materials is extremely scarce and limited to two records. The oldest known case concerns erythraeoid larva discovered in the Lebanese amber (c. 130 Ma). The second record pertains to two larvae (Erythraeoidea and Trombidioidea) from Canadian amber (c. 70-80 Ma). In both cases larvae were attached to dipteran hosts representing Ceratopogonidae (Diptera: Nematocera).

During the analysis of 1850 amber lumps (Burmese, Baltic and Ukrainian), containing terrestrial Parasitengona mites, 40 larvae of Erythraeoidea, Trombidioidea and Calyptostomatoidea captured in parasitic phase along with their hosts, were discovered. The majority of new findings (35) involves Diptera as hosts. Among other hosts parasitized by Trombidioidea larvae the representatives of the Hymenoptera were also stated.



Speaker

### Where were the mosquitoes? Differences and similarities between the Eocene Baltic amber and Recent fauna of Diptera Nematocera

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Baltic amber was created in the area of present Europe, mainly in the Scandinavian Peninsula during the Eocene period (40-42 Ma). At that time, most of today's Europe was submersed under warm ocean waters. The prevailing climate was much warmer than today (subtropical), interspersed by cooler periods. The consecutive changes of temperature can be evidenced by insect fauna which was different and very characteristic for each period; for example presence of members of the Tanyderidae (warm period) or Trichoceridae (cold period). This amber occupies a special position among all fossil resins because the last representatives of the extinct Mesozoic fauna can be found together with the first representatives of many living genera. Moreover, most genera and almost all families that occurred there are also represented in contemporary fauna; therefore inclusions in Baltic amber are of great importance for analyzing and understanding the evolutionary changes in many families of Diptera. Inclusions provide also information about paleoclimate and paleoenvironment at the time this resin had been deposited. However, only a few fossil genera are known only from the Baltic amber. Generally, the Eocene fauna of Diptera Nematocera is very similar to the extant fauna and differs only at species level.The most surprising is the nearly complete absence of mosquitoes (Culicidae) and other families, that are otherwise present and very diverse in almost all modern wet ecosystems.



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#### A mid-Cretaceous tree fern of Thyrsopteridaceae (Cyatheales) in Myanmar amber

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Numerous well-preserved fossils have previously been discovered in mid-Cretaceous (late Albian to earliest Cenomanian,  $\approx$ 100 Ma) amber from northern Myanmar, including new species, genera, and even families of plants and invertebrates. Compared to the 34 orders of insects and

252 families of arthropods already known from this site, researches on the botanical inclusions is far behind, as exemplified by only a few derived ferns (polypods) described from the Myanmar ambers. This is not surprising because, with only about 10,000 species, ferns are much lower in species diversity than the arthropods. However, the polypod fossils are significant not only in recovering the polypod ferns' diversity changes in history, but also in bridging the gap between the Cretaceous records of polypod ferns and divergence time estimates obtained based DNA sequence variation.

A new species of tree fern trapped in 100 MA Myanmar amber is described. It belongs to the Thyrsopteridaceae and closely resembles Thyrsopteris elegans Kunze, an endemic to the Juan Fernandez Islands. The fossil has short-lobed lamina segments, terminal sori, cyathiform indusia, clavate receptacles, and oblique annuli.The fossil adds to the diversity of previously described Thyrsopteridaceae from Upper Cretaceous to Eocene, and extends the family's fossil record back to the mid-Cretaceous. The palaeobiogeographic and palaeoclimatic scenarios are discussed.



Speaker

#### Ostracoda in Miocene amber from Chiapas, Mexico

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Miocene Mexican amber from Chiapas' Campo La Granja mines is special: it was formed in an estuarine environment with tidal marine influence and sea-level fluctuations, enclosing high numbers of semiand fully aquatic arthropods. We present our study on more than 250 submillimeter-sized individuals of Ostracoda (Crustacea) from Campo La Granja, trapped in the resin under water in a brackish coastal habitat.

Ostracods have a unique fossil record throughout geological history due to their calcified bivalved carapaces. However, some taxa with carapaces lacking solid calcification may not be represented in the regular fossil record. This is to be assumed for the tribe Thalassocypridini (Paracypridinae, Candonidae), the extant representatives of which typically possess a very weakly calcified carapace and which lack any fossil representatives. The Campo La Granja amber revealed an Early Miocene ostracod fauna predominantly consisting of such Thalassocypridini species, thus providing the first insight into the evolution of this taxon. Their transparent valves allowed a widely unobstructed view onto the appendages and made it possible to identify nine ostracod species, six of them new to science.

The exceptional finding of such a high number of individuals, even entombed together in single amber pieces, allowed us to draw conclusions on population composition, reproduction mode and taphonomy, and even on micro-environmental parameters of the amber's place of formation. In comparison with today's autecology of this taxon, we argue that the amber fossils may either reflect the taxon's evolutionary shift in habitat, or indicate an additional ancient distribution. Synchrotron micoand nanotomographic investigations proved to increase considerably the optical information retrieved from Campo La Granja ostracods. Gains from these methodologies will be shown by examples covering taxonomy, micromorphology, and reproductive biology of the amber ostracods.



Speaker

#### Trash-carrying green lacewing larvae from Early Cretaceous Lebanese amber

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Some animals possess morphological and behavioural adaptations aimed at selecting and carrying diverse exogenous elements for camouflage and physical protection. This is the case of the so-called "trashcarrying" green lacewing larvae (Neuroptera: Chrysopoidea: Chrysopidae), voracious predatory insects widely used in pest control. In 2012, the discovery of Hallucinochrysa diogenesi, a bizarre-looking chrysopoid larva from Early Cretaceous Spanish amber carrying a trash packet specifically composed of plant trichomes, revealed that trash-carrying has been present in the lineage leading to modern green lacewings for more than 100 million years. Since then, similar fossils have been found in other Cretaceous ambers, although most of these are still awaiting formal description. A conspicuous feature uniting most of the known Cretaceous diversity of trash-carrying larval chrysopoids, and distinguishing it from the extant diversity of the group, is that the setose tubercles present on the specimens' dorsa for retention of the trash packet elements are extremely elongate, tubular in shape. At least two morphotypes of chrysopoid larvae, one of them previously figured, are currently known from Lebanese amber, Early Cretaceous (Barremian) in age (about 130 Ma). The first morphotype represents a first instar without associated debris, and an aggregation of several individuals is known. Unlike H. diogenesi, this morphotype lacks setal specializations. The second morphotype is an advanced immature form, probably a third instar, and it possesses expanded setal endings. Remarkably, several irregular fragments of debris corresponding to an initially built trash packet or a partially dislodged one are entangled among the tubular tubercle setae of this latter morphotype. Both morphotypes have a pair of lateral and laterodorsal tubular tubercles on, at least, the mesothorax, and the tubular tubercle dotation on abdominal segments includes a variable number of pairs of shorter tubercles in submedial position, revealing a variety yet unknown. These new studies will be paramount to understand the diversity of early larval green lacewings and their relationships. Most importantly, chrysopoid larvae hold significant potential to inform of past ecological interactions and to shed light on the evolution of developmental patterns in holometabolous insects, particularly those associated to adaptations as critical for the species' survival as trash-carrying.



Speaker

#### The age and paleobiota of Ethiopian amber revisited

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Fossiliferous amber from Ethiopia was reported a decade ago and was considered to be early Late Cretaceous in age (Cenomanian, ca. 93-95 Ma) based on initial assignment of palynomorphs and physicochemical properties of the amber. This assumed Cretaceous age has recently been questioned, given subsequent discovery of extant genera among the arthropod inclusions, and identification of erroneously determined palynomorphs. An investigation of additional amber material and associated sediments is presented here, which provides compelling evidence that the material is much younger in age, datable to the Cenozoic, Early Miocene (16–23 Ma). Palynomorphs from the samples have yielded large numbers of typically long ranging Cenozoic pollen, some of which are known within nearby basins in South Sudan to be particularly common in terms of a climate controlled regional plexus of abundance in the Early Miocene. The newly-studied insect fossils mostly belong to extant families and genera. A particular reference to ants is made here with the report of 60 individuals mostly assignable to extant genera of Dolichoderinae (e.g., Ravavy, Technomyrmex), Myrmicinae (e.g., Carebara, Melissotarsus, Monomorium, Rhopalomastix), Ponerinae (e.g., Cryptopone, Hypoponera), and Pseudomyrmecinae (e.g., Tetraponera), but also some undetermined, possibly extinct genera. Chemical analysis indicates that Ethiopian amber belongs to the Class Ic ambers that were mostly produced by the Fabaceae (Legume family of flowering plants). The resin producer may have been allied to the genus Hymenaea that is well known in the prolific East African Zanzibar copal trade, and other Neotropical ambers. It is noteworthy that one of the more common pollen types recovered from the amber-containing sediments, the genus Striatricolpites (=Striatopollis) plus much rarer Margocolporites spp., come from within the order Fabales, that includes the Fabaceae family. Although much younger than previously estimated, Ethiopian amber remains of great interest as fossil insects are exceedingly rare in Africa, and the Miocene age permits comparison to coeval worldwide ambers of similar fabaceous origin such as Dominican, Mexican, and Peruvian amber.



Speaker

### Marine life captured in amber - exceptional preservation of small aquatic isopod larvae in Cretaceous amber from France

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Isopod crustaceans are commonly referred to as woodlice; however, terrestrial isopods (Oniscidea) are only one of many evolutionary successful lineages of this group of malacostracan crustaceans. A major share of isopod diversity is represented by the marine forms. Among marine isopods a large variety of ecological strategies has evolved, ranging from the adaption to deep sea environments to a strictly parasitic lifestyle. How and when parasitism evolved within isopods is still subject to recent investigations. Within the parasitic isopods, the group Epicaridea represents still a special case: While most isopods and their relatives have offspring that resembles the adult in most aspects, epicarideans show at least three distinguishable larval phases, each characterized by a distinct morphology and lifestyle. One of these stages (the cryptoniscium larva) is now investigated in detail from a Cretaceous amber site in France (Vendée). Besides one occurrence in Miocene amber from Mexico this is only the second and thus oldest record of body fossils for this animal group. With the help of high-resolution composite fluorescence microscopy, we shed light on the morphology of these very small animals. Although the body length of the fossil larvae does not exceed 0.5 millimetres, delicate structures like single sensory setae can be visualized. Our investigations contribute important insights into the developmental biology and ecology of these 90 million years old crustaceans and may help to further elucidate the evolution of parasitic strategies in isopods.

Speaker

# Diversity of the scorpionflies (Mecoptera) in fossil resins and its implications for evolutionary research

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Scorpionflies (Mecoptera) are of special significance for insects evolution and phylogeny, being the stem group for several biggest and recently important insect orders. Recently, scorpionflies are a small and relict order divided into nine families, while 40 families were described from fossil scorpionflies. Their greatest diversity is recorded in the Middle Mesozoic (~200-150 Ma), when they reached their main radiation. Thus, Mecoptera is a group of species of the highest scale of extinction among holometabolous insects.

Investigations of the scorpionflies preserved in fossil resins significantly enlarge our knowledge about morphology and diversity of their past fauna. Such inclusions with entire bodies preserved threedimensionally offer a fascinating chance of seeing insects with the accuracy of living forms. Till now such inclusions were known only from Baltic amber dated between 40-50 Ma. Altogether 12 species classified into three modern families of Mecoptera were described from this Cenozoic resin. Before the year 2005 Mesozoic scorpionflies were known only from compressions or impressions mostly of wings in sediments. Recently thanks to the access to new fossils mainly in fossil resin from Myanmar (Burmese amber), we got great chance of studying the mid-Cretaceous inclusions containing entire bodies. This epoch saw the final stage of the highest diversity of scorpionflies. To date six species of Mecoptera belonged to three families from Burmese amber were described, among them Pseudopolycentropodidae, which are the only extinct family of the Mecoptera and are of great importance for evolution of this order.

Abundant new inclusions which are studied by the Polish team will bring new species both from above mentioned families as well as new taxa of yet unknown taxonomical status. The Cretaceous inclusions offer a fascinating opportunity of investigation of all morphological details of ancient Mecoptera and promise a breakthrough in our knowledge of their diversity and evolution.



Speaker

## The Amphiesmenopteran fossils from Asia offering important information for the early evolution of this group

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Amphiesmenoptera is composed of two modern orders, Lepidoptera and Trichoptera. However, it is still questionable when these two groups diverged from each other because of poor fossil record. In recent years, we reported a series of lepidopteran and trichopteran species in Mesozoic sediments from Asia, including 6 genera 11 species of Trichoptera (referring to Vitimotauliidae, Rhyacophilidae, Philopotamidae, Hydrobiosidae and Necrotaulidae), and 12 genera 17 species of Lepidoptera (referring to Eolepidopterigidae, Mesokristenseniidae, Ascololepidopterigidae and Micropterigidae). These studies give important information of the origin, early evolution, palaeogeography, and paleoecological implications of these groups. The studies on necrotauliid specimens show their male genitalia with harpagones, a synapomorphy of Trichoptera. They also share some characters with Integripalpia on maxillary palps and forewings, indicating Necrotauliidae is probably a stem-group of Integripalpia rather than amphiesmenopteran. The diversity of late Middle Jurassic lepidopterans supports a conclusion that the Lepidoptera?Trichoptera divergence occurred by the Early Jurassic. Cretaceous moths (Lepidoptera: Micropterigidae) with preserved scales from Myanmar amber support that scales have developed various types and shapes by the Cretaceous.



Speaker

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# Hymenoptera in Burmese amber: new families and a review of the fauna

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The Burmese amber assemblage is now the richest for Hymenoptera in the Cretaceous, the number of described species of Hymenoptera is soared to 93 until September 2017. The collections of Burmite (Burmese amber) from the Hukawng Valley in NIGPAS were examined, the diversity of Burmite inclusions is very high and many new families were found. There are about 12800 insect amber pieces registered by our research team containing approximately one hundred thousand insects. A total of 1774 hymenopteran inclusions has been recorded from 1409 amber pieces. The data show presence of 46 hymenopteran families which give a considerable addition to any other lists. In this list, our records new for the Burmese amber are Anaxyelidae, Burmorussoidea, Myanmarinidae, Radiophronidae, Trigonalyidae (?), Peleserphidae, Roproniidae, Austroniidae, Sclerogibbidae, Angarosphecidae, Burmusculidae and possibly Mymarommatoidea fam.nov.? (undescribed). These add five transitional families (Anaxyelidae, Roproniidae, Austroniidae, Sclerogibbidae and Angarosphecidae), five endemics (Burmorussoidea, Myanmarinidae, Peleserphidae, Burmusculidae and possibly undescribed Mymarommatoidea fam.nov.?), and one the youngest fossil record (Radiophronidae). The Burmese hymenopteran assemblage shows the highest diversity (46 families) among all fossil assemblages except the Baltic amber one (55 families). This rich Cretaceous fauna coupled with the unusual concentration of endemics suggest a kind of exclusiveness in the biogeographic position of the respective source territory which undoubtedly deserves special study. On this occasion, the Hymenoptera fauna of Burmese amber is revised.

Speaker

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#### Brachyceran flies in mid-Cretaceous Burmese amber: diversity and ecological significance

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The Diptera (true flies) is one of the most species-abundant orders of Insecta, and they are certainly one of the most ecologically ubiquitous and significant orders of insects. Dipteran fossils are quite abundant in the Mesozoic, especially in the Late Jurassic and Early Cretaceous. Mid-Cretaceous Burmese amber yields abundant insect inclusions including dipterans. The three-dimensionally preserved insects in Burmese amber provide excellent medium to compare fossils with modern ones. Till now, at least 18 families of basal brachyceran flies have been found in Burmese amber, including the extinct long proboscis flowervisiting Zhangsolvidae, needle-shaped ovipositor endoparasitoid Eremochaetidae, enigmatic family Rhagionemestrinidae and nowadays predominant flower-visiting flies Bombyliidae. Bombyliidae (bee flies) are a large family with more than 4, 000 species described, and they are major pollinators, all their larvae are predators or parasitoids of arthropods. Fossil records of bee flies are quite patchy, with little knowledge about their early evolution. Remarkably, Burmese amber illustrates a quite high diversity of bee flies in mid-Cretaceous. In conclusion, these brachyceran groups of Burmese amber played an important role in the origin of co-evolutionary relationships with basal angiosperms. Moreover, the rise of angiosperms not only improved the diversity of flower-visiting flies, but also advanced the turnover and evolution of other specialized flies.



1 // Ora

Speaker

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### Bristletails from Myanmar amber provide phylogenetic insight into the evolution of Archaeognatha (Insect)

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Archaeognatha, commonly called jumping bristletails, are the sister group of all other insects. Fossil species of Archaeognatha are known from the Devonian to recent. Based on fifteen Archaeognatha specimens from Myanmar amber, two new genera and four species, *Cretaceomachilis longa* Zhang *et al.* 2017, *Unimeinertellus abundus* Zhang *et al.* 2017, *U. bellus* Zhang *et al.* 2017 and *Nullmeinertellus wenxuani* Zhang *et al.* 2017, are described.

Phylogenetic relationships within Archaeognatha have been discussed in several studies. However, the phylogenetic positions of the 'paleo-types', and the monophyly of Machilidae and their subfamilies, are still controversial. Herein we present a phylogeny of Archaeognatha. We sampled a total of 26 terminal species, comprising 24 ingroups (18 extant species and 6 fossil species) and 2 outgroups. Phylogeny is reconstructed by employing two phylogenetic methods: 1) maximum parsimony using morphology data, 2) bayesian inference using morphology and DNA sequence data (total evidence). Finally, we reach the following conclusions: 1) Meinertellidae are a monophyletic group; 2) Machilidae are probably a paraphyletic group, but Machilidae excluding *Ditrigoniophthalmus* and *Petrobiellus* form a clade; 3) *Charimachilis, Mesomachilis* and *Turquimachilis* are nested within Machilidae; 4) The monophylies of Machilinae and Petrobiinae are poorly resolved.

The oldest known meinertellid is from Lebanese amber. Lebanon is considered to be in a northeastern position in the Gondwana continent during the Early Cretaceous, which suggests a Gondwanan origin for the Meinertellidae. We also applied two approaches for inferring the origin of Meinertellidae. First, we used parsimony ancestral state reconstruction implemented in Mesquite. Second, we used a dispersal-vicariance (DIVA) optimization model implemented in the programme RASP2.0 Beta with default settings. The phylogenetic tree based on total-evidence obtained from Bayesian analysis was used for biogeographical analysis. Combining these two biogeographical analyses, the possibility of a Gondwanan origin of Meinertellidae is proposed.



Speaker

# S2 - Angiosperms, from the beginning to their diversification

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## On some angiosperm stem diversity from the Cenomanian of Envigne valley (Vienne, western France)

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Recently, two Konservat - and Konzentrat -lagerstätten fossil plant assemblages have been reported from the Envigne valley, Vienne, western France. Thousands of stem fragments were collected, and they consist of the tree fern Tempskya, and at least five conifers and seven angiosperms. In many known localities of Cretaceous fossil wood, only this latter tissue is conserved, the other stem tissues having been eliminated during both the degradation and fossilization process. There, the majority of them (medulla, wood and liber) are preserved very exquisitely in many specimens, particularly in some of which belonging to angiosperms. The wood of angiosperms show a great histological diversity for many features concerning the size of the vessels, the perforations, the vessel and ray pits, and the axial parenchyma arrangement. The ray features are more homogeneous (type of cells composing the ray, seriation) as well as the presence of thyllosis that appears frequent in the majority of the taxa. The presence of several specimens of each type of wood makes possible to comprehend intraspecific variability. In addition to these typical heteroxylous angiosperms, numerous specimens show a vesselless angiosperm, and they probably belong to Winteraceae. The very broad conformation of its rays may indicate a liana habit. Most specimens attributed to the other angiosperm taxa show a relatively small stem diameter compared to many coniferous specimens suggesting that they were smaller plants and most probably had a shrub habit rather than tree habit. The in-depth study of these two new deposits is particularly promising in the understanding of 1) Cenomanian forest ecosystems (diversity of taxa, size, habit), and, 2) the evolution of angiosperm histological features not only for wood but also for more less-known tissues as medulla and liber.



<sup>&</sup>lt;sup>°</sup> Speaker

## The Icacinaceae from the Palaeogene of the Paris Basin: diversity, affinities and changes through the PETM

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The Icacinaceae Miers is a family of trees, shrubs and lianas with an extant pantropical distribution. This group is well known in the fossil record from the Paleocene and Eocene, particularly in the Northern Hemisphere, although fossil evidence from the Southern Hemisphere has recently been increased. In the Paris Basin Icacinaceae are represented by numerous fossil endocarps from five main localities. Among these, two sites in Oise, Rivecourt (late Thanetian) and Le Quesnoy (early Ypresian) are geographically and temporally very close. The PaleoceneEocene thermal maximum (PETM) event occurs (temporally) between these two fossil outcrops. Thus, the study of the Icacinaceae fossils in those localities provides a good opportunity to elucidate the impact of the PETM on this family in the Paris Basin.

Based on 266 fossil specimens attributed to Icacinaceae, from the five Paris Basin localities, we conducted detailed anatomical (using SEM) and morphological studies. The fossil remains are mainly lignitic endocarps, but other endocarps preserved as quartzite sandstone imprints, as well as flowers and pollen preserved in amber have been studied.

This study allows the distinction of twelve species from only one extant genus (*lodes* Blume) and three extinct genera (*Palaeophytocrene* Reid and Chandler, *lcacinanthium* Del Rio & De Franceschi and *lcacinicarytes* Pigg, Manchester & Devore). This diversity within the Paris Basin is comparable to other major Palaeogene outcrops such as the London Clay or the Clarno Formation.

All species are related to tropical climber groups. The climbers are abundant in the riverbanks or channels and thus the representation of only climbers of this family could be a taphonomic bias. In this context, the overall ancient Icacinaceae diversity could be underestimated. Among Icacinaceae fossils from the Paris Basin, there are some evidences of affinities with extant IndoMalaysian vegetation, which seems to be a relict area of wider Paleocene and Eocene Eurasian vegetation. No clear extinction is shown through the PETM, but a floral enrichment across the PETM is demonstrated, in particular with a new *Iodes* form in the early Eocene, possibly part of incoming new floral assemblages that arrived together with new faunal elements.



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## A global overview of Early Cretaceous angiosperm records from Teruel province (Spain)

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The past 25 years of paleobotanical studies on the Lower Cretaceous (Albian) Escucha and Utrillas Formations of Teruel province (northeastern Spain) have yielded the most complete and diverse macroand microfloral assemblages of this age known to date in southwestern Eurasia, and they have contributed to a more comprehensive view of the evolutionary diversification and dispersal of early angiosperms during mid-Cretaceous times.

Sediments of the Escucha Formation (early-middle Albian), interpreted as deposited in a tidally influenced fluvial system, have provided an important angiosperm leaf record of lines related to the basal eudicot family Platanaceae (*Sapindopsis turolensis, Eoplatanus*), plus leaves of chloranthaceous affinities. Microfloral remains also include typically eudicotyledonous tricolpate pollen grains with foveolate, reticulate, and striate sculpture (*Phimopollenites, Rousea, Striatopollis,* and *Tricolpites*), with the dominance of monosulcate pollen grains representing basal angiosperm lines of uncertain affinities (*Dichastopollenites, Jusinghipollis, Pennipollis, Retimonocolpites,* and *Transitoripollis*), as well as taxa with more definite relationships to Chloranthaceae (*Clavatipollenites* and *Hammenia*) and monocotyledons (*Liliacidites*).

The uppermost part of the Utrillas Formation (latest Albian), which consists of fluvial and lacustrine sediments deposited on a tidally influenced coastal plain, yields several paleobotanical assemblages containing many elements shared with North America and others suggesting a northward extension of Northern Gondwanan taxa during this time. Key pollen taxa include *Afropollis jardinus, Senectotetradites varireticulatus*, and *Stellatopollis barghoornii*. Macrofloras are dominated by leaves of both terrestrial and aquatic angiosperms, representing probable Nymphaeales (genera *Ploufolia* and *Aquatifolia*), Nelumbonaceae, possible Ranunculales (*Klitzschophyllites*), Platanaceae (a more derived species of *Sapindopsis*), and an unexpected diversity of monocots, including both a leaf and inflorescences of the near-basal family Araceae.



Speaker

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### Implications of phylogenetic analyses for the Cretaceous radiation of Magnoliidae

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The name Magnoliidae was originally used for the whole basal paraphyletic grade of angiosperms other than monocots and eudicots, but it is now restricted to the largest clade in this grade. Phylogenetic analyses of the position of Cretaceous fossils in molecular trees clarify the timing of diversification of Magnoliidae and provide insights on character evolution, biogeography, and ecology. The oldest confirmed Magnoliales are Endressinia and Schenkeriphyllum from the late Aptian of Brazil. Our earlier analysis associated Endressinia with a clade of four basically Gondwanan families united by inner staminodes, but reanalysis associates both fossils with Magnoliaceae. This implies that the magnoliaceous line originally had inner staminodes (lost in crown Magnoliaceae) and included Gondwanan plants adapted to more arid conditions than modern Magnoliales. Archaeanthus, from near the Albian-Cenomanian boundary in Kansas, had flowers essentially like modern Magnoliaceae; it was recently placed in crown group Magnoliaceae, but the evidence for this is problematic. Futabanthus, from the Coniacian of Japan, is a near-basal crown group member of Annonaceae, the largest living family of Magnoliales. The middle Albian flower Virginianthus appears to be nested just above the base of Laurales; it shows that reticulate monosulcate pollen, variously modified in living Laurales, was retained into the early radiation of the order. Mauldinia, from near the Albian-Cenomanian boundary, had more derived trimerous, unicarpellate flowers like those of Lauraceae, another large tropical family. However, it is most likely a stem relative of both Lauraceae and the more derived family Hernandiaceae, not a member of crown Lauraceae. An increasing number of flowers representing intermediate levels in Laurales have been described from the Albian. Canellales, which include the vesselless austral family Winteraceae, are represented by monoporate pollen tetrads in the late Barremian of Gabon and similar Aptian-Albian tetrads with sculpture more like that of modern Winteraceae. The much larger (semi)herbaceous sister order Piperales has had a poorer record, but Hexagyne from the late Aptian of Brazil confirms its predicted early presence. These results imply that Magnoliidae began to diversify earlier than eudicots but continued to radiate alongside them and included some of the first locally dominant angiosperms.



S2 // Oral

Speaker

## Homologous or analogous? Morphological interpretations of permineralized glossopterid reproductive organs from Queensland, Australia, in comparison to angiosperm carpel and stamen

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The most comprehensive approach for obtaining the best estimate of the true phylogeny of land plants is an analysis combining extant morphological and molecular information with morphological fossil data sets. Although most fossil information is incomplete due to the tendency for plants to become disarticulated into separate organs, and inherent limitations in preservation, phylogenetic analysis requires the most detailed description of fossil characters possible. Exceptional preservation allows for more accurate assumptions of synapomorphies. Glossopterids are extinct gymnosperms representing the dominant plant associated with the biota of the Permian Gondwana supercontinent. They have been also considered one of the possible ancestral lineages leading to the angiosperms. We present a new interpretation of glossopterid reproductive organs based on anatomically preserved megaand microsporangiate organs from the Upper Permian strata of the Bowen Basin of Homevale, Queensland, Australia. Because of their exceptional preservation, these fossils provide evidence that allows for a more accurate understanding of the glossopterid reproductive organs.

Both megaand microsporangiate organs from Homevale are reproductive shoots consisting of a series of helically arranged vegetative leaves and distally formed reproductive units borne on the shoot axis. The megasporangiate unit consists of a vegetative leaf similar to *Glossopteris homevalensis* and several small megasporophylls attached to its adaxial surface. Each megasporophyll has an adaxial surface facing the vegetative leaf, and is adaxially infolded to enclose several tiny ovules. This megasporophyll unit might be compared to the angiosperm outer integument. The microsporangiate unit is composed of a vegetative leaf bearing a pair of microsporangiate axes. Both axes branch several times and bear terminal microsporangia. Of particular significance is the absence of an axillary bud, or comparable structure in axils of leaves in the studied reproductive shoots. The leaf bearing multiple microsporangiate axes on the adaxial side in two rows is morphologically comparable to the hypothesized angiosperm "primitive" stamen, a lamina with two rows of microsporangiate sporangia on the adaxial side. A case can be made that the Homevale glossopterid organs are most comparable to the angiosperm carpels and stamens, providing an example of extinct seed plant morphologies that could be one of assumed ancestral forms genetically transformable to the angiosperm carpel and stamen.



Speaker

## The role of grasses in the East African vegetation across the Oligocene-Miocene boundary: new results and perspectives from plant silica (phytolith) analyses at Chilga and Mush Valley (Ethiopia).

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The savanna biome today occupies about ~50% of the African land surface. Savannas are characterized by a continuous grass substratum, which feeds zebras, rhinos, and a variety of bovids, all known for possessing tooth morphologies adapted to withstanding abrasive grasses and soil particles ingested with them. We seek to document the history of savannas (i.e., the ecological dominance of grasses, in the family Poaceae) in the geologic past of Africa, in order to elucidate factors that may have triggered their expansion in this part of the world. On other continents, pollen and grass silica remains (phytoliths) indicate that the first grass- dominated habitats appeared asynchronously during the Oligocene to Pliocene epochs. In East Africa, paleobotanical data (macrofossils, palynofloras), functional morphology of fossil faunas, and carbon isotope ratios suggest that grassdominated vegetation started expanding at the expense of forests during the early/mid-Miocene, but likely not until 21 Ma. To test this hypothesis, we have conducted phytolith analyses on several deposits the Chilga (ca 28-27 Ma) and Mush Valley (ca 22 Ma) localities on the Ethiopian Plateau, which are dated from before grassdominated vegetation is thought to have spread in East Africa. Our new phytolith data support the existence of forested environments at these two localities, regardless of their different taxonomic composition. Diagnostic grass silica bodies make up < 25% of the total sum of diagnostic phytoliths, indicating that grasses were present, but not abundant in vegetation overall. Among these grasses, C3 taxa related to forest-dwelling early diverging lineages and/or the Bambusoideae subfamily were present in grass communities at Chilga, whereas these same lineages seemed to have likely co-existed with representatives of the cool temperature-adapted Pooideae subfamily at Mush. Furthermore, high percentages of non-diagnostic grass phytoliths (silicified bulliform cells, trichomes) in a few samples from both localities, but especially Chilga, suggest variations in evapotranspiration or water supply either caused by seasonal climate and/or by repeated or persistent underwater conditions. Our results add to the previous interpretation of Chilga and Mush as forests by showing that grasses existed in the understory or in forest openings. More broadly, our results are consistent with the hypothesis that significant grass expansion in East African environments did not take place until after 21.73 Ma.

<sup>&</sup>lt;sup>°</sup> Speaker

## A missing link in *Glossopteris* evolution: new species of *Lidgettonia* from a middle Permian Lagerstätte in South Africa

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South Africa is renowned for its unparalleled collections of seed bearing structures of the widespread Gondwanan fossil plant taxon, Glossopteris. These have been collected from either lower Permian coal-associated deposits (Artinskian) in the north-eastern Main Karoo Basin (MKB), or late Permian (Lopingian) localities in the eastern parts of the country. Two new localities near Sutherland in the southern MKB, have yielded an exceptional flora in association with an unprecedented abundance of insect fossils, and represent the first conclusively dated middle Permian fossil plant sites in South Africa. A Guadalupian (Roadian) age has been determined through proximity to dated ashes, vertebrate biostratigraphy and stratigraphic correlations. In addition to a low diversity of Glossopteris leaf species, a new species of Lidgettonia has been identified, along with the first record of Squamella, the pollenate cone of Glossopteris, outside of Australia. To date, Lidgettonia has only been found in the late Permian of KwaZuluNatal and at one site in the Eastern Cape. This occurrence expands the temporal range of this fertile organ into the middle Permian, and provides an exciting glimpse of a plesiomorphic form of the genus. Lidgettonia taxa comprise a scale leaf with one to three pairs of campanulate organs, each homologous with the larger dictyopteridiacean forms typically found attached singly to a Glossopteris leaf. The scale leaves lack a midrib, have flabellate venation and are coriaceous. The new taxon from Sutherland is approximately 30% larger than previously recognised forms, and up to eight pairs of large cupules are attached to the extended pedicel of the scale. The scale leaves have a well-developed midrib and venation that more closely resembles that of a vegetative leaf than a typical scale, forming a narrow morphological continuum with associated Glossopteris leaves. To inform our taxonomic decisions, detailed morphometric analysis were performed on the scale leaves, attached seeds and cupules. This form represents an evolutionary link between the Dictyopteridiaceae and the Lidgettoniaceae that has been long hypothesised, with the reduction of fructification size coincident with an increase in number of fructifications per Glossopteris leaf, with the subtending leaf closer in morphology to a vegetative leaf than the highly reduced scale typical of more derived species.



S2 // Oral

<sup>.</sup> Speaker

## The evolution of sporophyte development during the early Paleozoic

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Molecular phylogenetic analysis of the timing of embryophyte origins now places the origin of land plants by middle Cambrian time. While this does correspond to the earliest record of spore-like remains, cryptospores sensu lato, such a date is at odds with the record of macroscopic plant remains, which are not found in strata older than the Wenlock Series. One possible explanation of this discrepancy is to consider the mid-Cambrian to mid-Silurian interval as the time of the assembly of the embryophyte developmental toolkit from an evolving complex of aeroterrestrial, streptophyte algae. The morphological manifestation of this process was envisioned by Bower as the antithetic origin of the land plant sporophyte. Bower predicted that sporogenous tissues evolved prior to vegetative tissues during the evolutionary assembly of an evolving plant sporophyte. When viewed in this way, Cambrian cryptospores demarcate the initial stages of an evolving streptophyte algal complex. Meiotic sporogenesis was canalized by the Darriwilian, and spore tetrads from this time were probably produced in a unilocular sporangium which possessed a tapetum. The origin of callose corresponds to the time at which free trilete spores become common during the Llandovery. Nematoclasts and cuticles become common during the Llandovery-Wenlock interval. Paleobotanists currently view these fragmentary fossils as fungal, but their stratigraphic distribution as documented in Laurentian and Avalonian terrains are a good fit to the sporophyte-assembly model proposed here. The origin of the embryophytes represents the origin of complex multicellularity in a subaerial photosynthetic eukaryote lineage. This was achieved, not as a singularity in geologic time, but rather as a serial genomic assembly that was underway by the mid-Cambrian and was finished by the end of the Silurian.



Speaker

## Early Jurassic *Nanjinganthus* and its implications on angiosperm evolution

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There used to be some controversies over angiosperm evolution at the beginning of the 20th century. But such controversies were later replaced by the academic silence and constant favor over Arber and Parkin's (1907) hypothesis, which was claimed favored by fossil evidence of Bennettitales. There has been evidence favoring this hypothesis popping up in various fields of botany. According to this hypothesis, flowers with numerous helically arranged free parts, conduplicate carpels without obvious style but with adaxially inserted bitegmic ovules (just as seen in Magnolia) are the most ancestral among angiosperms. On the contrary, syncarpous gynoecium with few parts and inferior ovary are derived and should occur much later in the history of angiosperms. A fossil plant recently recovered from the Lower Jurassic of China, Nanjinganthus, has syncarpous gynoecium with 4-5 perianth parts, inferior ovary, and dendroidformed style. Such a plant is apparently at the odds with and undermining the traditional theory of angiosperm evolution. With this information in mind, it appears necessary to re-examine the former evidence favoring Arber and Parkin's hypothesis. First, Parkin (1925) admitted that there was no fossil evidence supporting their hypothesis. Second, the morphological and anatomic evidence of Magnoliaceae favoring the traditional theory documented by Canright (1960) was artificially manipulated and mis-presented. Third, early fossil angiosperms including Archaeanthus (Dilcher and Crane, 1984) and Archaefructus (Sun et al., 1998, 2002) were both mis-interpreted to favor the traditional theory. Fourth, the claimed two integuments in a Cretaceous angiosperm Monetianthus (Friis et al. 2009), just as expected by the traditional theory, did not exist. Therefore the truthful support from fossils for the traditional theory actually did NOT exist. Fifth, more importantly, a new study indicates that the carpels in Michelia are actually composite organs derived from former branches and leaves (Zhang et al. 2017). Sixth, most important, more than twenty years ago, functional gene study on Arabidopsis (Roe et al., 1997) indicates that ovules are borne on branches (not on the margins of any foliar parts as assumed by the traditional theory) and gynoecium is composed of two different parts that are developmentally controlled by two distinct sets of genes. Obviously, the traditional theory of angiosperm evolution and systematics is doomed to fail from the very beginning, and its collapsing is accelerated by increasing emerging evidence. Misled by this theory, botanists remain perplexed by the mystery of origin of angiosperms. Now, with new fossil evidence, it is necessary to refresh our perspective on angiosperm evolution.



S2 // Oral

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### The Jurassic flora of Nestares Formation, Neuquen Basin, Argentina

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Palaeofloristic assemblages from the Jurassic were shaped by the Late Triassic extinction, which led to the loss of dominance of the corystosperms in Gondwana, and the replacement of the floristic components in this region. During the Jurassic Period, Southern South America was in a warm temperate biome. Early Jurassic floras from Argentina were dominated by conifers, bennettitaleans and ferns in a relatively homogeneous flora, described from Mendoza to Antarctica. The Neuquén Basin developed from the Jurassic to the Early Cretaceous as one of the major sedimentological basins of the Mesozoic of Argentina, with economic importance by the exploitation of hydrocarbons. The Nestares Formation is on the southern margin of the Neuquén Basin. The age of the Nestares Formation is in dispute between the megafloristic and palynological records, with a Sinemurian age proposed by biostratigraphic correlation with other local, dated units, against a Toarcian age based in the development of the dinoflagellates. In this contribution we report for the first time for the Nestares Formation several fossil plants. We add Cycadolepis Saporta, Cladophlebis antarctica Halle, Dicroidium Gothan, Komlopteris Barbacka, Pagiophyllum Heer, Taeniopteris Brongniart, and Nododendron Artabe and Zamuner, to the previously described flora. The material is preserved as compressions with a good preservation of cuticles, which allow us to study the stomatal density of the conifer and bennettitaleans leaves, leading us to add information to the global studies about paleoclimates in this period. These descriptions result also in a more up-to-date palaeobiological knowledge of the present paleofloristic elements, and a better paleoecological characterization of the unit. The presence of taxa related to the older Triassic floras such as Dicroidium support the Lower Jurassic age of the Nestares Formation, but for the moment the floristic record does not resolve by itself the age dispute. Likewise, the floristic similarities between the Lower Jurassic floras of Argentina and Antarctica are reaffirmed.



Speaker

## Holocene vegetation of Faial Island (Azores archipelago, Portugal) buried by recurrent explosive volcanism: taphonomy, palaeodiversity and palaeoecology

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Due to their geology, isolation and relatively recent human colonization, oceanic Islands have been, since Darwin and Wallace's proposal of the evolution by natural selection, the ideal sites to observe and study ecological and evolutionary processes. Although these islands were recently settled, the rapid anthropogenic modification and the relatively late scientific description of the biodiversity and neoecology, can mislead to what was the original vegetation encountered by the first settlers. However, from a palaeontological point of view, the recurrence of volcanic events in active islands means that insular biotas can be exposed to destructive but taphonomical important events. In Faial Island (Azores archipelago, Portugal, central North Atlantic), numerous localities bearing leaf fossils, charcoal and palaeosols are known since mid-20th century. These remains were mainly used for radiocarbon dating but were seldom studied from a palaeobotanical and palynological perspective. Here we report the exploration of a palaeobotanical and paleopalynological record found within a sequence of 12 sub-plinian and phreatomagmatic trachyte eruptions younger than 16 ka BP, with special attention to a 1200 yr BP event that covered Faial Island and their palaeovegetation, from sea level to mountain top. A total of 41 charcoalified and unaltered trunks and 27 palaeosols and sediments were sampled from elevations ranging from 22 m to 977 m a.s.l. Two localities containing leaf beds were also explored. Our preliminary results reveal six wood morphotypes, including cf. Erica, Picconia sp., cf. Laurus, cf. Morella faya, and an unidentified morphotype. Leaf beds showed the presence of fern fragments and lauroid leaves associated with an ash fall tuff. Palynological records from palaeosols and sediments are still under investigation, but preliminary results indicate differential preservation within palaeosols, with higher altitude palaeosols showing well preserved palynoflora, while lower altitude presents poorly preserved palynofloras. Further investigations will contribute decisively to elucidate the palaeovegetation cover of Faial Island and test it against neoecological data.



<sup>&</sup>lt;sup>\*</sup> Speaker

## Clarification of the paleovegetation and paleoenvironments of the Upper Cretaceous Mifune Group, Southwest Japan

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Recently, new localities yielding terrestrial vertebrate fossils were successively discovered from various geological provinces of Japan. Among them, the Mifune Group is one of the most representative dinosaur localities for the Upper Cretaceous of Southwest Japan. The Mifune Group is divided into the Basal, Lower and Upper formations in ascending order. It contains offshore, deltaic and fluvio-lacustrine freshwater deposits with more than 2,000 m thick in total and its age is estimated as the Cenomanian to Campanian. We took sediments from all three formations of the group and performed a palynological analysis to reconstruct the paleoenvironments as well as to understand comprehensively the paleovegetation that sustained the biota. Very few research existed about plant fossils of the Mifune Group until this report except for a short report on fossil leaves discovered from the Upper Formation. In addition, few palynofloral studies were conducted in the Upper Cretaceous of Southwest Japan, while some data are available for those in Central and North Japan. We previously reported well-preserved palynofloras from the late Albian Sasayama Group of Hyogo Prefecture and from the mid-Campanian Mitsuse Formation of Nagasaki Prefecture in Southwest Japan. The present report on palynofloras from the Mifune Group thus allows to fill this gap for the first time. We could obtain a wide array of palynomorphs from the three formations, composed of spores, gymnosperm and angiosperm pollens, fungi, freshwater algae, dinoflagellates and foraminifers. Gymnosperm pollen is particularly abundant whereas angiosperm pollen is scarce, but we could observe some grains with affinities to magnoliids and palms, among others. This poor diversity of angiosperms in the Mifune Group is markedly different from the Yezo Group of Hokkaido and other areas of North Japan during the same period which yield abundant and diverse angiosperm pollens. This difference would support the hypothesis that the diversification rate of angiosperms was slowed down in dry regions. From the composition of the palynological assemblage, we could confirm the age of the formations. Moreover, by adding these new data to the existing palynological reports, we could also confirm that a warm climate basically prevailed in Japan during the Albian to Campanian period, which was however drier in Southwest Japan than in North Japan but with probably an increase in humidity from the Santonian.



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### The diversity of Fagaceae in Paleogene of South China and its implications

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Fagaceae is one of the largest and most economically important groups within the order Fagales with about 927 species, and is widely distributed in temperate, subtropical and tropical regions of both the northern and southern hemispheres. Cretaceous fossils assigned to Fagaceae have been considered unreliable. The earliest confirmed megafossil record of the family is a pistillate inflorescence and dispersed fruits of the subfamily Castaneoideae and trigonobalanoids from the Paleocene/Eocene boundary of western Tennessee, USA. During the Cenozoic, Fagaceae fossils have been widely distributed in the northern hemisphere, especially in East Asia. In this study, the diversity of Fagaceae from Plaeogene sediments are investigated. 28 species in 5 genera (including Berryophyllum, Castaneophyllum, Castanopsis, Lithocarpus and Quercus) of the Paleogene Fagaceae fossils recovered from South China are described in details, including leaves, woods and mummified acorns. Molecular data shows that Fagaceae had an estimated origin at 59.5 (50.6–66.1) million years ago (Ma), and diversified before Paleocene-Eocene boundary at 56.4 (50.5–63.2) Ma. The present fossils of discovered from South China support the above estimation, indicating that the family have been distributed in the lowest latitude of subtropical to tropical regions at least by the Paleogene. Moreover, the modern Fagaceae is tropical to subtropical distribution. According to the fossil records of the five genera in Fagaceae and the living environment of their nearest living relatives, we speculate that the climate of the tropical to subtropical of South China is warm and wet during the Eocene, which is adaptable for the growing of Fagaceae, especially that the tropical elements, Quercus subg. Cyclobalanopsis, are well-developed and highly differentiated during that time.



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## Albian Angiosperms of Partizansk Basin (Primorye Region, Far East of Russia)

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The well-preserved herbaceous angiosperms were found last summer in the Lower Cretaceous deposits of the Frenzevka Formation, southern Primorye, Far East of Russia. Locality Bolshoy Kuvshin is situated on the coast of Ussuri Bay on the Bolshoy Kuvshin Cape near the Bolshoy Kamen town. The geological age of the plant-bearing bed is determined to be early-middle Albian in age. Angiosperm assemblage includes six species: *Achaenocarpites capitellatus* Krassilov et Volynets, *Ternaricarpites floribundus* Krassilov et Volynets, *Jixia pinnatipartita* Guo et Sun, *Asiatifolium elegans* Sun, Guo et Zheng and two new undetermined species. The most part of specimens are represented by fragments of branching stems with attached leaves or fruits or by almost complete plants. Two species (*Jixia pinnatipartita* and *Asiatifolium elegans*) are common with angiosperm assemblage from the Chengzihe Formation (eastern Heilongjiang, China). Angiosperm remains are accompanied by fern *Onychiopsis psilotoides*, which is represented by almost whole young plants. The fossil plants were buried during one flooding event and very closely to their growth place. They formed pioneer open herbaceous community, consisting from fern and angiosperms with predominance of latter and adapted to colonize fresh sediments in periodically flooded areas.



Speaker

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## Palynological assemblages across the Hercynian unconformity in Western Iraq

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Recent study of samples from borehole KH-5/1 has allowed an assessment of the duration of the hiatus associated with the so-called Hercynian unconformity (also known as the 'Late Carboniferous unconformity' or 'pre-Unayzah unconformity') in western Iraq. KH-5/1 was drilled as a deep water well and fully cored to TD at 1620m. The well section spans the unconformity at 670m depth with the Raha Formation below and the Ga'ara Formation above. The unconformity appears to be associated with non-deposition or erosion of rocks corresponding approximately in age to part of the Serpukhovian and Bashkirian (latest Mississippian to early Pennsylvanian), similar to the duration associated with the same unconformity in well ST-8 situated to the south of KH-5/1 in northern Saudi Arabia. The Ga'ara Formation assemblages above the unconformity in KH-5/1 are similar in character to those described from 4620 to 4200 feet in ST-8. The age of these assemblages in both KH-5/1 and ST-8 is considered in this paper to be Westphalian. The composition of the Ga'ara Formation assemblages in KH-5/1 also shows some similarity to glacigene post-unconformity beds of the 2165 Biozone of the Al Khlata Formation of Oman.



## Ufadendron elongatum sp. nov., an Angaran element of lycopsids from the Upper Permian of inner Mongolia, China

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A new species Ufadendron elongatum sp. nov., placed in the family Tomiodendraceae Naugolnykh, represented by two well-preserved stems in the collection under study, was recently discovered from the Upper Permian Linxi Formation at the Jalaid locality in Inner Mongolia, China. The genus Ufadendron is characterized as leaf cushion long fusiform, with infrafoliar bladder, wings and heel well developed, leaf scar small and rounded, containing a central pointlike scar. The new species is different from the type species U. ufaense (Naugolnykh 2014) from the Lower Permian of the Cis-Urals, western limits of Angaraland, in the leaf cushion elongated and the heel marked. Interestingly, a large helical tracheid is occupied at the middle of central point-like scar. Ufadendron is very similar to Angarophloios in its infrafoliar bladder as well as wings and heel, but the former develops leaf scar with a central point-like scar containing conductive tissues, at the upper part of leaf cushion, while the latter only shows leaf base buried the matrix. So far, only 4 genera of Angaran elements of lycopsids have been discovered in the region geographically belonging to Angaran Phytogeoprovince in China. Lycopsids from the Euramerican phytogeoprovince with the most complicated leaf cushions and leaf scars infer that the Euramerican phytogeoprovince, which was located in the tropical continent, is the most suitable area for the development of lycopsids. Lycopsids from the Angaran and Gondwanan phytogeoprovince represent those plants from the temperate continent regions of North and South Hemispheres, respectively. They are similar in the absence of ligule for some taxa, implying that those plants did not develop very well in temperate continent regions because the leaf cushions of lycopsids from the tropical regions, i.e. the Euramerican and Cathaysian phytogeoprovinces, are more complicated. The new species U. elongatum not only enlarges our knowledge on taxonomy of Tomiodendraceae lycopsids, and also provides an opportunity to understand the difference between Angaran and Cathaysian floras in paleoclimatic, paleoenvironmental, and paleophytogeographic context.



Speaker

#### Assessing mid-Paleocene climate using fossil leaves

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The Paleocene was a globally warm period marked by several climatic variations. The most famous one is the abrupt warming event at the Paleocene-Eocene boundary, known as the PETM. Variations of the climate from middle to late Paleocene are comparatively less well documented, especially at middle latitudes. In this study, we analysed two famous fossil leaf assemblages, described during the 19th and 20th centuries by Saporta and Mai, namely Gelinden (Selandian, Belgium) and Menat (Selandian, France), in order to compare these two localities and to assess the continental paleoclimate for western Europe. Leaf morphology was used to calculate main paleotemperature and paleoprecipitation variables, using the Climate Leaf Analysis Multivariate Program (CLAMP) and the Climate Leaf Analysis with Neural Networks (CLANN) approaches. Preliminary results indicate a moderately warm, humid and seasonal climate for both localities. However, we observed some differences between the two approaches. CLANN leads to wider temperature and precipitation ranges, and higher MAT for both Gelinden and Menat. This is particularly a problem when the locality is outside of the model limits, and this approach might not be optimal for ancient floras without modern analogues as this is the case for both localities. CLAMP results showed that Gelinden paleoclimatic conditions were warmer and more humid as compared to Menat. According to the Köppen-Geiger climate classification, Gelinden climate represents an intermediate between subtropical humid climate (warm temperate without dry season climate) and Mediterranean-type climate (warm temperate with dry season), while Menat would be more representative of the second type. Subtropical humid climate is found nowadays for instance in China, in Southern Japan and in the southern part of North America. In agreement with oceanic proxies, both fossil floras suggest subtropical to warm temperate climates during the mid-Paleocene in western Europe.



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## S3 - Back to the sea: from Late Palaeozoic to Cenozoic, the Tetrapod adventure

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## When Nature is having fun: walrus-dolphins and aquatic sloths fom the Neogene of Peru

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Our knowledge of the present and past biodiversity is dreadfully poor. We probably know less than 0.5% of the taxa that existed and exist on Earth, that is to say, almost nothing. Given that, because past biodiversity is by far the most abundant, palaeontologists are constantly exposed to the most unexpected discoveries, resulting from the fantastically active imagination of Nature. The marine Neogene Pisco Formation of Peru has yielded two of such astonishing "jokes of Nature": a "walrus - dolphin" and an aquatic sloth. Odobenocetops is a delphinoid cetacean, which has lost the elongated rostrum characteristic of the order and instead bears postero-ventrally projected premaxillary sheaths bearing asymmetrical tusks, the right one being at least one meter long, and the left one barely erupting from the bone. The posteriorly located bony nares of extant cetaceans have migrated anteriorly, but are still dorsally facing and the maxillae are drastically reduced in contrast to the condition in other odontocetes. The large and deep palate suggests a feeding adaptation similar to that observed in the walrus, which uses its tongue as a piston to extract the foot and siphon of soft-shell mollusks that it firmly maintains in its powerful lips. Females of Odobenocetops have two small tusks and the function of the large right tusk of males was probably social as in living narwhals. Thalassocnus is a semiaquatic sloth represented by five species occurring in successive beds from the late Miocene to the Pliocene. The fact that the Peruvian coast was a desert during the Neogene and the abundance of articulated skeletons indicate that Thalassocnus was feeding there upon marine vegetation. The long premaxillae and mandibular symphysis with splayed apices suggest an increased capacity of grazing in more recent species. Thalassocnus used its powerful anterior claws to anchor itself on the sea floor to feed upon sea grasses, which are present in the sediments of the Pisco Formation. The pronounced osterosclerosis of the ribs and limb bones of Thalassocnus, which increases in the youngest species, served as a ballast to weigh down the body in order to graze with reduced efforts as is observed in sirenians. The limb bones anatomy indicates that Thalassocnus was not an efficient swimmer, but rather a bottom-walker as extant hippos. Odobenocetops and Thalassocnus were both benthic feeders, which peacefully coexisted on the coast of Peru during the late Neogene.



<sup>&</sup>lt;sup>°</sup> Speaker

## Endocranial microtomographic study of marine reptiles (Plesiosauria and Mosasauroidea) from the Turonian (Late Cretaceous) of Morocco: palaeobiological implications

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As windows into the deep history of neuroanatomy, endocasts may provide information about the central nervous system of fossil taxa. Based on exceptionally preserved specimens of coeval mosasauroids (Squamata) and plesiosaurians (Sauropterygia), from the Turonian (early Late Cretaceous) outcrops of Goulmima (Southern Morocco), the aim of this work is to describe for the first time in detail the endocranial anatomy of these two major clades of Mesozoic marine reptiles. This study aims at providing insights about the sensory abilities that accompanied the return of these amniote lineages to life in water. In addition, the endocranial anatomy of related extant squamates, mainly snakes but also varanids and amphisbaenians, also almost unknown until now, is described for the first time and used for comparative purpose to analyse the formfunction relationships associated to endocasts. The analysis of the endocranial variability in extant squamates pointed out that endocasts reflect both phylogenetic and ecological signals, and that the relative size of each endocranial structure can be related to differences in vision and olfaction according to taxa. Among fossil taxa, the 3D morphology of the endocast has been reconstructed, thanks to the resort to microtomography, for two elasmosaurid specimens of Libonectes morgani, an indeterminate polycotylid and the basal mosasauroid Tethysaurus nopcsai. The results show that the endocranial morphology of Plesiosauria is similar between the different taxa and differs from that know in other extinct and extant marine reptiles, being thus unique. Based on the relative size of the structures composing their endocasts, both the mosasauroid Tethysaurus and the plesiosaurians seem to rely more on vision than on olfaction to interact with their environment. However, these new endocast data, added to information already available in the literature suggest different modes of locomotion and hunting techniques, which probably allowed them to coexist in Goulmima.



Speaker

## **Comparative cranial morphology of the Late** Cretaceous Protostegid sea turtle Desmatochelys lowii

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The phylogenetic placement of Cretaceous marine turtles, especially Protostegidae, is still under debate among paleontologists. Whereas protostegids were traditionally thought to be situated within the clade of recent marine turtles (Chelonioidea), some recent morphological and molecular studies suggest placement along the stem of Cryptodira. The main reason why the evolution of marine turtles is still poorly understood, is in part due to a lack of insights into the cranial anatomy of protostegids. This study provides a detailed comparison of the internal and external cranial morphology of the protostegid Desmatochelys lowii Williston, 1894 with two extant marine turtles Dermochelys coriacea and Eretmochelys imbricata and the freshwater snapping turtle Chelydra serpentina. The studied skulls were scanned with X-ray microtomography and virtually segmented, in order to allow the examination of each bone individually. In total, 81 bones were described, including the nature of their contacts. The recent global phylogeny of turtle relationships was expanded and updated through the inclusion of the newly obtained anatomical insights. Additionally, a novel bone contact data was compiled and applied in a preliminary similarity study. The latter study that utilizes newly obtained bone contact data suggests that Desmatochelys lowii is least similar of the four turtles included, which would be concordant with a phylogenetic placement outside Americhelydia. The resulting phylogeny places the Protostegidae in the stem of Chelonioidea, which is a novel position for the group more congruent with recent molecular calibration analyses.

**S3 // Ora** 



## The fossil record of marine adapted snake lizards: origins, convergence, and phylogeny

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Despite the fact that the debate continues around the ecological origins of snake lizards burrowing versus terrestrial origins scenarios - the fossil record of snake lizards, when assessed against phylogeny, clearly indicates that numerous clades of snake lizards have secondarily, and thus convergently, invaded marine habitats. Beginning in the Middle Jurassic, with the oldest known snake lizards fossils, these animals are found in rocks deposited in sedimentary environments proximate to estuaries and beaches located on island archipelagos. Late Jurassic and Early Cretaceous snakes are found in back beach environments and coal swamps on island systems. By the Early Cenomanian, snake lizard clades have rapidly diversified with several form-types (grouped around cranial, vertebral, and rearlimbs present/absent) having radiated into marine environments in the Tethys Seaway of southern Europe, the Tethyan Platform and northern Africa and across the ProtoAtlantic to the north east margin of South America; these various snake lizards and their lineages show important skeletal aquatic adaptations (pachyostosis/osteosclerosis), and are also found in marine deposited carbonate rocks from a wide variety of depositional environments. There is a rich Late Cretaceous record of non-marine snake lizards from Gondwanan continents, but evidence of marine radiations is found only after the K-P Extinction Event. Beginning in the Eocene, and in many locations around the globe, numerous snake lizard clades (madtsoiids, macrostomatans, etc.) radiate into marine environments. While the majority of these Cenozoic snake lizards are known only from disarticulated elements of the axial skeleton, some are in fact known from beautifully articulated remains preserved in platy limestones deposited in lagoonal environments. These Eocene to Oligocene-aged snakes represent several different lineages of snake lizards, are found in a variety of marine environments, and some achieve gigantic proportions, while others are relatively small, though they have surprisingly large numbers of vertebrae. Modern marine snake lizards are found amongst higher caenophidians, including the freshwater/estuarine Java File Snake, and the sea snakes and sea kraits, which are highly derived elapids. Snake lizard evolution is currently understood to have undergone at least fifteen independent marine adaptive radiations, beginning as far back as the Middle Jurassic, and continuing forward to the present.

Speaker

### Form, function, and phylogeny in Late Oligocene tusked dolphins from New Zealand

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Late Oligocene dolphins from New Zealand include species with "spear-like" horizontally procumbent teeth, in long and slender jaws. Such long, delicate tusks are absent from living odontocetes. The function and phylogenetic significance of tusks are still uncertain, although feeding or display are possible functions.

The tusked dolphins are from marine mid-shelf strata, the Kokoamu Greensand and Otekaike Limestone (Chattian, to possibly basal Aquitanian) of the Waitaki region of New Zealand. The three key named species are *Waipatia maerewhenua*, *Otekaikea marplesi*, and *Otekaikea huata* (Waipatiidae). Phylogenetic analyses mostly place these in the Platanistoidea, a clade now restricted to the living South Asian river dolphin, *Platanista* gangetica but relationships are unstable. A fourth procumbent species from another New Zealand basin, cf. *Kentriodon* sp. (Delphinoidea), is probably Aquitanian.

Other undescribed "tuskers" from the Waitaki region are new species, known from parts or whole skulls with 6-10 horizontally procumbent apical teeth in their rostra and mandibles. The two most important specimens (OU 22397 and OU 22126) were briefly mentioned in print as species of Dalpiazinidae, a family otherwise known from Italy. The Dalpiazinidae is based ultimately on *Dalpiazina ombonii*, described from an incomplete mandible with empty alveoli and with no evidence of procumbent teeth (Belluno Sandstone, Aquitanian, Italy). There are no apomorphies with New Zealand fossils, and the Dalpiazinidae is thus unconnected to the New Zealand record. Both the New Zealand specimens have elongate, attenuate, and dorsoventrally flattened rostra, with the tusks in elongate premaxillae. The maxillary teeth are polydont: heterodont in OU 22397, and near-homodont in OU 22126. The periotic (earbone) has a parabullary sulcus, apparently apomorphic for Platanistoidea.

Phylogenetic analysis puts OU 22397 toward the base of the Platanistoidea, near *Waipatia maerewhenua*, and remote from Kentriodon and other Delphinoidea, with no tusks in intervening clades. This pattern could mean that tusks evolved convergently in the platanistoid and delphinoid clades. However, archaic Oligocene taxa are not well sampled between those clades, thus tusk plesiomorphy or homoplasy is still uncertain.



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## New insights in the evolution of true seals (Carnivora, Pinnipedia, Phocidae): diversity and paleobiogeography

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Historically, multiple attempts have been undertaken to elucidate the timing and geographical pathways of phocid (true seals) dispersal around the world. However, one major shortcoming is that researchers showed little interest in reassessing the original descriptions of extinct seals and their stratigraphic context. Another major issue is the use of syntypes in these original descriptions, allowing to question whether the fossil record of Phocidae truly reflects the actual diversity or may be oversplit/lumped.

Recent re-investigation of the fossil record of phocids from the North Atlantic Ocean and the Mediterranean Sea has important implications for the interpretation of the diversity and paleobiogeography of the family. First, the reassessment of the stratigraphy of *Monotherium gaudini*, from Italy, indicates that this species is the oldest confirmed and acceptably well-documented extinct seal, dated to the late Oligocene or early Miocene and comparable in age to the divergence date of Phocidae as estimated from molecular data. Second, dinoflagellate cyst analysis of sediment samples associated with phocid fossils from the Pliocene Kattendijk Formation, Belgium, indicates a late Miocene age instead of the commonly accepted early Pliocene age for the taxa considered. Third, the recent (re-)discovery of a 'southern' phocid humerus from the late Pliocene of Belgium suggests late survival of Monachinae at high latitudes in the North Atlantic. Additionally, new taxa have been described and the validity of others has been questioned, yielding implications on biogeographic ranges of different extinct phocid taxa and on phocid biodiversity through time, which may be related to climatic events.

Our findings indicate an early and fast diversification of phocids – and pinnipeds in general – during the late Oligocene and early Miocene. Stemming from northeast Pacific stem pinnipedimorphs, geographical dispersal of phocids to the eastern North Atlantic was rapid. The high number of seal taxa present during the late Miocene in Europe, predating the occurrence of the same taxa on the east coast of North America, suggests that diversification of part of the phocid seals from the Northern Hemisphere primarily occurred in Europe. Their rapid decline in diversity during the Pliocene may be related to climatic changes around the Mio-Pliocene boundary, such as the growth of permanent ice caps in the Northern Hemisphere.



S3 // Ora

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## Late Jurassic ichthyosaurs from the Neuquén Basin (Central-West Argentina): new insights into the phylogeny of the Ophthalmosauridae

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Ophthalmosaurids were advanced ichthyosauromorphs. Their evolution, from the Aalenian to the Cenomanian, encompassed half of the history of the whole clade. The traditional conception of ophthalmosaurids as the last representatives of a declining lineage has radically changed in the last decades. New discoveries and studies indicate that ophthalmosaurids dominated soon after they emerged, probably at the Aalenian-Bajocian boundary, and achieved a widespread geographical distribution. Although their oldest records were recovered from the Neuquén Basin (Argentina) most of their fossils have been collected from the northern hemisphere. Southern hemisphere records are mainly restricted to Australia, Argentina and Chile, and to isolated material from Madagascar. Four nominal ophthalmosaurid taxa are recognized from the southern margins of the eastern paleopacific: Mollesaurus periallus, Caypullisaurus bonapartei, "Platypterygius" hauthali and Arthropterygius sp. We assigned a new name for the reception of an ophthalmosaurid of Patagonia and included it in an expanded version of datasets to explore its phylogenetic affinities. The new taxon depicts a peculiar pattern of an "ophthalmosaurine-like" skull and a "platypterygine-like" forefin. Cladistic analysis recovered it forming a polytomy at the base of the platypterygine clade, and the "ophthalmosaurines" are found as a paraphyletic assemblage. All boreal forms are nested within platypterygines but only three of them (Cryopterygius, Janusaurus and Arthropterygius) form a subclade. Stratigraphic calibration of the tree indicates that the platypterygine radiation occurred earlier than previously supposed, probably during the late Middle Jurassic.



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## Towards an adaptive landscape for short-necked plesiosaurians

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Plesiosauria is the most diverse and probably the most disparate clade of secondarily aquatic tetrapods. The frequency and intensity of morphological convergences within this group and the strong constrains of the aquatic medium make Plesiosauria an ideal model for testing the processes of morphological diversification. The adaptive landscape of plesiosaurians has been summarised to two global morphotypes: one for short-necked forms (pliosauromorphs) and one for long-necked forms (plesiosauromorphs). Although these were historically conceived as long-liven, monophylogenetic clade, it is increasingly clear that these body plans each arose multiple times independently during the evolutionary history of Plesiosauria, providing evidence of a macroevolutionary adaptive landscape. We investigate the morphological diversification of the two major groups of short-necked plesiosaurians: Pliosauridae and Polycotylidae. Using an updated phylogenetic dataset incorporating most plesiosaurians and a morphological dataset summarising the Bauplan and diet-related features, we investigate the rates of evolution, patterns of morphospace occupation, and disparity over time of these two clades. Our results show that a handful of clearly distinct craniodental architectures exist within pliosaurids and polcotylids and that several episodes of convergent evolution affected these clades. This indicates that while there is probably no such thing as single 'pliosauromorph' morphotype, the craniodental adaptive landscape of these animals might be quite simple, with a few optimal morphologies.

Speaker

## An ancient beaked-whale mimic: a toothless presumed platanistoid dolphin from the Otekaike Limestone (latest Oligocene), Hakataramea Valley, New Zealand

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The Waitaki region in New Zealand is an important source of Eocene-Miocene cetaceans (whales, dolphins). These fossils are from the margin of the evolving Southern Ocean, in which the Antarctic Circumpolar Current influenced long-term climate trends and nutrient cycles potential drivers of cetacean evolution. The most fossiliferous units from southern New Zealand are the Kokoamu Greensand-Otekaike Limestone (Chattian, to basal Aquitanian). In Hakataramea Valley, these strata have produced diverse Cetacea including: the Mysticeti *Mammalodon, Waharoa* and other eomysticetids, the stem balaenopteroid *Mauicetus*, and the stem baleen whale *Horopeta*; and Odontoceti including a squalodontid, an apparent delphinoid, the platanistoid *Otekaikea*, and diverse smaller dolphins.

A new species of fossil odontocete from Hakataramea shows features reminiscent of suctionfeeding beaked whales (Ziphiidae, middle Miocene-Recent) and the Pliocene ziphiid-mimic *Australodelphis* (Delphinidae). Of note are: beak-like rostrum with robust maxillae, but no alveoli; uncertain number of tiny single-cusped teeth; mandible straight-edged with an indistinct alveolar groove; para-narial premaxillae strongly asymmetrical and elevated; and large facial fossa for nasofacial muscles. The dolphin is quite disparate, in these ziphiid-like features, from other coeval Southern Hemisphere taxa. Other features differ from those of Ziphiidae: the lacrimojugal is fused; the curved parabullary sulcus on the periotic matches archaic platanistoids; there is no enlarged posterior process on the bulla; and the pterygoid sinus fossa is not enlarged and has a rod-like hamulus.

The Hakataramea ziphiid-like dolphin is from a broad shelf setting facing the Southern Ocean. Burial was probably below storm wave base, judging from commonly-associated vertebrate skeletons and paraautochthonous invertebrate assemblages. Given the depositional setting, was the dolphin a neritic (shelf) species? Or might its ziphiid-like skull form imply pelagic foraging beyond the shelf break, and perhaps deep-diving? The dolphin adds to the taxonomic and ecological diversity of Oligocene Neoceti, consistent with Oligocene radiations in many lineages.



Speaker

## Anatomy of *Ferecetotherium kelloggi*, the earliest crown-group cetacean from the Oligocene of Caucasus

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An assemblage of Late Oligocene odontocetes from the South Caucasus, including a few representatives of different families and taxa with uncertain family affinities, has been originally described by Guram McHedlidze during the seventies and eighties. One of these cetaceans, Ferecetotherium kelloggi, was later identified as a sperm whale, thus being the earliest representative of crown odontocetes. The specimen consists of skull fragments, ear bones, mandibles, teeth, a few vertebrae, sternum, and both forelimbs. Here we interpret some of these fragments, which have not been discussed before. Apart from a typical physeteroid periotic, Ferecetotherium has a wide and deep supracranial basin with extremely telescoped facial bones and a high, rounded occipital shield, autapomorphic features for Physeteroidea. In addition, it has a slit-like antorbital notch, a large dorsal infraorbital foramen, somewhat reduced maxillary teeth, fused postaxial cervical vertebrae, a short and wide rounded sternum, contact between the 1st and the 2nd fingers, and other specific features observed in other Physeteroidea, including derived forms. Meanwhile, it has many primitive traits: nasals nearly equal in size, multiple maxillary teeth, a long zygomatic process with a long facet for the postorbital process, little transformed tympanic bulla and short forelimbs with advanced ossification and no traces of hyperphalangy. The combination of these characteristics is evidence for the evolution of advanced physeteroid anatomy (especially skull anatomy) by the Late Oligocene. It also shows that the earliest physeteroid was a pelagic, piscivorous cetacean with generalized feeding type and some evidence of suction feeding. The evolution of sperm whale apomorphies was independent of feeding or habitat adaptations, and evolution of the tympanic bulla and forelimbs was slower than the skull transformations.



Speaker

S3 // Ora

## *Kronosaurus boyacensis,* a Gondwanan marine mega-predator, from the 'Lower Cretaceous Gap' Paja Formation Lagerstätte of Colombia, South America

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In June 1977, the skeleton of a large sauropterygian marine reptile was discovered by local farmers in Vereda de Monquirá, Departamento de Boyacá, Colombia, South America. The skeleton was a large pliosaurid plesiosaur, almost complete and articulated, from the upper Aptian Arcillolitas Abrigarradas Member of the Paja Formation, which is now recognised as a Lower Cretaceous Gap (LCG) marine reptile Lagerstätte. The pliosaurid remains are preserved in situ, covered by the community run 'El Fósil' museum, and the skeleton has become iconic as 'The Fossil' of the Alto Ricaurte region. The scientific importance of the skeleton was recognised by its description as the holotype of a new species, *Kronosaurus boyacensis*.

Examination of the skeleton of *Kronosaurus boyacensis* has revealed the need for a detailed redescription, which indicates erroneous original interpretation of various features, including: the positions of the cranial bones and openings; the location of the atlas-axis; and the interpretation of the dorsal vertebrae. Hence, we undertake a full re-description, and clarification of the morphology of the specimen. Interpretation of the taphonomic trajectory of the fossilized remains indicates collapse of the skeleton on the sea-floor, rapid burial without evidence of scavenging or epibionts, and partial preservation in early diagenetic concretions, which together permit reconstruction the original three-dimensional shape of the animal.

*Kronosaurus boyacensis* is a remarkable specimen. It was the first of a growing number of newly described Lower Cretaceous pliosaurids from the LCG of Colombia. The holotype is an evolutionarily and palaeogeographically important Lower Cretaceous mega-predator, which highlights the importance of northern South America for the study of LCG pliosaurids. *Kronosaurus boyacensis* and its cohabiting marine reptiles are thereby critical to our understanding of Lower Cretaceous epicontinental seaways.



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## The inner ear reveals patterns of adaptation to aquatic environment in carnivoran mammals: seals, sea lions, fur seals and walruses

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Adaptation of terrestrial placental mammals to aquatic environment requires important modifications of anatomical, physiological and functional features of their body. Here we studied the transition from land to water in the carnivoran mammal clade Pinnipedimorpha, including living seals, sea lions, fur seals, walruses and their fossil allies. We investigated the evolution of their inner ear, the organ of balance and hearing in vertebrates, as its morphological transformations along the phylogenetic history of clades have proven to track sensory perceptual changes in response to locomotor and environmental shifts. We used high resolution X-ray microtomography to reconstruct virtually the bony part of the inner ear, the bony labyrinth, of 16 extant and 8 fossil pinnipedimorphs, representing a wide range of taxonomic and ecological diversity, with global geographical occurrences and a large chronological distribution from the Oligocene to present. We used 3D geometric morphometrics to investigate the relationships between inner ear shapes and species body size, phylogenetic proximity and environmental and behavioral factors. We built a time-calibrated phylogeny from molecular data and fossil occurrences for our sample. We found that the lateral semicircular canal of seals is smaller than in sea lions and fur seals. We found that species body size, phylogenetic relatedness and locomotion significantly influence inner ear shapes and that the shape of the cochlea is significantly correlated with diving parameters (duration and depth) in extant species. We also inferred the swimming modes of fossil pinnipedimorphs using a phylogenetic flexible discriminant analysis. The prediction model based on inner ear shapes suggested that the basal pinnipedimorphs Enaliarctos and Pteronarctos could have used mainly forelimb propulsion for swimming, while basal fossil seals and walruses could have used a hindlimb-dominated propulsion, like in their modern relatives. Pinnarctidion, alternately placed as a basal pinnipedimorph or in a fossil family closely related to seals (Desmatophocidae), could have used a forelimb-dominated propulsion while in water, as in modern sea lions and fur seals.



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## Evolution of body plan and the hydrodynamic properties of ichthyosaurs

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Ichthyosaurs were one of the most successful groups of secondarily aquatic tetrapods, which evolved from terrestrial ancestors in the aftermath of the Permian extinction and thrived in the Mesozoic oceans. During their ca. 160 myr of evolution, their bauplan changed from a narrow and elongated morphology in the primitive forms to the deep and highly streamlined bodies of the modern parvipelvians. By the Jurassic they had become highly specialised for aquatic locomotion and acquired fish-like body shapes, convergent with modern cetaceans or sharks, along with other adaptations to pelagic lifestyle like lunate tails for caudal propulsion. Until recently, studying the functional impact of these morphological changes has been hampered due to the lack of an objective, physics-based quantitative method. Here, we use 3D modelling techniques and Computational fluid dynamics (CFD) to evaluate the impact of these bodily transitions in the hydrodynamic properties of ichthyosaurs. CFD is a state-of-the-art engineering tool used to simulate fluid flows and to calculate the forces resulting from fluid-solid interactions. We create full-body digital reconstructions, scaled to the same length, of nine ichthyosaur specimens. We include the model of a living analogue, the bottlenose dolphin, for comparative purposes. We then perform flow simulations over a range of speeds to calculate the drag and lift, as well as to evaluate the contribution of the limbs to these forces. Our results demonstrate that modifications in the body plan of ichthyosaurs did not cause major changes in the drag coefficient across taxa or through evolutionary time. However, the values of drag relative to volume, here used as a proxy for muscle power, decrease substantially during the first 25 million years of ichthyosaur evolution. Before the end of the Triassic, ichthyosaurs had experienced a change in body proportions with a great impact in reducing the energetic cost of aquatic locomotion, contributing to a more efficient swimming.



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### The origins of forelimb-propelled swimming in pinnipeds

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When aquatic tetrapods swim, they typically propel themselves using either the front or rear end of their body. Ichthyosaurs, whales, and otters swim using their hind limbs or tail, whereas sea turtles rely on their powerful forelimbs. Pinnipeds (seals, sea lions and walrus) are unusual in employing both swimming styles, despite their monophyletic origin: sea lions propel themselves with flipper-like forelimbs, while true seals and walruses use alternating strokes of their crescent-shaped feet. Like true seals, early stem pinnipeds (e.g. *Enaliarctos mealsi*) are thought to have relied mainly on their hind feet. If so, why did some pinnipeds abandon this ancestral swimming style in favour of forelimb propulsion?

To unravel this question, we examined the forelimb anatomy of modern pinnipeds, linking morphology to differences in how the limbs are used. The most derived forelimbs are found in otariids, which use paired strokes of their flippers to generate propulsion. By contrast, phocine seals retained webbed paws bearing flexible digits and strong claws. These paws allow phocines to perform tasks like digging and holding prey, but they also make the forelimbs less effective tools for swimming. Monachines, or 'southern' phocids, show a peculiar intermediate state, with a trend towards increasing specialisation of the forelimb and – in some species – marked convergence on otariid-like flipper morphology. Observations of swimming in *Hydrurga, Neomonachus* and *Leptonychotes* suggest that they often use their forelimbs alongside their feet to generate propulsion. Together, these insights demonstrate that forelimb-based swimming and specialised flipper anatomy can be derived from a hind limb-propelled ancestor.

Early pinnipeds like *Enaliarctos* had forelimbs similar to modern phocines, with mobile digits and strong claws capable of grasping prey. Their paws likely remained important for feeding, as they do in phocines, which in turn may have constrained the adaptation of the forelimb for swimming. From this ancestral state, we suggest that the ancestors of otariids began targeting small schooling fish that could be swallowed whole without processing. Their forelimbs, freed from the need to grasp food, evolved into flippers, making early otariids even more mobile and adept at capturing evasive prey. Ultimately, sustained specialisation on fast-moving prey created the selective pressure that lead to the evolution of forelimb swimming.



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## The diversity and radiation of Machimosaurini (Crocodylomorpha, Thalattosuchia, Teleosauroidea) during the Middle Jurassic, and discussion on their morphofunctional adaptations

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Thalattosuchia was a unique group of marine crocodylomorphs that flourished during the Mesozoic Era, evolving a wide range of environmental adaptations and feeding specializations. One of the two major groups within Thalattosuchia is Teleosauroidea, a distinctive clade that superficially resembled modern gharials. They attained a near-globally distribution and frequented shallow marine and brackish ecosystems throughout the Jurassic. However, the major teleosauroid subclade Machimosaurini evolved into the crocodylomorph giants of the Jurassic, exceeding 7 m in body length and 1 m in cranial length. Moreover, their craniodental adaptations suggest a macrophagous and/or durophagous diet very different from other teleosauroids. Over the last five years, the taxonomy, comparative anatomy and phylogenetic relationships of Machimosaurini have begun to become well-documented, with at least nine synapomorphies identified (including parallelogram-shaped supratemporal fenestrae; dentition that is serrated with heavily ornamented enamel and blunt apices; and deep socket-like reception pits along the maxillae and dentaries). However, the origins of the group are little understood; machimosaurins were common in the Late Jurassic of Europe and Tethys, with the radiation of Machimosaurus (which may have been linked to the radiation of marine chelonians). Less is known about the subclade in the Middle Jurassic, with the bestpreserved material that of Lemmysuchus from the Callovian of England and France. Curiously, in these Callovian formations Lemmysuchus is a rare component of the ecosystems, hinting that machimosaurins did not become diverse until the Late Jurassic radiation of Machimosaurus. Prior to the Callovian machimosaurin material is fragmentary (such as from Morocco) or based on isolated teeth that might be referable to Machimosaurini (e.g. those from England). Here we evaluate the validity of the species Steneosaurus meretrix, S. megistorhynchus, S. larteti and S. boutilieri, and show that Machimosaurini was indeed present in the UK during the Bathonian. We also find there to be multiple cranial machimosaurin specimens from the Great Oolite Group. In addition, we evaluate the positioning of a potential machimosaurin from the Jurassic of Madagascar. This means that Machimosaurini had a wide geographical distribution prior to the radiation of Machimosaurus, known from the Bathonian of the UK, France, Morocco and possibly Madagascar.



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## A close relative of the Amazon river dolphin in marine deposits: a new Iniidae from the late Miocene of Angola

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Thanks to their highly specialized echolocation system, a few odontocetes (toothed cetaceans) have been able to independently colonize freshwater ecosystems. Although some species of delphinids (true dolphins) and phocoenids (porpoises) at least occasionally migrate upstream of large river systems, they have close relatives in fully marine regions. This contrasts with the three odontocete families only containing extant species with a strictly freshwater habitat (Iniidae in South America, the recently extinct Lipotidae in China, and Platanistidae in southeast Asia). Among those, the fossil record of Iniidae includes taxa from freshwater Miocene deposits of South America, whereas a few marine species from the Americas were tentatively referred to the family.

Based on a partial odontocete skeleton including the cranium, discovered in late Miocene (Tortonian-Messinian) marine deposits near the estuary of the Cuanza River, Angola, we identify a new iniid genus and species. This is the first time that the combination of a frontal boss with nasals being lower on the anterior wall of the vertex is observed in an extinct iniid found in a marine context. The new species further shares with the extant Amazon river dolphin *Inia geoffrensis* the laterally directed postorbital process of the frontal, the anteroposterior thickening of the nuchal crest, with a more developed left occipital protuberance, and robust teeth with wrinkled enamel.

Confirmed by our phylogenetic analysis, this record of a close relative of *I. geoffrensis* in marine sediments from the eastern coast of South Atlantic further corroborates the hypothesis that part of the iniids' early evolution (after the split with the sister family Pontoporiidae) occurred in the marine environment. Furthermore, morphological similarities with the extant species may indicate that the transition from the marine environment to the freshwater, Amazonian habitat may have occurred on the Atlantic side of South America. Finally, this first description of a Neogene cetacean from inland deposits of western sub-Saharan Africa reveals the potential of this large coastal area for deciphering key steps of the evolutionary history of cetaceans in the South Atlantic.



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### A hippopotamoid adaptative suite: the case study of Bothriodon velaunum (Cuvier, 1824) [Mammalia, Cetartiodactyla] from Ronzon

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Twenty years ago, several molecular studies on the phylogeny of extant mammals revealed an astonishing relationship between cetaceans and hippopotamuses. Shortly after, the nesting of Cetacea within Artiodactyla received support from new early cetacean fossil remains. Waterdependent lifestyles were hence interpreted as apomorphic to a cetacean-hippopotamus clade named Cetancodonta. Recent advances on the subclade, including the Hippopotamidae, revealed that extant hippopotamids emerged from a lineage deeply embedded within an anthracothere subfamily, the Bothriodontinae. The complex evolutionary history of these hippopotamoids led us to hypothesize that the acquisition of a semiaquatic lifestyle occurred multiple times within Cetancodonta.

Previous work on anthracothere paleobiology mentioned possible semiaquatic habits mainly based on the geological contexts of their discoveries or on overall resemblance with hippopotamids. A recent contribution using several methodologies such as dental microwear, geochemistry, fine anatomy and population variability, confirms that one of the most derived bothriodontines, *Libycosaurus bahri*, was water-dependent and more specialized for semiaquatic lifestyle than many hippopotamids. On these grounds, a research project (SPLASH) was created to investigate the Hippopotamoidea and detect the appearance of water-dependence even in the absence of obvious morphological specializations. This challenging aspect implies the use of a large array of methods to describe the paleobiology of key hippopotamoid species.

Here, we describe, as a preliminary result of the project, the paleobiology of *Bothriodon velaunum*, an early bothriodontine from the basal Oligocene of Europe. We performed combined analyses of a large specimen collection from the locality of Ronzon, housed in the Musée Crozatier at Le Puy en Velay. These results were integrated into an adaptive suite displaying the relationships between population structure, morphological features related to agonistic interactions, life history traits, senses, paleodiet, semiaquatic adaptations (revealed by oxygen isotopes, bones microanatomy, and inner ear morphology), and locomotion. This adaptive suite indicates that a semiaquatic behavior influenced the biology of bothriodontines at an early stage of their evolution. This approach will be subsequently applied to many other key hippopotamoid taxa and should allow deciphering the evolutionary history of the semiaquatic niche in this clade from the middle Eocene onward.



### The earliest ichthyosaur from the middle Lower Triassic of Thailand

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Biotic recovery from the Permian-Triassic mass extinction was accompanied by the invasion of the sea by several reptilian groups. Arguably the most important among these lineages is the ichthyosaurs. The ichthyosaur Thaisaurus chonglakmanii was discovered at a limestone hill in the Southern Peninsula of Thailand of putative Triassic age. Since its first brief description, however, T. chonglakmanii has never been restudied in detail and its exact stratigraphic and phylogenetic position remained elusive. Here we revisit the well prepared holotype specimen of T. chonglakmanii. The humerus of the holotype measures 21 mm long, suggesting a total body length of about 0.9 meter by extrapolation. This is even slightly smaller than the adult Chaohusaurus specimens from the Lower Triassic of South China, which was commonly taken as the smallest ichthyosaur before. Extensive cranial bone fusion and well-ossified limb bones, however, indicate an adult stage of the holotype specimen of T. chonglakmanii. Several characters suggest a much generalized morphology of T. chonglakmanii among ichthyosaurs, including notably the absence of the anterior terrace of upper temporal fenestra and an elongated humeral shaft without anterior flange. Parsimony analysis based on a published data matrix suggests T. chonglakmanii holds a basal position among ichthyosaurs. Field survey combined with a published conodont study confirms a late Induan (Dienerian) – earliest Olenekian (early Smithian) age (Sweetospathodus kummeli -Neospathodus waageni zone) for the *Thaisaurus* locality, which corresponds well with the basal phylogenetic position of the taxon. This is the earliest record of Mesozoic marine reptiles, two million years earlier than the earliest previous record. Our result thus indicates that ichthyosaurs invaded the tropical waters at least as early as the Dienerian, when the sea surface temperature was relatively cool and the Refuge Zone was enlarged. The generally small body size of Early Triassic ichthyosaurs in the tropical oceans supports the inference of a stressed environment in the upper water column during most of the Early Triassic.

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### The appendicular skeleton and the phylogenetic relationships among a cetancodont lineage, the Hippopotamoidea

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The Hippopotamoidea (Hippopotamidae + "Anthracotheriidae") is a mammalian superfamily that presents a wide spatial distribution and temporal extension. Indeed, representatives of this superfamily known from Africa, Eurasia, northern and central America, range from the middle Eocene to present. Nowadays, this clade is only represented by two hippopotamid species belonging to two distinct genera: the common hippo, *Hippopotamus amphibius*, and the Liberian hippo, *Choeropsis liberiensis*, both restricted to the African continent. They are the largest representatives of the ecological guild of the Large Semiaquatic Herbivores which was much more abundant during the Cenozoic.

Despite a consequent number of studies conducted on the Cetacea, which underwent the most complete return to aquatic life among mammals, only a few studies focused specifically on their less-known semi-aquatic sister-group, the Hippopotamoidea. Moreover, although much attention was paid on teeth and cranium, the postcranium, albeit abundant in museum collections, was generally ignored in cladistic studies performed on morphological characters. Nonetheless, the postcranial skeleton bears a non-negligible amount of characters that are potentially phylogenetically informative.

In the current study, we aimed at investigating the phylogenetic relationships within the Hippopotamoidea by considering morphological characters on the appendicular skeleton, more precisely on the bones of the stylopod and zeugopod, and testing the robustness of the phylogenies focusing on dental and cranial partitions. Various questions need to be further tested, such as the branching of Hippopotamidae within a particular anthracotheriid lineage, the archaic bothriodontines. Additional characters not previously considered on the postcranium have the potential to address such issues. Some characters also carry functional information, which can be related to locomotion and body mass that both shape the anatomy of the limbs by constant trade-offs between mobility and stability at the limb joints. The identification of such osteological traits will contribute to a better understanding of the functional constraints and abilities of extant and extinct hippopotamoids for a better characterization of the adaptive suite of characters linked to the semiaquatic way of life.

Speaker

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### Clinging to the shore: Oligocene whales of Australasia offer a rare insight into cetacean palaeobiogeography

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Baleen whales (Mysticeti) are the largest animals on Earth. Unfortunately, the very trait that makes them stand out also limits what we can learn about them: large body size means lower population sizes and, thus, fewer opportunities to gather data. This bias is exacerbated in the fossil record, where species are frequently based on just a single specimen, and thus offer little insight into intraspecific variability, geographic distribution, faunal structure, or habitat preferences. Even at higher taxonomic levels, limited sample sizes often render biogeographical and ecological evidence anecdotal. Here, we use the well-dated and abundant Oligocene fossil record of Australasia to present the first quantitative study of habitat preference and distribution in extinct mysticetes.

Separated by the Tasman Sea, south-eastern Australia and southern New Zealand are close enough to be directly comparable, yet far enough to accumulate meaningful faunal differences. During the Late Oligocene, both were located at similar latitudes and home to shallow-water environments, but they differed in water temperature and exposure to the open sea. Whereas Australian deposits accumulated in warm, sheltered bays, their New Zealand equivalents formed as cool-water carbonates around a scattered archipelago. The whales inhabiting these waters strikingly differed in size and ecology. Counts of tympanic bullae show that nearly 80% of the Australian specimens represent mammalodontids: small toothed predators and suction feeders. Toothless chaeomysticetes make up the rest, with eomysticetids clearly dominating. By contrast, mammalodontids contribute just 4% to the New Zealand record, which otherwise consists entirely of comparatively large chaeomysticetes.

Our results suggest a clear preference of mammalodontids for sheltered coastal environments, and a more open-water habit for toothless baleen-bearing whales. The proportion of eomysticetids is similar in both localities (roughly 20%), perhaps indicating a somewhat intermediate near-shore distribution. The close tie of mammalodontids to the coast likely explains their restricted distribution, and argues for the presence of endemism early in mysticete evolution. The preponderance of chaeomysticetes further from shore suggests that baleen evolved to exploit open-water resources, with filter feeding and/or the need for larger home ranges accounting for the associated increase in body size.



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#### Inner ear evolution in odontocetes

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Odontocetes (toothed whales) are the most successful lineage of marine mammals, highly specialised apex predators and a key component of modern ocean ecosystems. The proposed key innovation that has facilitated this is echolocation, a complex form of biosonar that utilises reflected sounds to construct a mental model of their environment. Whilst our understanding of this ability has increased, research into odontocete hearing has so far been biased towards physiological experiments and auditory pathway identification; quantitative studies on the organ of hearing the inner ear or cochlea are relatively lacking, despite its critical role in audition. Here, we analyse shape evolution of the odontocete inner ear using high-resolution

3D models and 3D geometric morphometric approaches. We analyse inner ears from a broad phylogenetic sample of odontocete species, encompassing nearly all extant genera and multiple fossil taxa. Using phylogenetic generalised least squares models, we find that the shape of the odontocete inner ear is correlated with multiple factors, including habitat, body size and prey type. Additionally we detect strong phylogenetic signal in odontocete inner ear shape. Finally, we reconstruct the macroevolutionary dynamics of the odontocete inner ear to reveal the tempo and mode of inner ear evolution in odontocetes.

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#### Iterative evolution of pelagization in sea turtles

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During the Cretaceous, three distinct turtle lineages adapted to a fully marine lifestyle; these include the extant hard-shelled Pan-Cheloniidae and leatherbacks or Pan-Dermochelyidae, and extinct Cretaceous Protostegidae. Pan-cheloniids and pan-dermochelyids constitute a monophyletic clade based on molecular and phenotypic data. However, phylogenies incorporating fossils place protostegids as the stem-lineage of leatherbacks. Because protostegids appeared in the Early Cretaceous (Late Barremian / Early Aptian), this topological positioning implies emergence of the chelonioid sea turtle crown at least 35 million year earlier than current molecular clock estimates suggest, unless an unusually accelerated tempo of evolution occurred after the basal sea turtle split. Evaluation of the skeletal anatomy of Eosphargis gigas, a pan-dermochelyid from the Eocene of Belgium, reveals that the key postcranial states uniting protostegids with leatherbacks are likely convergent. Indeed, an extensively revised and expanded sea turtle phylogeny shows that E. gigas is pivotal to reconstructing protostegid relationships because its transitional character state mosaic forces Protostegidae into a basal stem-lineage position relative to the chelonioid crown. The divergence timing of crown sea turtles thus no longer conflicts with molecular data, and extends between the Campanian–Eocene, although a more precise estimate remains problematic. The new phylogeny also identifies the type-Maastrichtian taxon Allopleuron hoffmanni as a potential Cretaceous stem-dermochelyid based on shared combination of unique cranial, postcranial and histological traits. Protostegids share a vast number of characters with crown sea-turtles, although experimental weighting and deletions demonstrates that these all correlate with marine adaptations, inferring that although protostegids are robustly retrieved on the chelonioid stem, they may still represent a potentially independent marine cryptodiran radiation. The cosmopolitanism of sea turtles has been previously dated to the Cenozoic and limited to pan-cheloniids and pan-dermochelyids but expanded sampling reveals that some protostegids independently achieved near-global distribution during the Cretaceous. Regardless the phylogenetic position of Protostegidae several of their ecomorphological and developmental features likewise evolved convergently to extant sea turtles.

### My head hertz: Hearing abilities in an early simocetid (Cetacea: Odontoceti) as reconstructed from microCT scans

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Whales, in their transition from terrestrial to fully aquatic lifestyles, have profoundly modified the mammalian form to support living and feeding underwater. Toothed whales (odontocetes) are the most abundant group among modern whales, and originated sometime during the Eocene/Oligocene transition <sup>~</sup>34 million years ago. Odontocetes are thought to have quickly, over the span of about 10 million years, evolved the ability to echolocate. The earliest transitions to fully aquatic biosonar usage are represented in early Oligocene odontocete members of the Simocetidae, Xenorophidae, and Agorophiidae. Simocetids exhibit unusual cranial and facial morphology compared with xenorophids and agorophilds, potentially related to suction feeding. Some aspects of their facial morphology, such as premaxillary sac fossae and expansion of the maxillae over the frontals, are consistent with biosonar capabilities. Here, we perform (to the best of our knowledge) the first in-depth investigation of simocetid inner ear labyrinth morphology. We use microcomputed tomography (microCT) to image and examine a petrosal belonging to a neonatal cf. Olympicetus. We obtain a wide variety of morphological measurements of the inner labyrinth, which we add to an extensive dataset of cetaceans and other artiodactyls to determine whether this individual had infrasonic or ultrasonic hearing. The semicircular canals and vestibule are also measured and described in detail as they relate to possible other aspects of ecology. These approaches provide a unique opportunity to better understand the evolution and ecology of simocetids, which occupy a crucial position in the evolutionary and ecological history of odontocetes.



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## Neotropical gavialoids: a case study to explore patterns of longirostry in crocodylians

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Gavialoidea is a clade of slenderand long-snouted crocodylomorphs with a single living species, the Indian gharial Gavialis gangeticus. Because elongated snouts (longirostry) have evolved independently in several crocodylomorph clades, this head shape has been interpreted as an ecological adaptation. How this condition affected patterns of diversification and how longirostrine-associated cranial features changed through adaptive radiations, remain poorly understood. By integrating phylogenetics and morphometrics, we focus on the diversification of the Neotropical gavialoids to investigate evolutionary patterns of longirostry within Crocodylia. Paleontological evidence indicates that Neotropical gavialoids might have originated in the early Palaeogene along the African coasts and dispersed via marine pathways to South America and the Caribbean. Neotropical gavialoids reached a diversity peak during the Miocene, with at least 10 species encompassing an enormous range of body sizes (ranging from 2.26 to 7 m) and inhabiting multiple environments (coastal marine, estuarine, lacustrine, riverine). Despite this extraordinary adaptive radiation, analyses revealed that the snout shape of the whole clade has occupied a small, distinct and almost invariable morphospace since the Cretaceous, in contrast with the morphologically labile snout shape of other crocodylians (crocodyloids and alligatoroids). Our results suggest iterative environmental shift occupations throughout gavialoid evolution without significant changes in snout proportions, but involving conspicuous rearrangements of the circumorbital bones. The longirostrine gavialoid morphotype is a distinct adaptation for seizing small prey and typically possesses short and wide premaxillae and enlarged 'caniniform' teeth only at the tip of the snout. Long-snouted crocodyloids (Tomistoma, Mecistops, Crocodylus intermedius) exhibit a different pattern of longirostry in which the 'caniniforms' are present in both the maxillae and premaxillae/tip of the dentary. The retention of powerful bites and 'caniniforms' closer to the jaw joints in these longirostrine crocodyloids allowed them to exploit a wider range of prey sizes, which could explain their snout shape plasticity. Because morphospace occupation of gavialoids widely differs from that of crocodyloids, we hypothesize that the Pliocene extinction of gavialoids from South America and the Caribbean responded to factors other than the coeval arrival of Crocodylus.



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### Patterns of growth and ossification in the Early Permian clade Mesosauridae (Sauropsida; Parareptilia)

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Mesosaurs represent a small and extinct clade of Early Permian reptiles, which are notable in that they represent the first fully aquatic amniotes, and are generally considered the basalmost parareptile clade. Although they are very commonly housed in collections worldwide due to the high productivity of their fossil sites in southern Gondwana, many aspects of their anatomy and ontogeny remain poorly understood. Here we analyse a set of measurements taken on a large sample of mesosaur specimens and describe the ossification sequence in Mesosaurus tenuidens and Stereosternum tumidum, two of the three mesosaurid species currently considered valid. In the smallest specimen, the skull seems fully ossified, whereas the ossification of the vertebral column is incomplete and shows a zipper-like pattern of fusion of the paired neural arches proceeding from anterior to posterior. This is a general pattern in tetrapods, but it is the first time this feature is being described in a Palaeozoic taxon. Based on several specimens, the limb ossification sequence in mesosaurs follows the pattern common to all amniotes, with stylopodial and zeugopodial elements ossifying first, followed by digit ossification with a postaxial polarity in the order of digit IV-(V or III)-II-I. This supports the idea that this pattern was the ancestral condition for Amniota. Only the youngest juveniles have incompletely ossified diaphyses, whereas in older juveniles or sub-adult individuals they are fully ossified and only the epiphyses, carpals, and tarsals remain partially ossified. In contrast, one of the specimens studied displays an aberrant ossification pattern, with some of the autopodial epiphyses being more ossified than the distal ends of the diaphyses. This suggests the presence of separate ossification centres in the epiphyses, which is rare in non-mammalian tetrapods and might represent a pathology in this individual. Our morphometric analysis highlights no allometric differences between the three species in terms of skull and long bones dimensions. Most parts of the skeleton show isometric growth, although the mid-shaft diameters of the long bones display a slightly negative allometry. This lag in growth rates highlights a slimming of long bones throughout ontogeny. Only the first digit of the pes, as well as the distal width of the fibula, which is quite enlarged in mesosaurs, exhibits positive allometry and therefore an accelerated growth.



Speaker

### Fossil odontocetes from Patagonia (Argentina) as a key to understand their evolutionary history during the still enigmatic early Miocene

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Cetacean history includes three major adaptive radiations. The first involves the Eocene northern origins of cetaceans. The second involves the Neoceti (Odontoceti + Mysticeti), which diversified from latest Eocene to earliest Miocene as the Southern Ocean opened. This radiation is linked to the rise of the Antarctic Circumpolar Current and to increased nutrients, leading to new niches for cetaceans. Details are uncertain for aspects of this second radiation, especially for the earliest Miocene, but clues come from early Miocene dolphins (clade Platanistoidea) from the Gaiman Formation of Patagonia (Argentina). The fossil record suggests that species of Platanistoidea were once diverse and widespread components of global marine ecosystems, but the lineage now includes only one extant species, Platanista gangetica. The radiation and later decline of platanistoids are still poorly understood. In Patagonia, platanistoids are represented by: Notocetus vanbenedeni, Phoberodon arctirostris and Prosqualodon australis. Surprisingly, these widely-cited species have been overlooked in recent phylogenetic studies, and their detailed anatomy and functional complexes need a modern assessment. We are analyzing key anatomical characters of these species to elucidate the different morphotypes represented in the earliest Miocene. Phoberodon has a long and robust rostrum, with a wide and toothed premaxilla. Prosqualodon has a short and narrow rostrum, also with a wide premaxilla. Phoberodon and Prosqualodon are heterodont and polydont; their robust cheek teeth have highly elevated denticulate crowns, suggesting a component of mastication. Short jaws in Prosqualodon may indicate sarcophagous feeding. In contrast, the small, more "modern" Notocetus has single-rooted teeth with short conical crowns, reminiscent of the extant Platanista, suggesting a more piscivorous diet. These characteristics indicate wide variation in feeding strategies and prey preferences in the early Miocene Patagonian communities, and are consistent with little or no ecological overlap. Moreover, all species have osteological correlates indicating the presence of the nasofacial sound-producing complex and pterygoid sinus system, consistent with echolocation abilities reported for all crown-clades of odontocetes. These fossils inform us on an important epoch of the evolutionary history of platanistoids, and can help us characterizing the early Miocene cetacean communities of Patagonia. The analyses continue.

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#### A new species of *Guizhouichthyosaurus* (Ichthyosauria, Shastasauridae) from the Ladinian (Middle Triassic) of Xingyi, Guizhou, southwestern China

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Ichthyosauria is a monophyletic clade of Mesozoic marine reptiles that secondarily adapted to the aquatic environment after the end Permian Mass Extinction. In the Middle Triassic, ichthyosaurs evolved rapidly and its diversity increased considerably. Not only small to midbodied genera like *Xinminosaurus* and *Mixosaurus* appeared, but more importantly, large taxa emerged, which indicates a rapid reconstruction of marine ecosystem after the mass extinction. Shastasauridae is a group of Middle-late Triassic ichthyosaurs with distinctively large body and world-wide distribution suggesting that this group contained top predators with the ability to swim over long distances. Therefore, researches on shastasaurids can provide information on ichthyosaurian evolution and palaeobiogeography, as well as Triassic marine ecosystem. Till early years of this century, Shastasauridae remained enigmatic due to its poorlypreserved and fragmentary skeletons, when compared to the Jurassic and Cretaceous materials. Since this century, abundant well-preserved materials of shastasaurid ichthyosaurs have been excavated from the Guanling Fauna (Carnian, Late Triassic) of Guizhou, Southwest China, namely*Guanlingsaurus* and *Guizhouichthyosaurus*. However, the taxonomic position of *Guizhouichthyosaurus* and the intra-group phylogeny of Shastasauridae remain controversial because the description of the holotype of the type species *Guizhouichthyosaurus tangae* is too brief to assign additional specimens to the species.

Here we report a new species of *Guizhouichthyosaurus* based on a new specimen from the Zhuganpo Member of the Falang Formation (late Ladinian, Middle Triassic) of Guizhou, Southwest China. The skeleton is almost complete, with a total length of about 5.3 meters. The skull, about 98 cm long, is visible in lateral view while the postcranium lies in ventral view. The specimen can be referred to *Guizhouichthyosaurus* on the basis of the size over 5 m; narrow and long groove anterior to external naris and scapula without proximal shaft. Despite of these similarities, a list of morphological features unambiguously suggests it could be a new species. The new specimen has a relatively higher presacral count of at least 73, unlike that of 63-69 observed in *G. tangae*. And the mandible is relatively robust compared to the type species. Furthermore, the interpterygoid vacuity of the new specimen is extremely reduced, but it is obviously present although small in *G. tangae* and *C. wolonggangensis*. The radio-ulnar foramina are present in both sides of forefin of this specimen but absent in other shastasaurids, except *Shonisaurus*. The hindfin of the new specimen is shorter than in *G. tangae* and lacks any accessary elements unlike the latter.

We performed a phylogenetic analysis. The strict consensus tree indicates that Shastasauridae is a monophyletic clade containing the new species. The new species is stratigraphically older than *G. tangae*, which is exclusively known from the Wayao Member of the Falang Formation (Carnian, Late Triassic). Along with thalattosaur *Anshunsaurus, Xinpusaurus* and the ichthyosaur *Qianichthyosaurus*, the occurrence of *Guizhouihthyosaurus* in Xingyi Fauna suggests a closer relationship between Xingyi Fauna (late Ladinian, Middle Triassic) and Guanling Biota (Carnian, Late Triassic).

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### The evolution of thalattosuchian crocodyliforms, neuroanatomical insights into the land-to-sea transition

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Thalattosuchians were a widely distributed group of marine crocodyliforms that thrived during the Early Jurassic–Early Cretaceous. This radiation evolved a wide diversity of body plans and ecomorphotypes ranging from gharial-like species to those superficially similar to living killer whales. While their osteological adaptations to a marine lifestyle are well documented, the full extent of their soft-tissue and neuroanatomical adaptations are still poorly understood. It is also unclear whether these soft-tissue adaptations evolved first, and therefore underpinned the thalattosuchian radiation, or evolved in concert with the osteology. Based on digitally segmented CT scans of thalattosuchian skulls, we begin to rectify this knowledge deficit.

Due to the regression and loss of bone-enclosed craniomandibular sinuses in cetaceans and pursuit-diving birds, we hypothesise that thalattosuchians underwent a similar trajectory. Our early findings show exactly that, with the pharyngotympanic sinus system already reduced and simplified in the basalmost thalattosuchians on either side of the MetriorhynchoideaTeleosauroidea split. The intertympanic diverticula were absent, with the dural venous system

hypertrophied dorsal to the brain cavity. The long-noted absence of aërum foramina in Thalattosuchia is here confirmed to be due to the quadrate diverticula regression, and the resultant lack of siphonia + articular diverticula. The infundibular diverticula still fill the dorsal quadrate, but also as longnoted in Thalattosuchia, there are no subtympanic foramina. We can confirm the presence of basioccipital diverticula, and the recessus epitubaricum + pterygoid diverticula in thalattosuchians. Both the quadrate and pterygoid diverticula are vestigial. Overall, the various pharyngotympanic diverticula are not well differentiated from one another, unlike in extant crocodylians. Moreover, the pharyngotympanic system in thalattosuchians does not dorsally enclose the bony labyrinths and brain cavity (as they do in extant crocodylians), with the semi-circular canals largely visible in lateral view when the neuroanatomy is digitally segmented out.

Thus at the base of Thalattosuchia, there was already a generalised simplification of the pharyngotympanic sinus system, a loss of diverticula and regression of others. This fits with osteological data, that show thalattosuchians had already become specialised for an aquatic lifestyle prior to the teleosauroid-metriorhynchoid split.

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<sup>\*</sup> Speaker

### Reassessment of *Undorosaurus* Efimov, 1999, a mysterious Late Jurassic ichthyosaur of the Boreal Realm

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Recent study of Late Jurassic ophthalmosaurid ichthyosaurs revealed a number of new taxa. However, the validity of several taxa from the Volgian (latest Jurassic-earliest Cretaceous) of European Russia still remains unclear, complicating comparisons and, in some cases, affecting taxonomic decisions. A revision of type specimens of *Undorosaurus* Efimov, 1999 reveals the potential validity of four species within *Undorosaurus*: *U. gorodischensis, U. nessovi, U. trautscholdi,* and *U. kielanae*. Furthermore, examination of the holotype of *Cryopterygius kristiansenae* from the coeval strata of the Svalbard archipelago shows that this taxon is a junior synonym of *Undorosaurus gorodischensis*. This supports the idea of faunal exchange between the Middle Russian Sea and other Boreal seas in the Late Jurassic. A new phylogenetic dataset including 33 taxa and 102 characters, 21 of which are new, was composed in order to resolve the phylogenetic position of *Undorosaurus*. The results of this analysis challenge all previous phylogenetic hypotheses for Ophthalmosauridae in a number of aspects, including the recovery of Undorosaurus spp. as deeply nested within Platypterygiinae as a sister group to derived platypterygines.



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Speaker

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### Ecomorphotypes in the family Phocidae (true seals) supported by evidence from other terrestrial and marine vertebrates

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The Family Phocidae (true seals) has four subfamilies: three extant (Cystophorinae, Monachinae, Phocinae) and one extinct (Devinophocinae). Each subfamily is classified based on distinguished morphological characters, mainly from the skull, with other sets of characters separating them into ecomorphological groups. In the Family Phocidae, ecomorphs of only representatives of the subfamily Phocinae have been demonstrated. This study will compare morphological characters of the other three subfamilies with those already described in Phocinae. Remains of fossil seals fall into analogous morphological and ecological groups as modern seals. In each subfamily, (Cystophorinae, Devinophocinae, Monachinae) characters do not fit precisely into the groups already created for members of subfamily Phocinae. The ecology of fossil seals will be extrapolated from what is known in modern seals, when they fit in same ecomorph group. Fossil seals have natural morphological units similar to those of recent species, providing a rationale for associating the many dissociated fossil elements. In order for fossil seals to be placed into ecomorphological groups, three of the most commonly found bones are used for examination: the mandible, humerus, and femur. Specific ecological distinctions (diving depths, environment, diet, speed and body size) of extant seals are examined to correlate to analogous fossil seals. Placing seals into specific ecomorphological groups does not use alpha taxonomy, instead combining morphological and ecological characters. Ecomorphs are also found in other vertebrates, including but not limited to: rabbits, anole lizards, finches and seacows.



Speaker

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### First Mosasauridae (Reptilia, Squamata) in the Late Campanian (latest Cretaceous) of Savoie (Chartreuse Massif, French Alps)

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Mosasaurid were a very successful clade of marine squamates, highly systematically and ecologically diversified and worldwidely widespread, known from the Cenomanian to the end of the Maastrichtian where they disappear during the K/Pg biological crisis. Mosasaurids are known from complete skeletons in several outcrops in the world like the extensive ones of the WIS of North America, Morocco, Belgium, the Netherlands, and New Zealand. The fossil record of mosasaurids is comparatively rather poor in France, and most discoveries dated from the end of the XIXth century. Here we report on the first discovery of mosasaurid remains in the Late Cretaceous of the subalpine massif of Chartreuse, a mountainous region of the Alps, a hundred kilometers southwest of the Mont-Blanc massif.

The specimen has been found by one of us (FD) during a walk in a forest located in the Chartreuse Regional Nature Park near the village of Entremont-le-Vieux, not far from Chambéry, in Savoie. The remains were found in a marly grey chalk deposited in the "dauphinois domain" of the Tethys Ocean. It is very rich in invertebrates remains, including mainly molluscs like Cephalopods (Ammonites, Belemnites, Nautiles), Bivalves and Gastropods, as well as Echinoids, Brachiopods and possibly Arthropods. Microvertebrate remains (fish teeth) have also been found, as well as possible plant ones. The ammonites found there, like *Nostoceras polyplocum* indicate a Late Campanian age for the outcrop.

The mosasaurid remains consist of around twenty caudal vertebrae found articulated. Though generally well preserved, they are slightly laterally compressed. The vertebrae include only the centra and part of the fused haemal arches in some of them. The centra are slighly procoelous and vertically oval in shape. Most are about 3 cm high and long, the smallest ones being half this size. The fact that these centra preserved both transversal processes and haemal arches indicatedthat they correspond to median caudals, located probably anterior to the caudal flexure. The fact that the haemal arches are fused to the centra also indicate that this specimen belong to the Mosasaurinae clade. In Europe, only *Mosasaurus* and *Prognathodon* have been already found. Only the detailed description of this new specimen would permit to precise its systematical attribution. This new discovery permits to improve the rather poor French mosasaurid fossil record. It represents the first discovery of mosasaurid remains in the Alps.



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### The palaeoenvironmental characteristics of Xingyi *Keichousaurus* fauna

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The Middle-Upper Triassic are well-developed, and abundant fossils of Ladinian marine reptiles and fishes were excavated from the mid Zhuganpo Member of Falang Formation at Xingyi (Guizhou Province, southwestern China). The same fossiliferous beds are well exposed at both Nimaigu Section in Wusha Town and Langmushan Section in Dingxiao Town, but the high-resolution stratigraphic correlation and paleoenvironmental variation between these two sections were not well studied. The field investigation, detailed section measurements and microfacial analysis indicate that the dominant microfacial types in Nimaigu Section are muddy microcrystalline limestone and microcrystalline limestone with bioclast of ammonite, bivalve, ostracod and crinoid, while the main microfacial types in Langmushan Section are microcrystalline limestone with fenestrated fabric and microbial mats. Nimaigu Section shows a transformation from lagoon to restricted sea, and then to open sea, while Langmushan Section shows the characteristics of a typical lagoon and tidal flat. It can be inferred that the lagoon was not very deep and the hydrodynamic force was weak, as only laminated bedding was developed with calcareous mud. Welldeveloped microbial mat and fenetrated fabric indicated that the sea floor had gone through an exposure and the lagoon became a tidal plat intermittently. The low-diversified benthic invertebrate might suggest a saline water. The study reveals that the assemblage of the Xingyi Keichousaurus fauna lived in this lagoon, which was enriched of Ladinian pachypleurosaur Keichousaurus and fish Habroichthys, associated with a large amount of Asialepdotus and Guizhouamia, but yielded few bivalve and ostracod. It shad lights on that Keichousaurus probably lived nearshore in the lagoon. The lagoon deposits in both sections can be well correlated, showed a wide distribution of this environment, and it might develop islands in between. Xingyi was a large carbonate platform in Middle Triassic, in which the west part was deeper and the east part was near the shores of islands.



Speaker

### The radiation of baleen whales (Cetacea: Mysticeti): insights from the Miocene record of Patagonia (Argentina)

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Mysticete (baleen whales) evolution is marked by major turnover events. The first one occurred during the Late Oligocene-early Miocene, with the extinction of toothed forms and the diversification of the baleen-bearing groups (= Chaeomysticeti). This is a critical time in the evolutionary history of the group, because it represents the time of diversification of crown lineages. However, there is an important early Miocene gap where fossil representatives of the living families Balaenopteridae (rorquals), Eschrichtiidae (grey whale), Neobalaeninae (pygmy right whale) and Balaenidae (right whales) are virtually unknown. Fossil baleen whales from the early Miocene of Patagonia (Gaiman Formation, Argentina) provide one of the best known records of mysticetes for this age interval. Some of the key species recorded include one of the most archaic rorquallike whales (Aglaocetus moreni) and the oldest right whale (Morenocetus parvus). These are pivotal fossils for the calibration and estimation of living mysticetes molecular clock divergences. The second important diversification event in baleen whale evolution is during the late Miocene-Pliocene, with the establishment of the modern mysticetes lineages. Fossil mysticetes from the late Miocene of Patagonia (Puerto Madryn Formation) also shed light on this critical time in mysticete evolution. Among the most relevant records are one the oldest Eubalaena -like right whales and a pygmy right-like whale (Neobalaeninae indet), as well as a new species of Balaenidae. In particular, the anatomical study of balaenids show that some of the specialized morphological traits of modern balaenids were acquired by the early Miocene and have remained essentially unchanged up to the present. Moreover, the study of an ontogenetic sequence of fossil balaenids indicates that an overall juvenile morphology is retained in the adult stage, also sharing some similarities with the juvenile form of Eubalaena australis. These observations suggest that a heterochornic process (i.e. paedomorphy) operated during the evolution of Miocene balaenids. The results of our studies provide novel insights into the evolution of living mysticete lineages and ultimately will contribute to elucidate the evolutionary driving forces of the Miocene baleen whale radiation.



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## Uncommon vertebral histological and microanatomical features in sauropterygians

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If the inner structure of various sauropterygian long bones has recently been widely investi gated, this is not the case for vertebrae, whose inner architecture (microanatomy) and osseous tissue features (histology) remain almost unstudied. The high variation observed in sauropterygian long bone features highlights the strong interest in analyzing other parts of the skeleton, in order to perform both physiological and functional inferences on these taxa. The analysis of the inner structure of various pachypleurosaurs, nothosaurs and pistosaurs reveals very uncommon traits. The occurrence of primary periosteal bone made of parallelfibred bone, but with also woven bone deposits in nothosaurs and pistosaurs (and the pachypleurosaur Anarosaurus), is not surprising. However, the endochondral territory essentially contains calcified cartilage because of paedomorphosis, which is so far unique among amniotes, though consistent with what is observed in their long bones. Moreover, there are specificities in the bone microanatomy. A large cavity occupies the center of the centrum in nothosaurs and pistosaurs. The centrum consists thus in a surrounding layer of compact cortex with a large cavity or light spongiosa in its core, and a spongious organization in the articular regions. Conversely, in pachypleurosaurs, the vertebrae are extremely compact with a strong inhibition in periosteal bone resorption. This high compactness is very rare in amniotes, being only documented in pachyosteosclerotic marine squamates (e.g., "dolichosaurs", hind-limbed snakes). The histology and microanatomy of these sauropterygians is clearly complex with specific features. Clear differences are observed between pachypleurosaurs and eusauropterygians. The further analysis of placodonts and plesiosaurs will enable to put these data into a larger context and to better understand physiological and functional changes along the evolutionary history of sauropterygians.



Speaker

### Origin and dispersal of true seals (Family Phocidae) based on recent fossil evidence

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Although classification of the Family Phocidae (=true seals) remains contentious, fossil evi dence supports the existence of three extant subfamilies (Phocinae, Monachinae and Cystophorinae) and one extinct subfamily (Devinophocinae). The discovery of Afrophoca libyca (subfamily Monachinae, ~21 Ma) further demonstrates that the origin of true seals was in the Paratethyan/Mediterranean basins, occurring no later than the Late Oligocene. Seals widely dispersed during the Middle and Late Miocene, crossed the Atlantic Ocean westward and prac tically ceased to exist in Europe by the Early Pliocene. Representatives of the subfamily Cystophorinae (two species of the genus Pachyphoca) also supports an origin in the Paratethys, followed by westward migration (~11.2 Ma) before dividing into two modern genera (Cystophora and Mirounga). Cranial material (Devinophoca claytoni and D. emryi) and the first record of mandibles/postcranial bones (D. emryi) of the subfamily Devinophocinae from the Central Paratethys (Vienna Basin; 13.8-16.5 Ma) presents unique, primitive characters as well as mixed characters with the other three subfamilies, demonstrating the possible ancestral morphotype for all four subfamilies. Leptophoca amphiatlantica (subfamily Phocinae) originated on the coast of Western Europe (16.4-15.8 Ma), dispersed across the Atlantic westward to the eastern shore of the North Atlantic in Calvert time (~15 Ma) and then spread southward in St. Mary's time (~10.5 Ma). Currently, Early-Middle Miocene phocines (L. lenis) and two new monachine species (Terranectes magnus and T. parvus) have been found on the eastern shore of the United States. The fossil record from Miocene deposits of Europe and North America supports a North Atlantic-Paratethyan origin of true seals, not a North Pacific origin. The North Pacific record of fossil Phocidae is relatively late, represents only a few genera and provides no evidence about the earlier evolution of the Family Phocidae.



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### New insights on *Diaphorocetus poucheti*: a Physeteroidea (Cetacea, Odontoceti) from the early Miocene of Patagonia (Argentina)

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The Pan-Physeteroidea represent one of the earliest diverging lineages of odontocetes with extant representatives. The extant diversity of the group - three species distributed in two genera - contrasts with the past diversity, as depicted by the rich Miocene fossil record – approximately 20 species divided in 16 genera. Most Miocene physeteroids were recovered from the North Atlantic (USA), North Pacific (USA and Japan), Mediterranean and North Sea (e.g. Italy, Belgium), Southeast Pacific (Peru), and Southwest Atlantic (Argentina). Among southwestern Atlantic collections, the most complete and diverse records are from Patagonia (Argentina), from which four species were named: Diaphorocetus poucheti and Idiorophus patagonicus (Gaiman Formation, Early Miocene, Chubut), Preaulophyseter gualichensis (Gran Bajo del Gualicho Formation, Late Miocene, Río Negro), and "Aulophyseter" rionegrensis (Barranca Final Formation, Late Miocene, Río Negro). These taxa were described from wellpreserved cranial materials and have not been restudied since their original descriptions. Miocene physeteroids from Patagonia are particularly relevant given that Diaphorocetus and Idiorophus are some of the oldest physeteroids known, being key taxa to assist in resolving the physeteroid phylogenetic relation ships. Thus, a detailed review of the Miocene Patagonian physeteroids is necessary to evaluate their primary diversity and analyze their phylogenetic relationships in the context of a modern phylogenetic analysis of Odontoceti. In particular, the anatomical study of Diaphorocetus resulted in an exhaustive description of the skull and the modification of several characters. In the brief original description of Diaphorocetus, illustrations showed regions of the skull that are not present nowadays. It was a very important point to review the phylogenetic relationships of Diaphorocetus and analyze its phylogenetic position, incorporating the new anatomic information. As a result, Diaphorocetus is recovered in a more basal position than in recent analyses, in a basal polytomy within crown Physeteroidea. Anatomic and taxonomic revisions of the other Miocene physeteroids from Patagonia are currently in progress. Future studies evaluating the ecomorphological disparity of the group will contribute to having a more accurate knowledge of the Miocene radiation of Physeteroidea.



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### Integrated biochronology and age of the Middle Triassic Xingyi Fauna, South China

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The Xingyi Fauna from the Zhuganpo Member of the Falang Formation of Guizhou and Yunnan Provinces, South China, containing exceptionally well-preserved marine reptiles and fishes, has been providing knowledge on the taxonomy, biodiversity, paleobiology and evolution of Triassic marine reptiles, fishes, ammonoids and other clades, and also on the paleobiogeography. The large shastasaurid ichthyosaur Guizhouichthyosaurus, the euichthyosaur Qianichthyosaurus, pistosaurs Yunguisaurus and Wangosaurus, and the thalattosaur Xinpusaurus, with a closer paleobiogeographic affinity to North America, occur only in the upper assemblage of the Xingyi Fauna, clearly showing an ecological turnover of marine reptiles from near-shore to the open ocean community. However, the timing of such a fauna turnover is not clear as yet, with two possibilities i.e. Late Ladinian or Early Carnian. Here we present new high-resolution conodont biostratigraphic data, calibrated with ammonoid data, from the Nimaigu section, Wusha District, Xingyi City, Guizhou Province. The strata from the Zhuganpo Member to the basal Wayao Member of Falang Formation at the Nimaigu section was exposed and sampled bed-by- bed during our large-scaled fossil excavations. Five conodont zones were recognized, they are, in ascending order, the Paragondolella inclinata Zone, the Quadralella polygnathiformis Zone, the Quadralella tadpole Zone, the Quadralella praelindae Zone, the Quadralella auriformis Zone. The first three conodont zones laterally correlate well with their counterparts for the Ladinian- Carnian boundary interval from Southwest China and British Columbia. Therefore, the occurrence of Xingyi Fauna within conodont Paragondolella inclinata Zone and slightly below the ammonoid Haoceras xingyiense Zone suggests the age of Xingyi Fauna should be late Ladinian, no younger than middle Longobardian. The ash layer within fossiliferous bed of Xingyi Fauna yielded a U-Pb zircon age of 240.8±1.8 Ma. Thus, it confirmed that the Xingyi Fauna was so far the only well preserved marine reptile fauna reported from the late Ladinian that withness the ecological turnover event of marine reptiles.



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## Plesiosaur remains associated with a rich marine fauna from the Albian of southeastern France

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The Early-late Cretaceous transition (Late Albian-Early Cenomanian; ~100\_Ma) witnessed marked environmental changes and a deep reorganization of the marine fauna. Nevertheless, the impact of these environmental and biotic changes on Eurasian marine vertebrates remains poorly understood, as specimens from this area are mostly represented by fragmentary and isolated remains occurring in reworked, bonebed-like deposits. Here we report vertebrate remains from an Upper Albian marine fossiliferous bed from the Geological Reserve of Digne (Alpes-de-Haute-Provence, southeastern France), recovered with diverse invertebrate species (ammonoids, belemnoids, brachiopods and inoceramid bivalves). The fossiliferous bed consists in glauconitic marls enriched in planktic foraminifera. It occurs within an expanded and monotonous succession of marllimestone alternations deposited in the hemipelagic domain of the SE French Basin. The ammonite fauna is quite exceptional by its abundance, diversity and quality of preservation (i.e., large specimens preserving very fragile shell features that are generally not fossilized) and indicates that the investigated bed belongs to the Mortoniceras fallax ammonite Zone (Late Albian). The diverse vertebrate fauna consists of chondrichthyans, ichthyosaurs and plesiosaurs. Chondrichthyans are represented by five shark species belonging to the order Lamniformes. This shark assemblage is dominated by Sphenodus teeth and comprises predator taxa probably living in open marine temperate waters. The site yielded a large, partial post-cranial plesiosaur skeleton with articulated elements probably belonging to an elasmosaurid (long necked) taxa and representing one of the most complete Albian plesiosaur specimens known from Europe. These findings indicate that this new paleontological site holds promising clues about the evolutionary history of major groups of marine vertebrates near the Early-late Cretaceous transition.



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## Evolution and disparity of pliosaurid teeth and the influence of the Jurassic-Cretaceous transition

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Pliosaurid plesiosaurians played important roles in marine food chains from the Middle Jurassic to the mid Cretaceous, frequently as apex predators. All hitherto described pliosaurid species of the Kimmeridgian to the Hauterivian possess trihedral and subtrihedral teeth with a smooth labial surface, while Aptian–Turonian pliosaurids have exclusively conical crowns with apicobasal ridges typically arranged around the entire circumference, suggesting, for each of these time intervals, a restricted range of tooth morphologies, and thus, possibly, of ecological niches. However, current knowledge of pliosaurids comes mostly from several restricted time intervals and areas; the Jurassic-Cretaceous transition remains a persistent gap in our knowledge of pliosaurid evolution. Consequently, the effect of the Jurassic-Cretaceous boundary faunal turnover on pliosaurids is poorly understood. To tackle this issue, we describe a series of pliosaurid teeth ranging from the upper Volgian (Tithonian, Upper Jurassic) of the Kheta river basin (Eastern Siberia, Russia), to the Berriasian and Valanginian (Lower Cretaceous) of the Volga region (European Russia) and analyse the evolution of pliosaurid teeth through time. Unexpectedly, these teeth belong to widely distinct morphotypes, including the first report of conical-toothed pliosaurids from the latest Jurassic-earliest Cretaceous interval. This challenges the hypothesis that only one lineage of pliosaurids crossed the Jurassic-Cretaceous boundary. It appears that conical-toothed pliosaurids coexisted with their trihedral-toothed relatives for at least 25 million years over the Jurassic-Cretaceous transition. In fact, our quantitative analyses indicate that pliosaurids reached their maximal dental disparity (in both size and shape) during this interval, showing little evidence of a turnover associated with the Jurassic-Cretaceous boundary. Instead, disparity decreased later in the Early Cretaceous, with the disappearance of trihedral-toothed forms in the Barremian. Pliosaurids thus decreased their dental disparity (and thus, possibly, their ecological diversity) long before their extinction in the early Late Cretaceous.



Speaker

# S4 - Big Data in Palaeontology: sharing knowledge for leveraging research options

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## Digitizing fossils to advance macroevolutionary research

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Databasing and georeferencing extensive palaeontological collections housed at the University of Kansas and partner institutions has been made possible via the U.S. National Science Foundation's Advancing the Digitization of Biological Collections program. In particular, this program led to the creation of two Thematic Collections Networks (TCNs), the Paleoniches and the Cretaceous World, which in total have thus far shared more than 1,000,000 specimen records. Here we discuss how these specimen data have been used in macroevolutionary studies, with a focus on studies that employed Ecological Niche Modeling (ENM).

As part of the Paleoniches TCN, specimen data were analyzed using ENM to examine how climate change during the Neogene influenced macroevolution. We focused on the exceptionally diverse molluscan fauna of the western Atlantic and considered the roles that niche breadth and geographic range played in determining species survival and extinction over the last 3 million years. The extent to which species niches evolved or displayed stasis was also analyzed. Species ranges were found to have shifted substantially, yet in the face of these changes the species niches were stable. Further, the geographic range a species occupied played the primary role in determining which species survived; species niches were far less predictive of survival.

ENM was also used to predict the fate of extant mollusc species in the western Atlantic in light of anticipated human mediated climatic warming through 2100. The species considered are important human food sources and key pillars of ocean food chains; several scenarios of climate change were investigated. The predicted impact on species is dramatic, and varied from moderate extinction to complete decimation, depending on whether more moderate or more extreme scenarios were utilized. The results suggest we should be seriously concerned about the fate of marine ecosystems, and ultimately humankind.

The Cretaceous World TCN is focused on databasing and georeferencing invertebrate and vertebrate fossils from the Cretaceous Western Interior Seaway, and using these data, in conjunction with ENM, to study a time period with a greenhouse climate. We are especially interested in focusing on whether species packing in communities may differ during times of profound warmth, and also considering the extent to which taxa display niche conservatism during episodes of phylogenetic divergence.



### The status and future of Big Data in paleontology and a roadmap for building a data synthesis center for the paleogeosciences

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Technological developments in data science and informatics are revolutionizing access to geoscientific data, breaking down barriers between disciplines, and opening new research frontiers, particularly within palaeontology. Successful database projects (e.g. Community Curated Data Repositories CCDRs) such as the Neotoma Paleoecology DB, Paleobiology Database, LinkedEarth, SedDB/EarthChem, NOAA Paleoclimatology, MorphoBank, VertNet have enabled data-driven science that have led to important insights into the palaeontological record with respect to extinctions, macroevolution, biogeography, and Earth-life systems. The pace of change within cyberinfrastructure is rapid, with respect to building the software, practices, linkages, culture, and other resources that together form the ecosystem for data-driven palaeogeoscience. Key challenges in this effort include reducing data friction by better integration, encouraging community input, and, most of all, sustainability. Cyberinfrastructure investments over the next decade should come from distributed, meso-scale investments, focused on the following six priorities: 1) reducing data friction by developing scientific workflows, structured vocabularies, semantic frameworks, and data-tagging systems to pass data and metadata seamlessly within and among community resources, 2) developing automated data-mining systems for extracting information from unstructured data in the scientific literature, 3) supporting the long-term sustainability of existing community cyberinfrastructure resources and the grassroots development of community informatics resources for subdisciplines that lack data sharing systems, 4) launching funded data mobilization campaigns to unlock existing data relevant to high-priority scientific research questions, 5) developing and training a distributed scientific workforce, for both early career scientists and current practitioners, and 6) establishing a Paleodata Synthesis Center to coordinate activities among individual geoscientists and the federation of CCDRs and sample repositories, promote community best-practices and data standards, and develop education and scientific workforce training initiatives. Accomplishing these aims requires the collaboration and cooperation of the entire paleogeoscience community on a global scale. We present an update on the status of database projects worldwide and propose a roadmap to create a Paleodata Synthesis Center to address the challenges of the future.



<sup>&</sup>lt;sup>•</sup> Speaker

#### MethoDB: a database of methods

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While databases are developed to manage the large amount of paleontological data, and other resources used by the scientific community, it remains difficult to have a clear understanding of available methods to treat those data. As a consequence, some paleontologists use methods without really knowing what they actually do, often without selecting the most appropriate tools for their data. Many researchers do not have the time to read and understand deeply all the methods that are published. Another limitation is the hardness of the literature with a specific vocabulary and, most of the time, the need of advanced skills in mathematics and programming for a clear understanding, which is not the core of paleontological research. The community needs tools to democratize knowledge and promote discussion on methods. MethoDB is a database with an interface aimed at filling this need. Its purpose is to provide an organized system of information on methods including steps of methods, softwares, algorithms, publications. Over the different aims, a specific attention is brought to allow users to quickly reach available alternatives of a data treatment they envisaged as well as their strengths and weaknesses to facilitate doing the best choice. To do so, the interface should be able to incorporate comments on methods in order to stimulate debates about concurrent alternatives.

Methods are mainly series of steps transforming data from inputs to outputs with the emergence of knowledge that allows drawing conclusions about a scientific question. Flow charts are thus well-suited to graphically represent them. The International Standard ISO 5807 will be used to build the flowcharts in order to facilitate the reading by the largest possible audience. The interface will be based on many blocks that can be detailed (i.e. predefined processes in ISO 5807). This hierarchical structure aims at getting general overviews of methodological domains for students or workers discovering a new field; but also, at reaching advanced levels up to programs and practical algorithms.

In the future, I plan that flowcharts based on MethoDB be readily locally writable by everyone. This could offer a powerful tool to develop new methods but could also potentially constitute additional contents for publication making the analyses of a paper more trackable for reviewers and readers.



### Cenozoic marine diversity is not exceptional for the Phanerozoic

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Analyses of the global fossil record suggest that marine animal diversity reached an all- time maximum in the Cenozoic. However, ubiquitous species-area relationships cause diversity to covary with the spatial extent of sampling. We show that this spatial bias explains ~64% of the variation in nominally 'global' marine animal diversity. Furthermore, spatial sampling does not track changes in habitable area. Controlling for this bias results in substantial revisions to paradigmatic diversity curves. Mesozoic–Cenozoic increases are substantially flattened, culminating in late Cenozoic diversities that are similar to those of several earlier intervals. Spatially-standardised diversity fluctuates within bounds that have persisted for hundreds of millions of years. Mass extinctions are followed by increases to levels comparable to those previously attained. Marine animal diversity similar to the present-day was likely attained early in the Phanerozoic. Our results provide the strongest evidence yet for long-term limits to regional- scale diversity in Phanerozoic marine animals, and suggest that past studies using potentially- misleading 'global' curves to evaluate the biotic and abiotic drivers of marine diversity may need to be revisited.



### The influence of inapplicable/secondary characters on disparity studies

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The use of discrete character data for disparity analyses has become more popular in recent years, in part due to the recognition that character data are useful for describing variation at large taxonomic scales, but also due to the increasing availability of both character matrices co-opted from phylogenetic analysis and software tools to run analyses. Although strategies for creating and coding characters vary, it is not uncommon for some characters to be inapplicable for some taxa in a study. This results from the need to describe variation in traits that are not present in all taxa, a need that often increases as taxonomic scope increases. In such situations, it is common practice to treat inapplicable characters as missing data when calculating dissimilarity matrices. However, for commonly used dissimilarity metrics like Will's GED and Gower's coefficient, this can lead to the re-ranking of pairwise dissimilarity values, resulting in datasets where taxa that share more primary character states are assigned larger dissimilarity values than taxa that share fewer primary character states because of the undue influence of the secondary characters that describe variation in the primary characters. Here we introduce a family of metrics which weight primary characters according to the secondary characters that describe them, effectively eliminating this problem, and compare its performance to that of common dissimilarity metrics as well as previously proposed weighting schemes. When applied to empirical datasets, we find that choice of dissimilarity metric frequently affects the rank order of pairwise dissimilarity values, but not necessarily enough to influence downstream macroevolutionary inferences.



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### Capturing intraspecific variability in the global ocean: Building the largest public database of planktonic foraminifera images and IDs for automated species recognition using machine learning

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Planktonic foraminifera vary widely in their morphology within both morphospecies and even genetic species. In any given assemblage, individuals that are morphologically intermediate between species concepts are encountered, constituting a real challenge for those looking to pick a single species for geochemical applications, and raising important ecological and microevolutionary questions. To date, studies have generally skirted around this complex problem. Here we report on a community effort to document and describe more than 46,000 individual planktonic foraminifera (comprising 32 species) from sediment core tops. Of those individuals identified by experts utilizing the Zooniverse platform for classification projects, more than

72% have received high quality identifications (*i.e.*,  $\geq$ 75% agreement among four independent classifiers) based on a single view of the individual in images taken under a stereolight microscope. These images, paired with corresponding morphological measurements including major and minor axes length and 2D and 3D meshes and outlines, constitute the largest database of expert-identified 3D morphological variability within a clade of modern taxa. They thus serve as an important new resource for those looking to learn modern foraminiferal taxonomy or study ecological or evolutionary patterns. In addition to reporting on the lessons learned from this community effort, we will also describe the efficacy of modern machine-based deep learning techniques, leveraging this dataset to automatically identify species from out-of-sample images. We provide a case study of the utility of this approach, considering within- and among- species trends in body size in the North Atlantic Ocean.

\* Speaker



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## Ecological and evolutionary drivers of temporal variations in body size

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Body size, being well accessible in fossils, has been a research focus for generations of paleontologists. Most studies focus on long-term evolutionary trends within or across lineages or on short-term variations in the context of evolutionary crises. Here we address, based on a compilation of more than 6000 interval-to-interval changes of body size in marine taxa, how the oft-cited Lilliput effect compares across spatio-temporal scales. To assess body-size changes, we used the log-ratio of the geometric means of body-size estimates from one interval to the next. This measure of effect size is theoretically independent of absolute body size and symmetrical for losses and gains.

There is a tendency of effect size and variance to increase with temporal and taxonomic scale suggesting that changes in body size are largely manifested in macroevolutionary rather than phenotypic processes. Some higher taxa such as fishes and ammonoids appear to be more prone to body size changes than others, but sampling issues prevent a conclusive statement. Effect sizes are weakly but significantly correlated with body size suggesting that larger organisms are more prone to body size change than smaller organisms.

To test if the Lilliput effect is significantly linked to environmental perturbations or rather deceived by the focus of pertinent studies on mass extinctions, we compared the large dataset of pure background changes with those of inferred background to crises changes. Negative changes of body size are significantly more pronounced during changes from background to crises intervals than in any other combination of the background-crisis-survival-recovery intervals. This maintains that the Lilliput effect is a common phenomenon during evolutionary crises, but the mechanisms still need to be better understood. Body size reduction cannot be taken as evidence of warming-induced crises, since it occurs during hypterthermals (e.g., end-Permian) as well as hypothermals (e.g., Late Ordovician).

### The R package 'divDyn': diversity dynamics from fossil occurrence data

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Methods to calculate accurate estimates of diversity dynamics are in constant development. These include different metrics of global taxonomic richness, extinction and origination rates, as well as sampling standardization protocols. With the increasing size of this toolkit, it becomes more and more difficult to keep track of the different methods, and to compare their performance and applicability.

Depending on their quantitative skills, researchers tend to implement their own solution to create time series of biodiversity dynamics. Students and less quantitatively inclined researchers either rely on snippets of code or collaboration with colleagues. As reconstructed trajectories of biodiversity dynamics are often the basis of hypothesis testing, the community would benefit from an accessible toolkit to calculate diversity dynamics from fossil occurrence data. We hope that a user-friendly implementation will facilitate the distribution and wider application of these approaches.

Here we present the R package 'divDyn' that allows the rapid calculation of a large array of raw and sampling-standardized metrics of diversity dynamics. The package is applicable to any sort of time-binned occurrence databases such as the Paleobiology Database. The 'divDyn' package also offers functions to generate matrices of survivorship probabilities, environmental affinities, and tests of extinction selectivity. The unique subsampling wrapper function allows the application of popular sampling standardization processes such as classical rarefaction, occurrences-weighted by-list subsampling, and shareholder quorum subsampling.

S4 // Oral



### The stability of coastal marine biogeography over the last 10 million years

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Although we have a detailed understanding of the geographic structure of life in the oceans, we still know little about its determinants and history. Seawater temperature and habitat areas have changed substantially over the last 10 million years. As both these variables have a significant impact on species distributions, we expected bioregionalisation patterns to have changed markedly over that interval of time. To compare past and present-day biogeography, we outlined benthic bioregions with the 'infomap' community detection algorithm on networks constructed from occurrences of both recent and fossil species (using data from OBIS and Paleobiology Database, respectively). We found that global patterns of benthic biogeography remained remarkably stable in the last 10 million years. Current bioregions are traceable back in time and they had similar positions in the past. Our results suggest that continent configuration and the latitudinal temperature gradient jointly define marine biogeography. Landmass barriers and open ocean barriers control habitat space and its connectivity, while changes in seawater temperature slice the connected areas to latitudinal series of bioregions.

Speaker

## Reproducibility in phylogenetics: the importance of accuracy in data matrices for phylogenetic analysis

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Large phylogenetic data matrices often contain problematic scores: typographic and similar accidental errors; redundant characters whose scores are predictable from each other; characters with only one described state; plesiomorphies in morphologically immature specimens scored at face value; even taxa scored after presumed close relatives. Further, even continuous characters are usually unordered. We find that the frequency and the impact of these issues has been underestimated.

As an example, we report thousands of misscores in the largest published matrix of early limbed vertebrates, which failed to recover several widely accepted clades and found the "temnospondyl hypothesis" on the origin of Lissamphibia (TH) to be more parsimonious than the "lepospondyl hypothesis" (LH). After improving the mentioned issues, we find much longer trees with more conventional clades and with the LH markedly shorter than the TH; the sister-group of Lissam-phibia is a large clade that includes adelogyrinids, urocordylid "nectrideans" and Á'istopods.

Adding 56 OTUs to the original 102 increases the resolution. The added taxa range in completeness from complete articulated skeletons to an incomplete lower jaw. Even though three particularly lissamphibian-like temnospondyls (e.g. *Gerobatrachus*) and an extremely peramorphic (thus temnospondyl-like) salamander are added, the difference between LH and TH rises slightly, despite low support; a clade composed of Brachydectes (Lysorophia) and Brachystelechidae ("Microsauria") is the sister-group of Lissamphibia. The TH requires several more regains of lost bones than the LH, contrary to recent literature.

Bayesian inference of the enlarged taxon sample mostly agrees with parsimony. High posterior probabilities are found for Lissamphibia (1.00) and for the LH (0.92); many other branches are weakly supported and short, as expected from the character/taxon ratio (< 3:1).

We discuss phylogeny, approaches to coding, methods of phylogenetic inference, some character complexes, and prospects for further improvement of this matrix. In its present state, even after our changes, the matrix cannot provide a robust assessment of the phylogeny of early limbed vertebrates; sufficient improvement, however, will be laborious but not difficult.

Similar ongoing work on a recent matrix for analysis of dinosaur phylogeny confirms that every cell in a matrix can impact the resulting trees and that published support values do not always stand up to scrutiny.



### Setting biostratigraphical data free: a collaboration between the British Geological Survey and the Nanjing Institute of Geology and Palaeontology

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The British Geological Survey (BGS) palaeontological collection of around 3 million fossils has been systematically gathered over 150 years from all over the United Kingdom to exacting and consistent standards. The collection is supported by a large amount of supporting biostratigraphical information spanning around a century and containing a large number of sections and spot localities. The collection and its supporting information is the most representative database of British fossil occurrences, and as such has the potential for underpinning significant scientific research. To release the value of this data, much of which is contained within analogue documents or simple document scans the BGS is working with the Nanjing Institute of Geology and Palaeontology (NIGPAS) to transfer data to the NIGPAS-hosted GeoBioDiversity database which is almost unique in being the only large database to hold sequences of fossils tied to sections, rather than just spot collections, and can be used to improve the quality of international correlation. GeoBioDiversity is the International Commission on Stratigraphy's official nominated database. Another aim of the project is to develop innovative ways of extracting meaning from written texts using artificial intelligence and automation so that large amounts of biostratigraphical information can rapidly and easily be accessed. BGS and NIGPAS carried out a pilot project between October 2017 and January 2018, at the offices of the BGS. A UK database was developed and a method was investigated to establish workflows for extracting stratigraphic and palaeontological data from BGS scanned and other paper reports. The ultimate aim is to develop very large databases for standard sections, CONOP and graphic correlation. These will improve BGS models and stimulate UK and international science and bring palaeontology into the realm of 'big data'.



## Large-scale study of ecomorphological trends in conodonts

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Conodonts have one of the best fossil record of any animal group, and an important morphological diversity. Through history, many authors have noted repeated and phylogenetically independent evolution of various morphological characters, notably in the P elements: changes in size, appearance of a platform and reduction of the basal cavity. More recent works have shed light on the function of these elements, which allowed the breakdown of food. In this context, the study of these repeated evolutionary events, over a large time span, may help understand and test which ecological variables could have influenced their appearance. To achieve this, we are collecting morphological and associated paleo-environmental data from the bibliography and available collections to create a large conodont database. The relationships between the various data obtained may then be explored and tested via multivariate statistics. Ultimately, identifying ecological conditions in which conodont morphology was modified, combined with the arising functional knowledge of the conodont apparatus, may hint at potential adaptive interpretations for these evolutionary trends.

Speaker

# Catalyzing new research on the Cretaceous seas of California

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The Invertebrate Paleontology collection at the Natural History Museum of Los Angeles County (LACMIP) is digitizing the world's largest collection of Cretaceous marine invertebrates (bivalves, gastropods, cephalopods) from California, USA and Baja California, Mexico to create research-ready resources promoting international collaboration. By the end of this two-year grant (NSF DBI 1561429), at least 21,000 specimen lots (126,000 specimens) will be cataloged, 2,930 localities will be georeferenced, and a representative selection of species (about 5% of all cataloged lots) will be imaged. Significant effort is being made to standardize and modernize the taxonomic and stratigraphic nomenclature used for this project to promote consistency internally, as well as across future research endeavors, so as to enable the highest quality research by downstream users of these data. In addition to the resulting taxonomic dictionary and stratigraphic lexicon, digitization products will include a bibliography, image library, and searchable inventory of LACMIP Cretaceous collections, all of which will be made publicly accessible online. The vast majority of these collections represent decades of field work and are from localities no longer accessible due to land development, highlighting the value of digitally-accessible museum collections in the future of paleontology. Relatively few studies have explored the Cretaceous marine invertebrate faunas from the Pacific Slope of North America. Those that do exist typically focus on the descriptive taxonomy of bivalves and gastropods (see Saul, Squires, Popenoe, et al.), yet there is great potential for robust paleoecological and biogeographic analyses across these fossil communities. Likewise, while heavy research emphasis has been placed on Cretaceous marine invertebrates from the epicontinental seaways of North America and Europe, these faunas should also be juxtaposed with their open-ocean counterparts. Further disparities between the published and unpublished diversity of Cretaceous Pacific Slope marine faunas have come to light over the course of this project. Digitization of the LACMIP collections described here will soon permit such comparisons, thus facilitating opportunities for future research to close important knowledge gaps in Cretaceous paleontology.

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## S5 - Biodiversity changes through times: crisis and radiation

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Speaker

# Novelty, adaptive radiations and evolutionary diversification

Douglas Erwin \*

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In 1960, G. G. Simpson argued that the history of life can be described as a series of adaptive radiations, essentially the point illustrated by the only figure in Darwin's *Origin of Species*. The term adaptive radiation has been applied to a wide range of diversification patterns, some of continental extent or extending over long time spans, and which are inconsistent with ecological models of adaptive radiations. This has led to proposals of many other types of evolutionary diversifications, although the boundaries between these are often indistinct. In particular, while many biologists since Simpson have held that adaptive radiations reflect response to ecological opportunity, the relationship between adaptive radiation (both ecological and from deep time), I evaluate evidence for the relationship between adaptive radiations, evolutionary novelty (defined here as the formation of newly individuated characters or character suites), taxic diversification, and evolutionary innovation (changes in the structure of ecological communities). These have been seen as linked through the origin of 'higher taxa', but case studies where well-resolved phylogenies exist demonstrate that they are not necessarily correlated, and novelty is largely uncorrelated to adaptive radiation.



## Near coincidence of maximum Deccan volcanism with the Cretaceous-Paleogene boundary : evidences from U-Pb geochronology and mercury chemostratigrahy

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Mercury (Hg) as indicator of large-scale volcanism in marine sediments provides new insights into relative timing between biological and environmental changes, mass extinctions and delayed recovery. The bulk (80%) of Deccan Trap eruptions occurred over a relatively short time interval in magnetic polarity C29r. U-Pb zircon geochronology reveals that the onset of this main eruption phase around 250 ky before the Cretaceous-Paleogene (KPg) mass extinction and continued into the early Danian suggesting a cause-andeffect relationship. We investigate the mercury (Hg) contents of 15 KPg sections. In all sections, results show Hg concentrations are more than 2 orders of magnitude greater during the last 100ky of the Maastrichtian up to the early Danian P1a zone (first 380 ky of the Paleocene). These Hg anomalies are correlative with the main Deccan eruption phase. At Gams (Austria), Bidart (France) and Elles (Tunisia), Hg anomalies correlate with high shell fragmentation and dissolution effects in planktic foraminifera indicating that paleoenvironmental and paleoclimate changes drastically affected marine biodiversity. Hg isotope data from Bidart support a direct fallout from volcanic aerosols. PGEs data from Mishor Rotem (Israel) from the KPg transition provide some important clues about the Hg deposited in the KPg layer, which appears to be more linked to volcanism than impact, suggesting a major pulse of Deccan activity just before and at the KPg that resulted in rapid climate warming and ocean acidification, increasing biotic stress that predisposed faunas to eventual extinction at the KPg.



S5 // Ora

<sup>&</sup>lt;sup>°</sup> Speaker

## The Frasnian-Famennian boundary mass extinction – widespread seismic events, the timing of climatic pulses, "pelagic death zones", and opportunistic survivals

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The Frasnian/Famennian mass extinction has remained enigmatic due its complexity, with rapid climate and sea level fluctuations, anoxia, stepped and regionally different extinction patterns, and highly variable opportunistic survival and re-radiation in different fossil groups and fragmented ecosystems. We present data for new and refined sections of the Rhenish Massif (Germany) and Morocco. The youngest Rhenish reef complex is exposed in a large quarry near Wülfrath. There, a thick stromatoporid-coral carbonate platform drowned in the upper Frasnian and turned into an open microbial biostrome. Currentoriented large orthocones indicate shallowing upwards. The microbial phase ended sharply with the transgressive, black, goniatite-rich Upper Kellwasser Limestone. However, a rapid turn of sea-level is marked by a long sedimentary gap below pelagic black shales of the top termini Zone. A temporary lateral section showed that the hiatus was caused by a major tectonic event, which uplifted the northern flank of the Velbert Anticline, resulting in a significant angular unconformity. Long known other Rhenish sections indicated a F-F boundary seismic event. At Beringhauser Tunnel (eastern Sauerland), unique, microbial Kellwasser Beds are sharply overlain by a thin, dark mudstone with torn pieces of the underlying wackepackstone. Its strange microfacies defies currently a sedimentological explanation. This F-F boundary bed is free of macrofauna and overlain by an equally unique mudclast mass flow. The reported sudden cooling (up to 7°) occurred at this level, not in the Upper Kellwasser beds, which developed in a very hot phase. It is probably not a coincidence that major mass flows characterize also the basal Famennian of the distant carbonate platforms of South China. Accordingly, pelagic top Kellwasser Beds of SE Morocco were resedimented by seismic shocks in the basal Famennian. In a deeper shelf basin of the eastern Anti-Atlas, fine siliciclastic sedimentation continued through the Kellwasser Crisis. But, despite the absence of any sedimentary perturbation, the top Frasnian conodont and homoctenid extinction occurred, as on the adjacent platform. This left a fossil-free, basal Famennian "death zone". The opportunistic survival of just one ammonoid, Phoenixites frechi, was restricted to the western Prototethys. New findings from the Ardennes prove that the loss of competition enabled a post-extinction ecological expansion into shallow brachiopod facies.



S5 // Ora

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## The evolutionary, biogeographical and ecological history of Cenozoic Crocodylomorphs: an updated review with new perspectives

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Crocodylomorphs and birds were the only Archosaurs to survive the K-Pg extinction. Seven crocodylomorph lineages survived: Crocodyloidea, Alligatoroidea, Gavialoidea, Planocraniidae, Borealosuchus (Neosuchia, Crocodylia), Dyrosauridae (Neosuchia, Tethysuchia) and Sebecidae (Metasuchia). The first five lineages inhabited former Laurasian continents (North America, Europe and Asia), while Sebecidae has a South American origin and Dyrosauridae inhabited all continents surrounding the Atlantic Ocean and the area of modern India. The survival of Crocodyloidea, Alligatoroidea and Borealosuchus may be related to the freshwater habitat of these groups, while that of Dyrosauridae and Gavialoidea to an estuarine (but not fully marine) habitat and dispersal capabilities. The survival of Sebecidae may be due to the peculiar crocodylomorph fauna of the Late Cretaceous of South America, while that of Planocraniidae is yet to be properly addressed. A global cooling in the Eocene may have caused the extinction of the high-latitudes inhabitants Planocraniidae, Borealosuchus and the European sebecids, as well as the estuarine Dyrosauridae. The sebecids are likely totally extinct after the Middle Miocene trough their disappearance from South America, possibly due to environmental changes caused by the orogenesis of the northern portion of the Andes. After that, Gavialoidea, Crocodyloidea and Alligatoroidea would be the only groups remaining. Due to their salt-water tolerance, the Crocodyloidea were able to disperse largely from their original "laurasian" distribution, reaching Australia and Africa. They also reached the American continents again at least twice through the Cenozoic: one from Africa through Crocodylus, in the Oligocene, and other through the Tomistomines, which have three genera (Gavialosuchus, Thecachampsa and Charactosuchus) occurring from the Eocene to the Miocene in the continents. Gavialoids may have had salt-water tolerance in the beginning of the Cenozoic, which may be related to their dispersion from Africa or Asia to South America in the Paleogene, forming the Gryposuchinae clade. Alligatoroids have no record of a high level of salt-water tolerance but have also performed significant dispersions. Among these, one from North America to South America during either the Late Cretaceous or the Paleocene (originating the clade Caimaninae) and at least two towards Asia during the Cenozoic (related to the occurrences of Krabisuchus and Alligator) stand out.



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### Middle Triassic ostracods from the North Dobrogean Orogen (Romania): between long-term survival and emergence of Triassic taxa

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Ostracods are minute crustacean characterized by their calcified bivalve carapace, which provides them with a good fossil record from the base of the Ordovician to present days. In neritic marine environments, ostracods have been deeply affected by the end-Permian extinction and it is widely considered that their assemblages where fully recovered during the Anisian (Middle Triassic). However, many questions are still pending as to the mechanisms of their recovery and the characteristics of the associated environments. The North Dobrogean Orogen in Romania is a pivotal area to characterize the post-extinction evolution of both shallow- and deep-water ostracods during this time interval. Several works have documented deep-water ostracod assemblages during the Anisian and reported the exceptional survival of Palaeozoic taxa (such as the genus Acanthoscapha). Recently, the analysis of a synchronous neritic assemblage has recognized for the first time the occurrence of typical Triassic taxa including the genus Liuzhinia. Here we propose the first comprehensive summary of Anisian ostracods in North Dobrogea, which brings new powerful arguments to the ideas on the environmental stability in deep waters during most of the Late Palaeozoic and Permian-Triassic transition. We also demonstrate the homogeneity of deep-water ostracods and the heterogeneity of shallow-water assemblages around the Palaeo-Tethys during the Anisian. In spite of slight disparities, a peri- Palaeo-Tethyan province is identified for marine ostracods during the Anisian and could be related to a surface circulation cell bathing this area.

Speaker

5 // Ora

## Ostracod diversity and environmental conditions of the Aras Valley section (NW-Iran) during the end-Permian mass extinction

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The end-Permian mass extinction, one of the most severe biotic crises in Earth history, is still a matter of debate regarding the responsible environmental and climatic conditions. In our study, we investigate the ostracod diversity of the north-western Iranian Aras Valley section in combination with geochemical proxies, such as d13C and d18O, to examine environmental changes during and after the extinction. The Late Changhsingian Paratirolites Limestone and the subsequent "Boundary Clay" (= Aras Member) are assumed to display continuous successions without major gaps in the sedimentary record. The diversity patterns right before and after the extinction show a restructuration of the ostracod community from a normal diverse assemblage with occurrences of possibly predatory planktonic forms in the upper Paratirolites Limestone to an abundant and diverse benthic assemblage up to the middle part of the Aras Member. This transition furthermore indicates the onset of different trophic conditions after the extinction with the disappearance of possibly predatory ostracods and occurrences of Platycopida in the Boundary Clay. The generally high species richness and high abundance of ostracods in the Aras Member, which is, in contrast to other Permian-Triassic sections, not linked to an onset of possibly protective microbial mats, leads to the assumption that significant anoxic conditions were not affecting the Aras Valley section right after the extinction horizon. A decreasing diversity in the upper part of the Aras Member, together with mass occurrences of Bairdiacypris ottomanensis and pustular representatives of this species are correlated with a persistent temperature rise (data from conodonts); these suggest changing environmental conditions.



5 // Ora

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#### What is a conodont species? The case of *Novispathodus* ex gr. *waageni*

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In Palaeontology, the concept of species is usually based on a combination of discrete morphological characters. This is particularly true for extinct fossil groups such as the conodonts characterized by their high abundance and evolutive rate, and for which there exists no extant analogue. Authors' views on what defines a fossil species may differ substantially, depending also on the quality of their collections. Thus, to avoid the biases due to the lumping *vs.* splitting efforts of previous authors, it is advisable to 'standardize' the taxonomy of conodonts to study the temporal evolution of their diversity. Conodonts are mainly known from their mineralized feeding elements, also called conodont elements. We are interested in the evolution of their diversity, in particular in the aftermath of the end-Permian crisis.

Novispathodus waageni and Novispathodus pakistanensis are iconic species of Early Triassic Smithian substage (Early Olenekian, ~251 Ma), usually considered as being clearly distinct taxa. In large conodont collections from Oman representatives of these species co-occur with many seemingly intermediate forms, which suggests they may not be as distinct as one thought. On the other hand, many different morphotypes of *N. waageni* have been described by various authors as elements of *N. ex gr. waageni*, although they may belong to distinct species.

Using microtomography, we scanned about 170 P1 conodont elements from that conodont-rich Smithian sample from Oman. Applying 3D geometric morphometrics as outline analyses, landmarks and sliding landmarks, and angle measurements, we are quantifying the morphological characters typically used in conodont systematics. We want to decipher which traits drive the morphological variation within such assemblage, and to assess whether and how specimens cluster in the morphospace. Are *N. waageni* and *N. pakistanensis* two distinct species? Are there more than two distinct morphometrical clusters, and thus possibly species? How may this modify our interpretation of the Early Triassic conodont record? We will present and discuss our preliminary results.



<sup>&</sup>lt;sup>•</sup> Speaker

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# Impact of the end Triassic mass extinction on insect diversity and ecology

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The fossil record is not a perfect record of past life but it can give us important insights into how past events affected the diversity and evolution of organisms through time. Insects are one of the most diverse and important groups of animals in terrestrial ecosystems and this is thought to have been true throughout their evolutionary history, therefore understanding the effects of large scale environmental perturbations on entomofaunas is important for understanding changing terrestrial ecosystems. Utilising museum collections and online databases we constructed the first species level dataset of insect diversity across one of the five largest extinction events to have occurred on Earth, the end Triassic mass extinction. Past studies have suggested that the ETME did not impact insects as much as some other groups, but this may not be the case. British deposits from this time provide highly resolved stratigraphy coupled with abundant insect fossils providing a resouce for a thorough investigation of the ETME, but much of the taxonomy of the collections was historic. We therefore taxonomically revised key orders of insects from the British collections and compared diversity changes at the local level with changes at the global level.

Speaker

#### Repeated extinctions by cosmoclimatological driver: GCR flux and global cooling

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The end-Paleozoic extinction that determined the fate of modern animals including human beings occurred in two steps: first around the end-Middle Permian (Guadalupian-lopingian boundary; G-IB) and then at the end-late Permian (Permian-Triassic boundary; P-TB). Biological and non-biological aspects unique to the G-IB event include significant drop in biodiversity, isotope ratios (C, Sr etc.) of seawater, sea level, ocean redox state, episodic volcanism, and geomagnetism, suggesting the ultimate cause was related not to the planet's surface phenomena but to those in the interior. As the G-IB and end-Ordovician extinctions share multiple similar geologic phenomena including the appearance of global cooling, the same cause and processes were likely responsible for the two events. In addition to the currently most popular scenario of mantle plume-generated large igneous provinces (LIPs), an emerging perspective of cosmoclimatology is noteworthy. Galactic cosmic radiation (GCR) and solar/terrestrial responses in magnetism could have had a profound impact on Earth's climate, in particular, on extensive cloud coverage (irradiance shutdown). The star-burst events detected in the Milky Way Galaxy apparently coincide in timing with the cooling-associated major extinctions of the Phanerozoic, e.g. end-Ordovician and G-IB episodes, and also with the Proterozoic snowball Earth episodes at ca. 2.3 Ga and 0.7 Ga. As an ultimate cause for major extinction, the episodic increase in GCR flux from the source (dark clouds derived from starburst) against the strength of geomagnetic shield likely determined the major climate changes, particularly global cooling in the past. Apart from these observations on timing, material-based evidence for the extraterrestrial forcing immediately before the main extinctions is lately appearing. The study of mass extinctions on Earth is entering a new stage with a new cosmoclimatological perspective.



#### Diversity dynamics of slit band gastropods (order Pleurotomariida) at the Paleozoic - Mesozoic transition

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During the Paleozoic-Mesozoic transition, the marine fauna suffered severe extinctions and underwent major changes. Although gastropods were less affected than other groups, major shifts occurred within Gastropoda. One of the most diversified gastropod groups of the late Paleozoic seas, the slit bearing nacreous vetigastropods (pleurotomariids), decreased significantly during the transition period and became a minor component of the post-Paleozoic fauna. A global Triassic gastropod species database includes 2,150 nominate Triassic species representing 430 genera, 122 families and 53 superfamilies. Permian pleurotomariid genera were analyzed from the Paleobiology Database. Diversity of pleurotomariid genera decreased gradually starting from the mid-Permian; only a quarter of the Permian genera survived into the Triassic. Despite gastropod recovery on the species level during the Triassic, pleurotomariids could not reach the level of diversity they had before the mass extinction. The ratio of global pleurotomariid genera to the total gastropod genera declined from 30 % to 14 % from the Permian to the Triassic. Abundance of pleurotomariids in gastropod assemblages decreased from 30-40 % in the late Paleozoic to 1-5 % in the early Mesozoic. Caenogastropods became the most diversified group in the Triassic and comprise 39 % of the global gastropod species diversity during the Triassic, whereas the species diversity of pleurotomariids comprises only 11 %. Standing species diversity of the four major subclasses (Caenogastropoda, Heterobranchia, Neritimorpha, Vetigastropoda) show similar trends and increased until the Carnian and decreased afterwards. However, pleurotomariids (comprising roughly half of the vetigastropod species diversity) had a diversity decline during the Ladinian. This suggests that they have failed to recover during the Triassic. The generic standing diversity of the four major subclasses, similar to the diversity trends on the species level, peaked during the Carnian and boundary crossers peaked at the Carnian-Norian boundary. By contrast, the generic diversity of pleurotomariids rose only slightly until the Carnian and the boundary crosser genera decreased earlier after the Ladinian-Carnian boundary. The failure to fully recover and the other mentioned differences in diversity dynamics to other gastropod clades show selectivity against pleurotomariids. Possible reasons, among others, are predation pressure or limits in tiering and feeding.



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### Molecular and morphological evidence for a rapid recovery of crown snakes after the Cretaceous-Palaeogene mass extinction

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Despite their astonishing diversity, with over 3400 living species, the early evolutionary history of crown group snakes remains poorly understood. Factors such as limited fossilisation potential and homoplastic vertebral characters have made phylogenetic inference and the dating of divergence events difficult. Previous analyses have focused on reconstructing ancestral conditions in crown and stem snakes, but continue to be plagued by uncertainty in tree topologies and the timing of diversification events. Here, we apply molecular clock methods to a dataset of 52 nuclear and mitochondrial genes to elucidate the early evolutionary history of crown snakes. We infer that as few as 5 extant lineages of crown snakes crossed the Cretaceous-Palaeogene boundary. We suggest that the major radiation of Afrophidia (which comprises most of the extant snake diversity and disparity) occurred in the wake of the K-Pg mass extinction, as did the origination of Leptotyphlopidae, Typhlopoidea, and Amerophidia. To investigate changes in snake disparity across the end-Cretaceous mass extinction, we performed Principle Component Analyses on vertebral fossils from the Late Cretaceous and early Cenozoic, and infer that morphological disparity was lower in the Palaeocene than in the Late Cretaceous and Eocene. Biogeographical analyses suggest that the diversification of snakes in the Palaeocene coincided with the colonisation of Asia by Afrophidia. Furthermore, aquatic snakes rapidly attained much larger sizes following the K-Pg transition than their Cretaceous counterparts. Our results support the hypothesis of a post-K-Pg extinction radiation, and simultaneous invasion of new niche spaces and landmasses by snakes. Together with mammals, birds, frogs, and teleosts, snakes were an important component of the global post-extinction recovery of vertebrate diversity.



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# Discrepancy between Early Paleozoic trends in diversity and evolutionary rates

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The Early Palaeozoic diversification in the marine realm comprises two main events, the Cambrian Explosion" (CE) and the Great Ordovician Biodiversification Event" (GOBE). Traditionally the two events are seen as either one coherent process within a unifying macroevolutionary dynamics or as the composite result of processes at multilevel spatial and temporal scales. The diversification can also be conceptualised as a pattern emergent from lower taxonomic levels and lower spatial scale. In this perspective the global marine diversity trend would represent more than a trivial addition of more and more taxa, but the appearance of new structural phenomena that in itself led to ever increasing numbers of coexisting taxa.

We estimated diversity trends and evolutionary rates for the Cambrian–Silurian interval in unprecedented time resolution, applying capture-recapture modelling methods. As a result we identified two main Early Palaeozoic diversity shifts reflecting the CE and GOBE peaks, respectively. Here we provide additional statistical evidence for the significance of these events and present the results of several tests for detecting significant diversity change-points.

Our estimated evolutionary rates are diversity independent and hence, diversity and turnover can be interpreted as variables describing the state of the Early Palaeozoic marine ecosystem independently from each other. This is most evident in a major temporal discrepancy between change-points of diversity and diversification rates and change-points of per-capita rates of extinction and origination. The global per capita turnover rates dropped drastically during the earliest Ordovician and at the same time the average genus longevity increased. This Early Ordovician drop in turnover rates and the simultaneous rise in genus longevity can be interpreted as a condition, setting the stage for the GOBE.



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#### The morphological disparity of Parareptilia throughout their evolutionary history

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The clade Parareptilia, the sister taxon of Eureptilia, is a group of sauropsids that thrived during the Late Palaeozoic and Early Mesozoic. The earliest known parareptile appeared in the Late Carboniferous, and from there the clade began to diversify, achieving considerable diversity and a cosmopolitan distribution by the end of the Permian, as well as becoming an important component of Permian terrestrial ecosystems. However, most major parareptilian clades go extinct during or before the end-Permian mass extinction event, with only one clade, the Procolophonoidea, surviving into the Mesozoic, before eventually going extinct at the end of the Triassic. Parareptilia is notable in that members of the clade exhibit a wide range of morphologies. Examples include: small, predatory superficially lizard-like taxa, secondarily aquatic taxa, and large, armoured herbivorous taxa. The wide array of morphologies present in the clade allowed parareptiles to occupy and be successful in a variety of ecological niches. In order to better understand parareptilian evolution and the numerous morphologies that appeared within the clade we investigated both the morphological disparity and phylogenetic diversity of parareptiles over the course of their evolution. To accomplish this our study uses phylogenetic data and statistical techniques to quantify the morphological disparity of parareptiles during the Palaeozoic and Mesozoic, as well as comparing it with their phylogenetic diversity. The results of our study indicate that there is an overall increase in parareptilian disparity during the Permian with the highest peak occurring in the Early Permian. From there parareptilian disparity fluctuates slightly, before it eventually declines sharply towards the end of the Permian and into the Triassic, seemingly corresponding with the end-Permian extinction event. Interestingly, this is a different trend to what is observed regarding parareptile phylogenetic diversity during this same time frame. As the diversity of the clade does not experience the same sharp drop at the end of the Permian, not being as heavily affected by the extinction event. This is likely in part due to the fact that, despite the extinction of several morphologically distinct parareptile clades, the procolophonoids, one of the largest parareptilian clades, were diversifying at the same time, resulting in the evolutionary patterns that are observed here.



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## Extinction, evolution and recovery of the Gondwanan flora through the Permian–Triassic biotic crisis in southern high palaeolatitudes, Australia

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The Permian–Triassic biotic crisis, ca 251.9 million years ago, was the largest of the 'big five' massextinction events in Earth's history. Nearly 60% of families and 80% of genera were extinguished. Most previous studies of this crisis have focused on marine and Northern Hemisphere successions. We are undertaking the first detailed investigation of extinction and recovery patterns in the terrestrial flora at high (>  $65^{\circ}$ ) southern palaeolatitudes by extensive sampling of drill cores and outcrops in the Bowen and Sydney basins, Australia. Initial results indicate a dramatic termination of coal sedimentation at the end of the Permian, and a gradual increase in red-green iron-rich mudrocks through the Early Triassic. Forests of broad-leafed glossopterid gymnosperms dominated the latest Permian peat-forming communities and were the main casualties of the extinction event on land amongst plants. Several subsidiary gymnosperm (conifers and seed-ferns), fern and horsetail groups also became extinct at this time. These extinctions are reflected in both the leaf macrofossil record and pollen assemblages. Stepwise recovery and evolution of the Triassic vegetation is characterised by the appearance of small-leafed Lepidopteris (Peltaspermales) and Voltziopsis (conifer) trees, followed by successive spikes in abundance of lycophytes (club-mosses), then Dicroidium (Corystospermales). The spore-pollen record has facilitated the identification and correlation of six palynostratigraphic zones (one Permian, five Triassic) across multiple sections in the Sydney Basin, with no consistent evidence of a depositional hiatus across the P-T boundary. Quantitative palynology was employed to reveal the fine-scale changes across the P-T boundary. The stepwise recovery and replacement exhibited by the macroflora was also observed in the palynological record; several common Permian palynofloral elements persist in low abundances until the upper Lower Triassic, and several other spore-pollen groups show a protracted increase in abundance and diversity over the same interval. The end-Permian extinction was probably linked to the largest known continental flood basalt eruptions in Siberia, which affected the atmosphere and climate and led to intensification of the Pangaean monsoon system at that time.



<sup>&</sup>lt;sup>\*</sup> Speaker

#### Dinoflagellates cyst from K/Pg boundary at Oued Malah section, northern Tunisia

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The Cretaceous/Paleogene boundary at Oued El Malah section, Tunisia, revealed the presence of marine organic-walled microfossil dominated by well-preserved and diversified dinoflagellate cysts. The biostratigraphic study of dinocyst assemblages identified the K/Pg boundary just above the Latest occurrence from *Dinogymnium cretaceum*, *Dinogymnium acuminatum* and *Alysogymnium eucleanse* and immediately below the first occurrence of the basal Danian markers *Damassadinium californicum and Carpatella cornuta*. This recognized boundary based on dinocyst assemblages coincides with the K-Pg boundary previously known based on lithostratigraphy (the iridium anomaly) and planktic foraminiferal biostratigraphy. The dinocysts assemblage is dominated by *Cerodinium*, *Lejeunecysta*, *Senegalinium*, *Andalusiella* and *Phelodinium* groups that characterize the Malloy suite (Lentin and Williams, 1980), and therefore confirms a deposit in a tropical or subtropical province Tethyan for the interval studied at Oued El Malah section.

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# The impact of the Mulde bioevent (Lower Silurian) on Ostracod ecological dynamics

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The Mulde bioevent (428 million years ago) was one of the most important geobiological events which affected biota during the dynamic Silurian period. At that time, most of the graptolites went extinct. However, so far, it is not much known about the impact of this event on to the benthic biota. Ostracods are an important component of benthic communities and the ostracods of the Silurian period are insufficiently investigated at global scale. The purpose of this work is to analyse the impact of the Mulde mass extinction (Lower Silurian) on Ostracoda ecological dynamics. In order to achieve this goal, detailed sampling of the Ge luva-118 core was performed, with processing of samples and extraction of ostracod shells. The taxonomic identification and statistical analyses diversity were accomplished. During this study, 99 samples (in 952,1 m - 1049 m depth interval) were analysed, which span approximately two million years, - starting from the pre-extinction phase and the onset of the Mulde biotic event at the beginning of the Ge luva regional stage to the final recovery. For the purpose of the chemostratigraphy  $\delta$ 180 and  $\delta$ 13C stable isotope analysis were performed. It was determined that immediately after the end of Mulde extinction in concert with a sea levels rise, the increase of abundance and of diversity began and the maximum ostracod abundance was reached. Statistical analysis shows high abundance of several dominant species, which shows the decrease of complexity of ecosystems in the initial post-extinction stage. However, the upper Wenlock is characterized by the decline of dominance and increase in entropy and species evenness. Probably one of the most important factors driving biodiversity and abundance changes during this time interval was eustatic change. It should be noted that maximum of abundance and diversity were reached at the higher sea levels.



Speaker

#### Combined climate and ecological niche modeling predicts the relative severity of marine extinctions during three Phanerozoic episodes of climatic cooling

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The Late Ordovician Mass Extinction (LOME) was one of the largest extinction events of the past 500 million years. This event has been closely linked to climate change, with the first major extinction pulse coinciding with cooling, expansion of south polar ice sheets, and sea level fall near the Katian-Hirnantian boundary. However, it remains puzzling that the magnitude of extinction during the first pulse of the LOME far exceeds that associated with other Phanerozoic glaciations. This disparity has led to suggestions that cooling alone cannot account for the LOME. Here we integrate global circulation models and ecological niche simulations to compare expected impacts of cooling on shallow marine fauna during the Late Ordovician, Late Eocene-Oligocene, and Plio-Pleistocene climate transitions. We simulate six different types of species, varying in both thermal tolerance range and dispersal ability. We randomly assign a range center for each species and allow it to expand to fill the adjacent coastal cells that have pre-transition sea surface temperatures within its thermal tolerance range. We then simulate a transition to glacial conditions and determine which species would be able to disperse along paleocoastlines to stay within their tolerance range, and which would be driven to extinction. We initially test whether paleogeography alone could have resulted in higher extinction rates during the LOME, then add known changes in extent of continental flooding and cooling from interval-specific global climate models. Our simulations predict much higher extinction magnitude during the Late Ordovician transition than during the Cenozoic transitions, particularly among species with narrow thermal tolerance ranges. These predictions are consistent with observed extinction patterns, and bolster evidence that cooling could have been one of the major drivers of Late Ordovician extinctions. Experiments with artificial thermal gradients only weakly support the hypothesis that paleogeographic configuration of the Late Ordovician placed Late Ordovician species at greater risk of climatically-driven extinction than their Cenozoic counterparts. However, when changes in continental flooding are considered along with paleogeography, Late Ordovician species were at elevated risk of extinction. We show that high extinction rates in the LOME are to some degree expected given current constraints on paleogeography and rate and magnitude of cooling.



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### Turning over a new leaf: the trophic evolution of herbivorous archosauromorphs through the Late Triassic and Early Jurassic

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A series of faunal turnovers in the Late Triassic saw a progression from archosauromorph to archosaur-dominated faunas, and helped establish dinosaur terrestrial supremacy through the remainder of the Mesozoic. Despite extensive study, the principal drivers of these turnovers remain hotly debated with competition, increased volcanism, and bolide impacts suggested as possible triggers. Modern investigation has shown that Triassic dinosaurs exhibited lower taxonomic and ecological diversity than contemporaneous pseudosuchians and non-archosaur archosauromorphs, and refutes traditional ideas of competitive superiority. Thus, attention is now focused on the impacts of environmental pressures, such as the Carnian Pluvial Event (CPE) and Central Atlantic Magmatic Province (CAMP) eruptions. Understanding the exact effects of these events is difficult, as imprecise chronostratigraphy has hampered attempts to compile an accurate account of global events during the Late Triassic and Early Jurassic. Nonetheless, recent biostratigraphic and geochronological revisions warrant fresh examination of macroevolutionary events through this interval. Here we apply quantitative morphometric and multivariate, comparative phylogenetic methods to infer patterns of trophic ecology and evolution in key herbivorous archosauromorph clades. Using mandibular functional morphology, we compare the feeding ecology of rhynchosaurs, aetosaurs, sauropodomorphs, and ornithischians, and assess the influence of climatic change on their macroevolution. Our disparity and morphospace results support an extrinsic driver for the rise of the dinosaurs, and reveal surprising patterns of eco-morphological evolution that suggest intrinsic factors may have played a greater role in driving archosauromorph macroevolution than currently thought.



Speaker

#### Body size downgrading across the late Quaternary

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Since the late Pleistocene, large-bodied mammals have been extirpated from much of the Earth. While all habitable continents once harbored giant mammals, the few remaining species are largely confined to Africa. This decline is coincident with the global expansion of hominins over the late Quaternary. Here, we quantify mammalian extinction selectivity, continental body size distributions and taxonomic diversity over five time periods spanning the last 125,000 years and stretching ~200 years into the future. We also compile and analyze the global pattern of mammalian extinction over the Cenozoic as a baseline. Our results clearly demonstrate that size-selective extinction was already underway in by the late Pleistocene, that it occurred on all continents, within all trophic modes, and across all late Quaternary time intervals, with the degree of selectivity decreasing towards the modern. Moreover, the degree of selectivity was unprecedented in 65 million years of mammalian evolution and was not driven by climate change. The distinctive selectivity signature implicates hominin activity as a primary driver of taxonomic losses and ecosystem homogenization. Because megafauna have a disproportionate influence on ecosystem structure and function, past and present body size downgrading is reshaping Earth's biosphere.



Speaker

## How is biodiversity produced? Biotic immigration events, speciation, and the accumulation of biodiversity in the fossil record

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Biotic Immigration Events (BIMEs) record the large-scale dispersal of taxa from one biogeographic area to another and have significantly impacted biodiversity throughout geologic time. BIMEs associated with biodiversity increases have been linked to ecologic and evolutionary processes including niche partitioning, species packing, and higher speciation rates. Yet substantial biodiversity decline has also been documented following BIMEs due to elevated extinction and/or reduced speciation rates. In this review, we develop a conceptual model for biodiversity accumulation that links BIMEs and geographic isolation with local ( $\alpha$ ) diversity, regional ( $\beta$ ) diversity, and global ( $\gamma$ ) diversity metrics. Within the model, BIME intervals are characterized by colonization of existing species within new geographic regions and a lack of successful speciation events. Thus, there is no change in  $\gamma$ -diversity, and  $\alpha$ -diversity increases at the cost of  $\beta$ -diversity. An interval of regional isolation follows in which lineage splitting results in successful speciation events and diversity increases across all three metrics. Alternation of these two regimes can result in substantial biodiversity accumulation.

We tested this conceptual model using a series of case studies from the paleontological record. We primarily focus on two intervals during the Middle through Late Ordovician Period (470– 458 Ma): the globally pervasive BIMEs during the Great Ordovician Biodiversification Event (GOBE) and a regional BIME, the Richmondian Invasion. We further test the conceptual model by examining the Great Devonian Interchange, Neogene mollusk migrations and diversification, and the Great American Biotic Interchange. Paleontological data accord well with model predictions.

Constraining mechanisms of biodiversity accumulation provides context for conservation biology. Because  $\alpha$ -,  $\beta$ -, and  $\gamma$ -diversity are semi-independent, different techniques should be considered for sustaining various diversity partitions. Maintaining natural migration routes and population sizes among isolated regions are vital to preserving both extant biodiversity and biogeographic pathways requisite for future diversity generation.



Speaker

#### Fine-scale diversity analysis of Jurassic Chondrichthyes disproves competition between Jurassic elasmobranch and hybodontiform fishes

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Elasmobranchii (i.e., sharks, skates, and rays) constitutes a speciose group of marine vertebrates encompassing more than 1.100 extant species, and according to our current knowledge, elasmobranchs had their first appearance in the Permian, but they already might have originated even earlier. They formed, together with hybodontiform sharks, their sistergroup ranging from the Devonian to the Late Cretaceous, the most dominant chondrichthyan lineage during the Mesozoic. The late Early Jurassic (~180 Ma) is considered to mark a key time interval in the evolutionary history of elasmobranchs, because the Toarcian witnessed a first major radiation event, as recorded by different published palaeodiversity analyses, suggesting an abrupt and nearly simultaneous colonisation of a wide range of marine habitats. Jurassic hybodontiforms are generally assumed to have been negatively affected by this event due to increasing competition resulting in a diversity decline towards the end of the Jurassic while elasmobranchs flourished. However, no detailed analyses have been conducted so far to test this hypothesis. In an attempt to gain deeper insights into macroevolutionary patterns of Jurassic chondrichthyans, we analysed the generic diversity of Jurassic elasmobranchs and hybodontiforms using published data as well as information from new fossil material from the late Early Jurassic of Germany. Two diversity peaks can be discerned in Lower Jurassic elasmobranchs, a weak one spanning the Pliensbachian-Toarcian boundary, followed by a high peak in the latest Toarcian, indicating a stepwise rather than sudden increase during late Early Jurassic times. Additional diversity peaks of high intensities are confirmed for the Middle (Bathonian) and Late (Kimmeridgian) Jurassic. Diversity patterns of Jurassic hybodontiforms markedly differ from those of elasmobranchs in showing only two weak peaks, one in the early Toarcian and one in the Bathonian. Mean standing diversity and number of boundary crossers indicate a strong taxonomic increase in elasmobranchs throughout the Jurassic, while in hybodontiforms a weak diversity increase across the Pliensbachian-Toarcian boundary is recorded, before reaching a diversity plateau spanning from the middle Toarcian to the end of the Jurassic. This pattern suggests that Jurassic elasmobranchs were not in direct competition with hybodontiform sharks and thus may have used different adaptive traits to partition available niche spaces efficiently.



<sup>&</sup>lt;sup>\*</sup> Speaker

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### Late Triassic predator-prey escalatory dynamics in the marine realm: macrofossil, microfossil, sedimentological, and ichnological evidence

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The paleoecological structure of marine predator-prey interactions has undergone significant transitions over the Phanerozoic, often in the aftermath of mass extinctions, but trophic cascades driven by biological interactions may have contributed to substantial macroecological shifts. Identifying the nature and timing of these biologically-driven restructuring events is convoluted by differential fossil preservation of common marine predators and prey, which leads to complications in analyses of populations and interactions between particular groups. During the Norian Stage of the Late Triassic, dramatic shifts among predators and prey suggest that a global escalatory interval took place in shallow marine systems among benthic taxa. Shelly invertebrate populations became increasingly infaunal, and several adaptations developed independently among epifauna such as ability to cement and swim. Vertebrate predators present a more complicated fossil record for this interval, but deposits of exceptional preservation suggest a taxonomic radiation among groups specialized for shell-crushing, especially among benthicdemersal taxa. Here, in order to elucidate the causal relationship between these changes, we present preliminary results of a dual database documenting population shifts of predator microfossils and invertebrate macrofossils, in a sedimentary and stratigraphic context.



Speaker

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#### The Permian-Triassic macroevolutionary history of Echinoids

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The Permian–Triassic bottleneck has long been thought to have drastically altered the course of echinoid (sea urchin) evolution. Previous hypotheses postulated that the entire echinoid stem group, which were abundant and morphologically diverse in the Palaeozoic, went extinct as a result of the end-Permian mass extinction. However, recent fossil finds of stem group echinoids from the middle Triassic of Germany and China are revising the scenario for the extinction of echinoids during the end-Permian extinction. We herein present results using phylogenetic analyses of stem group and crown group echinoids from the Late Palaeozoic and Early Mesozoic to document a revised macroevolutionary history of echinoids during the end-Permian mass extinction. By including both stem group and crown group echinoids in our analyses, including new and recently described species from the Early and Middle Triassic, we show that stem group echinoid did survive into the early Triassic, and thus were not limited in their occurrence to the Palaeozoic Era. We propose that stem group echinoids exhibited the Lazarus effect during the latest Permian and Early Triassic, implying mass rarity, restricted distribution, low diversity or all of these conditions in the post-Paleozoic stem group. Crown group echinoids, however, were comparatively diverse in the Early Triassic. The crown group and stem group echinoids thus overlap over 20 million years in their stratigraphic ranges, and the initial post-Palaeozoic diversification of the crown group echinoids accompanied the decline of the echinoid stem group.



Speaker

## Impact of the Grande Coupure event (Eocene-Oligocene transition) on European rhinocerotoids: rates of speciation and extinction as an explanation of diversification patterns?

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Extant rhinoceroses (five species) are some of the most endangered species on Earth. Yet, Rhinocerotidae were some of the most diversified large mammals after the Eocene, especially in Europe, where they are now completely extinct. They are also the only vestiges of the superfamily Rhinocerotoidea, which included diverse taxa such as the emblematic *Paraceratherium* (Hyracodontidae) and the peculiar Amynodontidae.

Rhinocerotoids notably appear in Western Europe only after a faunal turnover termed the Grande Coupure event, which is mainly explained by the closing of the Turgai Strait, leading to a connection between Europe and Asia. This connection is considered to be responsible for the migration of Asian Rhinocerotoids in Western Europe, leading to the extinction of endemic Perissodactyls such as paleotheres. However, in detail, little is known about this event and its impact on perissodactyla, one of the prevailing groups of large mammals during this period.

Here, we investigate the impact of this crisis through new phylogenetic hypotheses of two families: Rhinocerotidae and Amynodontidae. These new phylogenies allow to study the diversification and extinction rates of these clades. We expect to observe a peak of speciation and/or extinction rate near the Grande Coupure event (around 34 Ma). This peak was previously observed in a recent study based on a very large scale molecular supertree of mammals, calibrated in time by 30 fossil species. The rates of speciation and extinction were estimated by birth-death-shift models.

The method that we use here to estimate speciation and extinction rates deeply focuses on the contrary on extinct species, and in particular on their fossil record (not only last and first appearances), instead of divergence times. Because extant species are clearly under-represented within Rhinocerotoidea (only 5 species), morphological characters are preferred over DNA data, which prevents the use of divergence time or fossil calibration. Therefore fossil occurrences are here very helpful for the estimation of speciation and extinction rates. These rates will be discussed in the light of the Grande Coupure event, as well as the Oligocene-Miocene transition for example, and compared between two families: Rhinocerotidae and Amynodontidae. This will help to the understanding of these faunal changes among perissodactyla. Rates could also later be compared to those estimated by other methods, such as the Fossilized-Birth-Death process.



**S5 // Ora** 

<sup>&</sup>lt;sup>\*</sup> Speaker

### Assessment of morphological richness in morphospace: a case study for analysis of disparity in ammonoids

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A new method to assess amount of the morphospace occupation, or morphological richness, is introduced herein. It is based on multi-dimensional kernel density estimation of measurement data in a morphospace. The abundance of each species is taken into account, and the landscape of the probability density is depicted on the morphospace for each sample. Apparent morphological richness is estimated by an extent of the Bayesian highest posterior density region of the probability density. In order to remove sampling intensity biases, randomized subsampling of data is designed based on the sampling incompleteness of the subsample. The sampling incompleteness is assessed using a morphological rarefaction curve which depicts the relationship between the expected apparent morphological richness and the sample size. The slope at a point on the rarefaction curve represents the sampling incompleteness at the corresponding sample size. Subsampling is stopped when the final slope of the rarefaction curve falls below a given value, and the apparent morphological richness of the subsample in this case represents a standardized index of the morphological richness. This approach is closely related to the Alroy's shareholder quorum subsampling rather than classical rarefaction. The present method was applied to the analysis of change in morphological disparity of ammonoids. The Raup's parameters were estimated from the figures of ammonoids published in the literature. Data were collected from more than 6000 species registered in the Paleobiology Database (PDBD) ranging in age from the Devonian to the Cretaceous. The abundance of each species was estimated by the collection-based occurrence data deposited in the PDBD. Measurement data were transformed to remove skewness from the data and subsequently were standardized so that the mean and variance are zero and one. The standardized morphological richness was computed for each chronological bin. The standardized taxonomic richness was also estimated for the utilized data set for each bin using the shareholder quorum sampling method. The comparison between taxonomic richness and morphological richness in ammonoids reveals the following: morphological richness relative to taxonomic richness was generally high from the Lower Devonian to Guadalupian; but suddenly dropped in the Lopingian and remained at low levels until the Upper Triassic; and it had remained low throughout the Jurassic and Cretaceous.



<sup>&</sup>lt;sup>°</sup> Speaker

## Preliminary results of a morphometric analysis of Permo-Triassic ammonoid suture lines: morphogenetic and phylogenetic implications during a diversity bottleneck

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The end-Permian mass extinction was the most severe extinction in the history of life, wiping out more than 90% of marine species. Only one order of ammonoids survived it on a long term: Ceratitida. These are widely used for the construction of biochronological time scales, and as such play an essential role in our understanding of the biotic crisis and the subsequent rediversification. Their phylogeny, and thus systematics and taxonomy, is however still relatively poorly resolved. Many previous hypotheses are mostly based on their suture line morphology with a purely descriptive, typological method, mostly without considering the asymmetry and the ontogenetic and intraspecific variation. For example, some authors differentiated Proptychitidae from Gyronitidae exclusively by the presence of an auxiliary lobe in the suture line. Recent collecting and analyses of large populations showed that within some species, this trait is actually highly variable and tends to be absent in evolute variants. Additionally, some specimens have an auxiliary lobe only on one side, making their classification in previously established schemes impossible. In contrast, some details of the suture line such as the size and position of the indentations in the lobes were previously most often disregarded but proved to be stable within assemblages and rather easily traceable between different species. Here we quantify suture line morphology using a morphometric method (Fourier transforms) on a large dataset of Changhsingian (late Permian) to Smithian (Early Triassic) ammonoids. This method is used for the first time on such a long time interval. It allows a better understanding of the intraspecific variability, covariation with whorl section shape, ontogeny and taxonomic and phylogenetic significance of suture lines. In turns, combined with a stratophenetic approach, it allows the establishment of a new phylogenetic scheme for Permo-Triassic ammonoids, supported by quantitative rather than descriptive data. Obtaining such a well-established phylogeny is fundamental for the understanding of the response of ammonoids to this mass extinction and of their following recovery.



<sup>\*</sup> Speaker

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#### Extinction selectivity of corals during the Paleocene-Eocene Thermal Maximum

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The Paleocene-Eocene Thermal Maximum (PETM) is a well-known carbon cycle perturbation event associated with a rise in atmospheric pCO2 and sea surface temperature, increases in weathering and turbidity and potential surface ocean acidification. Coral reefs are particularly sensitive to these disturbances and previous analyses suggest a lack of coral reefs in the fossil record during the late Paleocene and early Eocene. However, in spite of this loss of habitat, corals do not appear to experience extinction during this period; in fact their generic- and species- level diversity increases. Studying corals during the PETM therefore provides unique insight into how these keystone organisms respond to environmental stress over long periods of time. Coral taxa vary in many aspects of their ecology: coloniality, feeding and reproductive strategies, habitat preference, and behavioral flexibility (among others). The aim of this study is to identify whether ecologic selection (based on physiology, behavior, habitat, etc.) plays a role in the survival of corals across the PETM. Many of the coral genera and species from this time are extant, allowing reasonable paleobiological assumptions of their ecology from modern coral relatives. Origination and extinction rates of corals during the late Paleocene and early Eocene are calculated and statistical analyses are used to identify traits common amongst coral taxa that were able to survive and/or diversify during the PETM. Multivariate models are used to highlight whether there are correlations between these ecological traits and coral taxa extinction or survival. We show that corals with certain traits (coloniality, flexibility of zooxanthellate symbiosis, high morphological integration, hermaphroditic brooding, living at high latitudes and in mixed carbonate-clastic settings) are more likely to survive the PETM. These findings have important implications for modern coral ecology and can help us to understand how corals may respond to future changes in climate.

**S5 // Ora** 

Speaker

#### The palaeobiodiversity of the Azores Archipelago (NE Atlantic): from the Early Pliocene to the Recent

#### Sérgio Ávila \*

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Santa Maria Island is the oldest and southeasternmost island in the Azores. This island is remarkably rich in exposed marine fossiliferous sediments of Pliocene-Quaternary age. The marine fossils of Santa Maria Island are known since the 16th century. Recent studies herein documented, based on a multidisciplinary approach by an international team of researchers, increased our knowledge on the palaeobiodiversity of the Azores. As a result, several papers covering a wide range of topics were published, e.g., the evolution of marine organisms in oceanic islands, systematics, palaeoecology, palaeobiogeography, geology, geochemistry, sedimentology, ichnology, conservation and sustainable touristic management, educational purposes, geoconservation and historical reviews. Our revised list of species reports 185 taxa from the early Pliocene outcrops of Santa Maria and 126 taxa from the Pleistocene (Last Interglacial). During this talk, a pictorial summary will be done, displaying the most important fossils of the studied marine groups.

Speaker

### Survival of vertebrates after the Cretaceous– Paleogene mass extinction event: did body-size matter?

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The Cretaceous–Paleogene (K–Pg) mass extinction event is associated with rapid restructuring of terrestrial ecosystems as a result of the Chicxulub asteroid impact event. A common hypothesis for explaining the observed extinction selectivity at the K–Pg is that large body-sized groups, such as non-avian dinosaurs, would be more sensitive to ecosystem devastation due to smaller population sizes compared to other smaller animals, such as mammals. These faunal changes are well documented thanks to the fossiliferous terrestrial deposits of the Hell Creek (HC) and Fort Union (FU) formations in Southwestern North Dakota.

We present new results from a systematic screenwashing of the first  $\_3$  meters of the FU Formation at PRTM site V02017. Excavation was stratigraphically controlled at a centimeter scale and each individual rock unit, identified by lithology and/or color, was individually processed through a 380 µm screen using a new method based on water agitation through bubbling by injected compressed air in a water tank. A total of 2,742 vertebrate fossil remains (fish, salamanders, frogs, turtles, crocodilians, champsosaurs, lizards, and mammals) were recovered from 5,162 kg of screen-washed material, across 20 distinct lithological units. Each specimen's long and short axis was measured to build a size-spectrum database. Vertical evolution of depositional environments at V02017 show a dark, massive mudstone sequence (Units 1 though 6) interpreted as a ponding event, followed by more energetic deposits of siltstone and sandstone (Unit 7 through 20) interpreted as fluvial and overbank deposits. The K–Pg boundary was identified at ~50 cm above the HC/FU formation contact using palynology.

Results show that despite unit 16 being the only unit producing visible fossils on the outcrop, all other units produced fossils when screen-washed, with the exception of unit 1 (lignite) and unit 7 and 8 (coarse sandstone, high energy). The vast majority of fossils recovered from the screenwashing are very small (1 % < 0.5 mm; 18 % < 1 mm; 40 % < 1.5 mm; 55 % < 2 mm long axis), emphasizing the importance of using the 380  $\mu$ m screen. Fossils from the basal lacustrine mudstone sequence show a broader size range spectrum than the overlying fluvial siltstone and sandstones. While the immediate recovery fauna is represented by small body-sized vertebrates, large fossils from unit 16 include three large (> 50 cm diameter) *Axestemys* turtles indicating widespread post-impact freshwater aquatic environments favored opportunists with broad tolerances and rapid reproductive potential.



<sup>&</sup>lt;sup>°</sup> Speaker

## Paleoecological analysis of benthic recovery after the late Permian mass extinction event in eastern Lombardy, Italy

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The late Permian mass extinction was the most severe biotic crisis of the Phanerozoic, with associated environmental changes that included the expansion of hypoxic and anoxic conditions in shallow shelf settings. It has been hypothesized that wave-aeration promoted oxygen transport to the seafloor providing a 'habitable zone' in the shallowest marine environments that allowed the survival and rapid recovery of benthic invertebrates during the Early Triassic. We test this hypothesis by studying the rock and fossil records of the Early Triassic Servino Formation, Italy. We also provide the first bulk carbonate d13C isotope curve, and present new occurrence data of stratigraphically important fossils, to improve the stratigraphic framework of the Servino Formation. The low-diversity fossil assemblages of the Servino Formation have similar compositions to other western Paleotethyan localities. Facies analysis demonstrates that benthic invertebrates were restricted to wave-aerated settings, supporting the proposed 'habitable zone' hypothesis. However, there is no evidence for rapid recovery in the 'habitable zone' prior to the Spathian, which may indicate additional environmental stresses. In the lower Spathian Myophoria Beds Member, an increase in taxonomic and functional richness, the appearance of stenohaline, erect taxa, a significant turnover and increased heterogeneity in the composition of benthic assemblages indicate significant benthic recovery, which is attributed to reduced environmental stress.



Speaker

# The advent of Neogastropoda according to the fossil record

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Since their emergence in the Palaeozoic times gastropods occupy an important place in the marine ecosystems. Changes in their abundance and taxonomic diversity reflect therefore the general trends in evolution of ecosystems. Emergence of carnivorous Neogastropoda and their rapid and extremely successful adaptive radiation was a significant part of the reorganizing benthic fauna in Mesozoic times known as the Mesozoic Marine Revolution. Nevertheless, in spite of implementing new research methodsespecially SEM examination of larval and juvenile shells- the origin of Neogastropoda remains elusive. The fossil record shows that the rapid radiation of neogastropods took place in the early Late Cretaceous and in the late Late Cretaceous (Campanian-Maastrichtian) all but one major neogastropod groups were already present, while the pre-radiation record is uncertain. The oldest published record of juvenile neogastropod attributed to Muricoidea comes from the Valanginian of Poland (early Early Cretaceous). However, there are also two families of extinct Mesozoic gastropods, which may form stem and/or sister groups of Neogastropoda. Pseudotritoniidae (=Maturifusidae) with genera Pseudotritonium and Maturifusus are known already from the Late Triassic and are characterised by fusiform shells commonly with clear anterior channel, weakly expressed posterior channel and multispiral larval shell similar in gross morphology to protoconchs of cerithioids. First occurrence of this family is known from Carnian reefs of the Cassian Formation in northern Italy. Coincidentally Cassian Formation is also known to yield several traces of drilling predation with the highest rate in the Triassic times. Purpurinidae with the genera Purpurina, Khetella, and Cretadmete appeared in the Jurassic boreal/subboreal seas and are characterised by fusiform shells with anterior channel and multispiral, smooth protoconchs or, in case of some Early Cretaceous forms with cancellate ornamentation. The latter forms are reminiscent of Tonnoidea and may actually be ancestral to the latter group.



Speaker

# The K–PG boundary: geological events, marine acidification and collapse of primary producers

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The severity of extinctions among pelagic calcifying species compared to non-calcareous taxa (~50% siliceous diatoms, Macleod et al. 1997) or non-calcifying phytoplankton suggests that a massive acidification of the oceans occurred at the K-Pg boundary (Keller, 2014; Tyrrell et al. 2015). This study presents the respective influence of the Chicxulub asteroid and Deccan traps using a coupled climatecarbon numerical (GEOCLIM) in which a biodiversity model is implemented, species being sensitive to abiotic factors (temperature, pH, calcite saturation state). Key points addressed in this study include a quantification of environmental changes provided i) by the Chicxulub asteroid, ii) by a pulse-like degassing of over a 250 kyr-long period combining CO<sub>2</sub> and SO<sub>2</sub> emissions (Deccan traps emplacement), iii) their respective impacts on the marine biomass and biodiversity, and iv) highlights the amplifying response to an initial perturbation caused by the inorganic and organic carbon cycles. Based on a standard scenario combing the Deccan traps emplacement with the Chicxulub impact our model simulates a global warming reaching 3.5 °C due to the rise of atmospheric CO<sub>2</sub> (+450ppmv) only interrupted by intense and brief cooling events due to S-aerosols derived from SO<sub>2</sub> emissions. In addition to climate changes, the pH of the surface ocean decreases by 0.2 units, from 8.0 to 7.8 while deep ocean pH drops by 0.4 pH units (from 7.8 to 7.4). Without requiring any additional perturbations, these environmental disturbances lead to decrease dramatically the biomass of calcifying species and their biodiversity by about 80%, while biodiversity of non-calcifying species are reduced by about 60%.



S5 // Poster

Speaker

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### Palynological succession across the terrestrial Triassic – Jurassic boundary in the Junggar Basin, NW China

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The terrestrial Triassic-Jurassic boundary is well documented in the Junggar Basin, NW China. An indepth comprehensive study of flora, palynology and carbon isotope was carried out to understand the response of terrestrial ecosystem to the fifth mass extinction event at the end of Triassic.

The palynological succession is divided to four zones, which are briefly introduced in ascending sort as following:

1. Triassic zone is characterized by the occurrence of some Triassic-diagnostic taxa, such as *Canalizonospora, Lycopodiacidites minus, L. rudis, Aratrisporites, Taeniaesporites, Protohaploxypinus, Striatopodocarpites* and *Hamiapollenites*.

2. Transitional zone shows coexistence of the Triassic-diagnostic taxa mentioned above and some elements which are common in Jurassic, e.g., *Cyathidites, Neoraistrickia, Densoisporites, Lycopodiumsporites* and *Perinopollenites*.

3. Spore peaks zone is comprised of several peaks of contents of spores. The most abundant spores are: *Densoisporites scanicus, Densosporites crassus* and *Cyathidites* sp.. The maximum content may rise to 80%, significantly greater than those from underlying and above beds.

4. Jurassic zone lacks Triassic indicator and comprises some Jurassic indicator, including *Cibotiumspora, Undulatisporites, Contignisporites, Cerebropollenites, Classopollis* and *Callialasporites*.

The spore peaks zone is greatly narrower than transitional zone, and is usually missed out or neglected. Therefore, from a long-term point of view, the giving away of Triassic zone to Jurassic zone is gradual.

Nevertheless, similar spore peaks have been also found at the Triassic-Jurassic boundary of Newark basin, America, St. Audrie's Bay, SW UK, and Hochalplgraben, Austria. Moreover, it is no exception accompany by negative shifts of carbon isotope in these sites and the Juggar basin. Hence, we believe that a rapid and strong change of ecological environment had happened at the terrestrial T/J boundary in the Juggar basin, China.



Speaker

### Palynoflora at the K-T boundary in Amur (Heilongjiang) River region, Russia

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Upper Cretaceous and Paleocene deposits are widely distributed in the Zeya-Bureya Basin located in the higher part of the stream of the Amur (Chinese name - Heilongjiang) River. Based on study of fossil spores and pollen obtained from these beds, seven successive palynological assemblages (the Santonian-Danian) were revealed and correlated with age-equivalent assemblages of eastern Asia and western North America. We studied fossil spores and pollen from K-T boundary beds both on left (Russian) and right (Chinese) banks of the Amur River. The late Maastrichtian assemblage in Zeya-Bureya Basin was revealed from lower part of stratotype section of the Tsagayan Formation near Belaya Mount on left bank of the Amur River and from lower part of the Furao Formation. This palynological assemblage is dominated by Taxodiaceae and Ulmaceae. *Laevigatosporites* predominates among spores. The angiosperms are rather diverse. They are represented by Betulaceae, Salicaceae, Juglandaceae, Myricaceae, Myrtaceae, Loranthaceae, and Proteaceae. The diversity of the triprojectate pollen is rather high.

The early Danian assemblage was revealed from the upper part of the stratotype section of the Tsagayan Formation near Belaya Mount, lower part of section of Arkhara-Boguchan coal mine on left bank of Amur River and upper part of Furao Fm and Wuyun Fm on the right bank of the Amur River. This palynological assemblage is characterized by *Triatriopollenites confusus*, *T. plicoides*, *Quercoidites minor* and by predominance of Ulmaceae. This assemblage is dominated by ferns and gymnosperms. Among gymnosperms, the Taxodiaceae, Cupressaceae, and Pinaceae predominate. The angiosperms are locally abundant. The Juglandaceae and Fagaceae predominate. The plants produced the triprojectate pollen suffered a sharp decrease in amount.

The changes of taxonomical composition of palynoflora in Zeya-Bureya Basin were gradual at the K-T boundary. Only plants produced the triprojectate pollen suffered the most significant extinction. The palynospectra sampled just above the K-T boundary comprise an increased number of fern spores (so-called fern peak).



<sup>&</sup>lt;sup>\*</sup> Speaker

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# Morphology and osteohistology of new Early Triassic ichthyosauriform fossils from the Russian Far East

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During the Early Triassic, ecosystems were recovering from the end-Permian mass extinction (EPME). Ichthyosauriformes is one major clade of reptiles that colonized the ocean after EPME. Their oldest fossil records are found from Spathian substage (Olenekian, late Early Triassic) strata in China. Here, we report on two reptilian remains from the early Spathian *Neocolumbites insignis* ammonoid zone of South Primorye in the Russian Far East. The first specimen comprises two centra, a neural arch, and the proximal portion of a rib. The vertebrae exhibit a combination of morphological characters that is often reported for Ichthyopterygia. The height-to-length ratio of the centra is around 1, suggesting that the current specimen represents a basal ichthyosauriform. The other specimen is the large isolated femur of an ichthyosauriform. The *N. insignis* zone correlates to the *Procolumbites* zone of southern China, from which the oldest known ichthyopterygian reptile, *Chaohusaurus*, (was) derived. The minimum estimated body length based on the femur specimen is around 5 m, so approximately five times larger than an adult *Chaohusaurus*, and twice as large as the basal ichthypterygian *Utatsusaurus*. This size variation among the earliest ichthyosauriforms might illustrate an explosive diversification in size and ecology in this clade immediately after the EPME. Both vertebrae and femur exhibit an extremely cancellous structure, suggesting that this animal had a high degree of aquatic adaptation despite their short-time evolution in the ocean.

<sup>&</sup>lt;sup>'</sup> Speaker

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## Upper Permian bivalves from the Bellerophon Formation (Dolomites, northern Italy) and biodiversity drop related to the end-Permian mass extinction

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The Upper Permian Bellerophon Fm of the Dolomites (northern Italy) is an overall transgressive succession, which consists of a lower sulphate-evaporite unit, deposited in a barren basin, and an upper shallow-marine carbonate unit, deposited along a low-energy ramp setting. This succession, mainly Changhsingian in age, contains rich fossil assemblages, which have been studied since 19th century. Although some taxonomical groups have been object of recent revisions (e.g. nautiloids and brachiopods), the stratigraphic and systematic knowledge of the bivalves is not supported by recent studies, which are necessary to evaluate the survival rates after the end-Permian mass extinction.

In this study, the biodiversity and stratigraphic distribution of the bivalves occurring in the Bellerophon Fm of western Dolomites is investigated with the aim to define the extinction patterns through the comparison with the taxa occurring in the Lower Triassic Werfen Fm. The specimens have been collected bed-by-bed from the Val Gardena and Val Badia sections aligned along a south west-north east transect, which records a slight deepening of the marine environment.

Systematic assessment, based both on newly collected material and on historical collections analysis, has revealed 18 genera with 24 species. The studied material has been ascribed to the genera: Bakevellia, Chaenomya, Cosmetodon, Dyasmya, Edmonia, Eumorphotis, Palaeolima,?Palaeonelio, Permophorus, Pernopecten, ?Pleurophorella, ?Promytilus, Schizodus, Solemya (Janeia), ?Tambanella, Towapteria, Volsellina and Aviculopectinidae gen. nov.

Infaunal suspension and detritus feeders suffered extinction rates higher than the semi-infaunal and epifaunal suspension feeders. The studied bivalves show a richness drop at genus level lower than other marine taxa. This higher survivorship can be related to the adaptation of the Upper Permian bivalves towards very shallow and stressed (e.g., high temperatures and low oxygen levels) marine environments, which characterized the western Dolomites during the deposition of the Bellerophon Fm.



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# Paleocommunity dynamics in the western Tethys following the end-Triassic extinction

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The marine biosphere is currently experiencing one of the greatest biodiversity losses in Earth's history, driven in part by rising concentrations of anthropogenic carbon dioxide in the atmosphere, warming, and ocean acidification. The end-Triassic mass extinction is thought to have been propelled by similar disruptions, thus examining how Mesozoic ecosystems responded and recovered could provide crucial insights into the potential range and magnitude of changes in community structure in the near future.

Communities following the end-Triassic extinction are thought to have undergone significant changes in the relative abundance and composition of organisms within various trophic levels and modes of life. Here we compare models of fossil food webs from two western Tethys shallow marine communities before (Anisian) and after (Bathonian) the end-Triassic extinction to identify differences in ecosystem structure and functioning. Differences in food web topology and general network structure were used to evaluate differences between ecosystem structure and complexity. Richness was higher in the Bathonian paleocommunity relative to the Anisian and had more guilds and links (interactions). This increase in diversity, functional richness, and intensity of biotic interactions in the Bathonian suggests that new evolutionary innovations and biotic expansions observed during the Mesozoic may have triggered significant ecosystem restructuring and major changes in energy transfer pathways such as patterns of interactions and the distribution of taxa among trophic levels. These structural changes in the marine communities may be due to rapid diversification and increasing predation pressure and suggest greater complexity in the Bathonian.

The examination of ancient food webs presents an opportunity to determine whether trophic organization has changed and to understand the evolutionary mechanisms that have contributed to historical patterns of community structure. Given the current biodiversity crisis, understanding how and why ecological changes occur is vital for effective resource management.



S5 // Poster

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# Diverse hemipteran insects from the Upper Triassic of Argentina

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In the last years, plenty of insects have been found in the Triassic continental sediments of Argentina, which is the main palaeoentomological region of South America and one of the most important from southern Gondwana, together with South Africa and Australia. The Potrerillos Formation yields abundant and diverse Carnian entomofauna with more than 300 well-preserved fossil insects within 27 species that include hemipterans, beetles, blattids, odonatans, mecopterans, orthopterans, plecopterans, grylloblattids, dipterans, hymenopterans and miomopterans. Hemiptera is the most abundant and diverse order with more than 100 specimens collected (more than 40% of the total insect fossils) and 9 species have been described so far. The abundance of hemipterans may be due to the robust and flexible nature of the forewings, increasing their preservational potential. The hemipterans come from two environmentally different sections at the south of Cerro Cacheuta, southern extreme of the Precordillera range, Mendoza Province: Puesto Miguez and Quebrada del Durazno. The hemipterans are represented by Scytinopteridae, Eoscarterellidae, Dysmorphoptilidae, Chiliocyclidae, and Protopsyllidiidae and they are preserved as impressions of complete sclerotized forewings (common element), membranous hindwing, forewing+clavus, clavus (less frequent), and complete insects (rare). Like their modern counterparts, these fossil hemipterans are phytophagous and occur in association with typical and diverse Dicroidium Flora which occupied middle to high palaeolatitudes (S30°) in the extratropical belt of Gondwana, where temperate/warm and humid conditions prevailed under maximal development of the Late Triassic megamonsoonal climates. Richness and diversity of insect assemblage is remarkably high in the fluviodeltaic sequence of the Quebrada del Durazno, whereas in the fluvial-environments of the Puesto Miguez is low. Thus, the difference of the insect content could be mainly related to different palaeoenvironmental setting, however, could also be as a response of collection/taphonomic biases. The hemipteran records in Potrerillos Formation provide evidence that Hemiptera was a key component in Late Triassic continental ecosystems. Its abundance suggests that they were probably the most dominant primary consumers within the palaeoentomofaunistic communities developed in this part of south-western Gondwana.



<sup>&</sup>lt;sup>°</sup> Speaker

#### Permian rugose corals in the world

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Permian rugose corals underwent the evolutionary episodes of assemblage changeover, biogeographical separation, and extinction, which are closely related to the geological events during this time. Two coral realms were recognized: the Tethyan Realm and the Cordillera-ArcticUralian Realm, which are characterized by the families Kepingpphyllidae and Waagenophyllidae during the Cisuralian, Waagenophyllidae in the Guadalupian, and the subfamily Waagenophyllinae in the Lopingian; and the families Durhaminidae and Kleopatrinidae during the Cisuralian and almost disappearance of colonial and dissepimented solitary rugose corals from the Guadalupian to the Lopingian, respectively. The development of these coral realms is controlled by the geographical barrier resulting from the Pangea formation. According to the changes in the compostion and diversity of the Permian rugose corals, a changeover event might occur at the end-Sakmarian and is characterized by the mixed Pennsylvanian and Permian faunas to typical Permian faunas, probably related to a global regression. In addition, three extinction events are present at the end-Kungurian, the end-Guadalupian, and the end-Permian, which are respectively triggered by the northward movement of the Pangea, the Emeishan volcano eruption and subsequently global regression, and the global climate warming induced by the Siberian Trap eruption.

Speaker

## A new species of *Lobatannularia* recorded from the Middle Triassic of China with its paleoclimate and paleoenvironmental implications

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A new species Lobatannularia linjiaensis sp. nov., under the order Equisetales and represented by 9 specimens in the collection, was recently recorded from the Middle Triassic Linjia Formation at the Qiandianzi of Benxi in Liaoning, Northeast China. The new species is characterized by leaf-whorls very small, generally composed of 20 leaves forming two marked lobes; leaves linear to oblanceolate, united for 2/3 to 3/4 of their length; midvein clear. The upper epidermis and the lower upper epidermis are different. Stomata are amphistomatic. The upper ordinary epidermal cells along the veins rectangular, about 90-100  $\mu$ m in length, and 35-50  $\mu$ m in width, while those between the veins polygonal, attaining 70-80  $\mu$ m in length, and 50-60 $\mu$ m in width. Stomatal apparatus haplocheilic, monocyclic, with stomata aligned in longitudinal rows parallel to the midvein. Subsidiary cells polygonal, attaining 50-80  $\mu$ m in length, and 40-80  $\mu$ m in width. The lower ordinary epidermal cells along the veins also rectangular, about 30-50  $\mu$ m in length, and 15-30  $\mu$ m in width, while those between the veins polygonal, attaining 45-55  $\mu$ m in length, and 25-45  $\mu$ m in width. Stomatal apparatus haplocheilic, monocyclic, with stomata aligned in longitudinal rows parallel to the midvein. Subsidiary cells polygonal, attaining 30-80  $\mu$ m in length, and 30-40  $\mu$ m in width. Since Kawasaki erected the genus Lobatannularia in 1927, at least 17 species have been described on the basis of the morphology of the megafossils. Most of them are collected from the Permian, seldom collected in Triassic. As a relict Cathaysian element, the new species not only enlarges our knowledge in taxonomy and epidermal structure of Lobatannularia as well as the Middle Triassic stratigraphy of North East China, but also provides an opportunity to understand how to change the diversity of typical elements of Cathaysian flora from Permian to Triassic in the background of the Mass Extinction and Recovery from Late Permian to Middle Triassic.



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## S6 – Biominerals through time: evolution, taphonomy and traces in the geological record

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# Skeletal calcifying matrices in metazoans: evolution and diagenesis

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In metazoans, calcium carbonate skeletons comprise a small amount of organic macromolecules, mostly proteins and polysaccharides, which constitute the calcifying matrix. Because these macromolecules are occluded in the skeletons, they can be preserved over a long period. From a historical perspective, the calcifying matrix has been extensively studied in extant skeletonized metazoans, successively *via* classical biochemical approaches, *via* molecular biology and in recent years, *via* high-throughput screening techniques (transcriptomics, proteomics). These latter approaches have made possible the rapid identification of large sets of mineralassociated proteins, which constitute the 'skeletal repertoire' or the 'calcifying secretome' of several skeleton-building metazoans ranging from sponges to echinoderms. The profusion of molecular data allows comparisons between the skeletal repertoires of several metazoans, shedding light on some peculiar macro-evolutionary mechanisms that may have affected skeletal matrix components: surprisingly, some protein components of the matrix, in particular the ones that are lineage-specific, suggest a rapid evolution while other skeletal protein components that are identified in very distant lineages suggest either an ancient recruitment of the corresponding function (and subsequent massive loss in intermediate lineages) or independent co-options for calcification. These aspects will be discussed in my talk, in particular through key examples such as the evolution of molluscan nacre.

Since molecular information acquired on skeletal tissues of extant metazoans is large enough to constitute a reference dataset, high-throughput approaches may also be applied to ancient skeletons (archaeological samples or true fossils), in order to revisit diagenetic processes, *i.e.*, how proteins of the matrix degrade during fossilization. These aspects, which deal with an emerging discipline in Earth Sciences, paleoproteomics, will be discussed too.



Speaker

## Why Carboniferous Gigantoproductini grew so large and thick shelled? A possible explanation for gigantism in fossils

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The species of *Gigantoproductus* are well-known giants within the Brachiopoda. This is a dilemma as living brachiopods have a low-energy lifestyle. Why these taxa have acquired such a large size (over 30 cm in width) and thick shells (over 1 cm) has never been investigated in detail. Even if brachiopod metabolic rates were higher during the Paleozoic than today, and they experienced a general directional trend towards larger size, the massive size reached by species of *Gigantoproductus* is still surprising. This increase in size during the Paleozoic has been related to increases in oxygen availability, high primary productivity, or high predation pressure; nevertheless, gigantism in fossil and Recent plants and animals remains poorly understood. By examining their diet, we are seeking to understand the mechanisms that enabled these low- metabolism brachiopod species to become giants. Were they suspension feeders, similar to all other brachiopods or did endosymbiosis provide a lifestyle that allowed them to have higher metabolic rates and become giants? We suggest that the answer to this persistent conundrum may be located in the identification of the biosignatures of symbionts through combined analyses of the carbon-and nitrogen-isotopic compositions of the occluded organic matrix within the columnar layer of the pristine fossil shells. This consists of remarkably long and a few hundreds of micrometers wide substructured columnar units.



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# Atomic scale transformation of bone in controlled diagenesis experiments

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The chemical and isotopic compositions of biogenic apatite, i.e. the mineral component of vertebrate's bones and teeth, are important geochemical markers, used to infer past climates, dietary preferences and habitat. However, they can suffer modifications during the fossilisation process. Fossil apatites generally exhibit an overall decrease in carbonate content, enrichment in fluorine, incorporation of trace elements and an increase in crystallinity. Detailed understanding of these transformations induced by fossilisation should help assess the preservation of geochemical records in apatites and validate their use as palaeoenvironmental proxies. In this contribution, we investigate the crystal-chemical transformations and more specifically the environment of carbonate groups and fluoridation mechanisms, in modern bioapatites altered under controlled conditions. Modern bone wafers and powders were soaked in aqueous solutions of neutral to alkaline pH for periods up to 3 weeks at various temperatures (20-70°C), with each experiment duplicated in fluorine-free and in 10-2 M NaF solutions. Their transformation was monitored through chemical (F, Ca, P) and isotopic ( $\delta^{13}$ C,  $\delta^{18}$ O<sub>c</sub>,  $\delta^{18}$ O<sub>o</sub>) analysis, and probed using vibrational (Attenuated Total Reflectance - Fourier transform infrared, Raman) and solid-state Nuclear Magnetic Resonance (NMR) spectroscopies. Systematic incorporation of fluoride in the channel sites is observed in all samples altered with a sodium fluoride solution. In contrast, the formation of secondary carbonated fluorapatite, associated with the presence of a clumped ( $CO_3^{2-}$ ,  $F^-$ ) defect in the structural B site, depends on the type of buffer solution used for the alteration experiment. Fluoride ions thus act as a probe revealing dissolution- recrystallization pathways in bone. Based on the experimental results, we discuss the fluoride incorporation mechanisms and their implications for palaeo-environmental reconstructions based on fossil apatites.



Speaker

#### Can fossil traces of intracellular carbonates formed by cyanobacteria be found in the geological record?

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Cyanobacteria have played an important role in mediating the formation of carbonate sedimentary deposits such as stromatolites for billions of years. It has been usually suggested that this occurs through extracellular carbonatogenesis, a process associated with CO2-concentrating mechanisms operated by the cells. Yet, this dogma of a systematically non-controlled and extracellular biomineralization of CaCO3 by cyanobacteria has been recently challenged by the discovery of several cyanobacterial species forming amorphous calcium carbonates (ACC) intracellularly (Couradeau *et al.* 2012; Ragon *et al.* 2014). This ACC formation capability is a synapomorphy that might have appeared several hundred million years, possibly 2-2.5 Gyrs ago (Benzerara *et al.* 2014). Moreover, one of the species forming intracellular ACC was recently shown to be the present-day closest cultured relative of primary plastids (Ponce-Toledo *et al.* 2017). This suggests that this capability to form intracellular ACC may have been present in early plastids, reinforcing the importance to test the preservability of such intracellular carbonates in the geological record.

Here, we will present the results of several approaches addressing the issue of finding and identifying traces of intracellular biomineralization by cyanobacteria in the geological record. In a first approach, we tested the preservation potential of ACC inclusions upon cell death by heating cells at varying temperatures. In a second approach, we determined partition coefficient of Ca, Sr and Ba between the extracellular solutions and the intracellular ACC. We showed that some cyanobacterial species tend to accumulate Sr and Ba preferentially, creating chemical heterogeneities (Cam *et al.* 2016; Blondeau *et al.* 2018). Finally, we measured isotope fractionations of Sr, Ba and Ca in order to determine if isotopic compositions may be used to trace the involvement of cyanobacteria forming intracellular ACC (Coutaud *et al.* in prep).

Benzerara K. et al (2014) Intracellular Ca-carbonate biomineralization is widespread in cyanobacteria. Proc. Natl. Acad. Sci. USA 111, 10933-10938.

Blondeau M et al (2018) Impact of the cyanobacterium Gloeomargarita lithophora on the geochemical cycles of Sr and Ba. Chemical Geology, 483, 88-97.

Cam N et al (2016) Selective uptake of alkaline earth metals by cyanobacteria forming intracellular carbonates. Env Sci Technol, 50, 11654-11662.

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Couradeau E. et al (2012). An early-branching microbialite cyanobacterium forms intracellular carbonates. Science, 336, 459-462.

Ponce-Toledo RI et al (2017) An early-branching freshwater cyanobacterium at the origin of chloroplasts, Current Biology, 27, 1-6.

<sup>\*</sup> Speaker

IPC 5

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# Burial-induced biases in paleotemperature reconstructions from fossil biocarbonates

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Geochemical studies of biogenic calcite in the marine sediment record have contributed enormously to the understanding of Earth's climate evolution. In particular, the oxygen isotope compositions of fossil planktonic and benthic foraminifera tests are used as proxies for surface- and deepocean paleotemperatures, respectively. Interpreted at face value, these compositions indicate Eocene deep-ocean and high-latitude surface-ocean temperature in the range of 10- 15°C, and deep-ocean even warmer during the Cretaceous. However, we demonstrated that oxygen isotope re-equilibration through solid-state diffusion can create large errors in ocean paleo-environmental reconstructions, even under the close-to-ambient pressure and temperature conditions characterizing shallow sediment burial. We investigated this diffusion-controlled reequilibration process with experiments exposing foraminifera tests to elevated pressures and temperatures in isotopically heavy artificial seawater (H<sub>2</sub><sup>18</sup>O), followed by scanning electron microscopy and quantitative NanoSIMS imaging: oxygen-isotope compositions changed heterogeneously at submicrometer length scales without any observable modifications of the test ultrastructures. In parallel, numerical modelling of diffusion during burial showed that oxygen- isotope reequilibration of fossil foraminifera tests can cause significant overestimations of ocean paleotemperatures on a time scale of tens of millions of years under natural conditions. Our results suggest that the late Cretaceous and Paleogene deep-ocean and high-latitude surface- ocean temperatures were significantly lower than is generally accepted, thereby resolving the early Eocene equable climate paradox.



Speaker

### Preferential origin of calcitic cephalopod structures during calcite seas

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Based on the aragonite composition of extant cephalopods and exceptionally preserved fossil cephalopods going back to the Paleozoic, it is commonly assumed that externally shelled cephalopods had an aragonitic shell wall. We present evidence that at least two lineages of orthoconic nautiloids in the Silurian and Devonian calcite seas were originally bimineralic, which developed convergently with gastropods and bivalves. We quantitatively analyzed the timing of the evolutionary origin of these and other reliably dated carbonatic cephalopods structures in relationship with calcite or aragonite seas as inferred from the rock record or Ca/Mg-models. Our log odd ratio tests support a preferential origin of calcitic structures during calcite seas, particularly in the Paleozoic. This further corroborates the hypothesis that seawater chemistry at the time a particular mineralized structure was first acquired within a lineage was particularly crucial for its mineralogy – even in pelagic organisms like cephalopods. These finds also highlight the need to verify the shell composition of exceptionally-preserved mollusks more comprehensively – even at sites where aragonite has typically been dissolved or replaced.



S6 // Oral

Speaker

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## Alteration in the hierarchical architecture of the calcite layers of fossil rhynchonelliform brachiopods - example of the Cenomanian Sellithyris cenomanensis

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Attempts to understand the hierarchical organization of the inners layers of the calcite shell during the process of biomineralization has been made on selected modern rhynchonelliform brachiopods, using the Atomic force microscopy (AFM) to complement the observations from the Scanning electron microscopy (SEM) to reach a nanometric level.

Drawing our attention to biomaterials from the fossil record (cf. *Sellithyris cenomanensis* from the upper Middle Cenomanian) allow to reveal alterations occurring in the shell components (organic and inorganic fractions) in the course of taphonomy.

Using the same techniques, SEM and AFM, reveal partial loss of primary information and emphasized the disorganization p. pr. of the former results from the observations illustrating the welldefined hierarchical process. Among alterations observed are: silicic result due to bacterial activity or, more often, the disappearance of part of the organic matrices (more estimated is that of the peri-crystalline organic matrix), in such situation, boundaries of the calcite fibrous elements of the secondary layer are p. pr. or completely merged and the nanoparticles or elementary granules previously highlighted are amalgamate progressively leading to shape secondary blocky calcite. Like that, the hierarchical organization observed at the sub-micrometric level can be rubbed out completely or partly with as results of diagenesis the presence or recrystallized calcite or silicic nodules in the shell thickness.



Speaker

#### Muscles and muscle scars in fossil malacostracan crustaceans

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Exceptionally preserved fossils yield critical information about the soft-part anatomy and the evolution of organisms through time. We compiled the first global dataset of exceptionally preserved muscles in malacostracan crustaceans including many new occurrences. Muscles are found predominantly in Mesozoic Konservat-lagerstätten, where specimens with muscles preserved experienced early diagenetic mineralization through phosphatization. The majority of specimens with muscles preserved are compressed, but rare three-dimensionally preserved individuals allow for more detailed studies of muscles. One example are specimens of a fossil ghost shrimp from the mid-Holocene of Panama showing exquisitely preserved strings of muscle fibers attached to the shell interior, resembling the muscle arrangement of modern representatives. Other fossil malacostracans, including the oldest fossil shrimp, also show muscle patterns similar to modern taxa. We hypothesize that this conservatism may be related to the confined space within the decapod shell in conjunction with the relatively stable body plan of several clades. Unlike the uncommon presence of muscle fibers and bundles, muscle scars are more common with a substantial percentage of papers containing evidence of muscle scars, albeit not always recognized. Muscle scars are common from the Late Jurassic onwards, and are found primarily in Brachyura and Axiidea. They do not suffer from a Konservat-lagerstätten-effect. We suggest that much more research on fossil muscles and muscle scars can be done, and that targeting rocks with well-preserved specimens should yield an additional wealth of information on the soft-part anatomy and internal functioning of muscles in crustaceans through time.



S6 // Oral

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# Homologous shell microstructures in Cambrian hyoliths and molluscs

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The origin and key transitions in the evolution of major lophotrocozoan clades (annelids, molluscs, "lophophorates") have advanced remarkably in the light of numerous discoveries of crucial stem-group fossils in Cambrian and new molecular phylogenetic investigations. Hyoliths are extinct palaeozoic lophotrocozoans with a calcareous exoskeleton that consist of up to three parts: a conical conch, a lid-like operculum, and some taxa may produce an additional pair of lateral curved spines or 'helens' of uncertain function.

Although hyoliths have been known for two centuries, their precise position within lophotrocozoans is still a subject of debate. Traditionally, they have been regarded as an extinct Class within the Mollusca, mainly based on the presence of crossed lamellar microstructure in some younger taxa, or a type of aragonitic microstructural fabric limited to Mollusca. Alternatively, they have been assigned to sipunculan worms or their own phylum. The core of the debate is whether the evolutionary derived crossed lamellar microstructure is homologous or convergent between hyoliths and molluscs, which has been hard to assess. Recently, a significant discovery from Cambrian Burgess Shale-type Lagerstätten revealed that the hyolithid hyolith *Haplophrentis* had evolved a lophophore, a characteristic tentacular filter-feeding apparatus confined to 'lophophorates' (modern brachiopods, phoronids, probably bryozoans and some fossil taxa: tommotiids and tentaculitoids). Consequently, hyoliths would be regarded as derived total group lophophorates, closely related to brachiopods.

Here, we provide broad microstructure data of hyolith conchs and opercula from the Cambrian Xinji Formation of North China, including two hyolithids and four orthothecids as well as unidentified opercula. We show that most hyolith conchs contain a distinct aragonitic lamellar layer that is composed of foliated aragonite except in the *Protomicrocornus* with a unique crossed foliated lamellar microstructure. Some opercula also express foliated aragonite microstructure. All these aragonitic lamellar microstructural fabrics are widely distributed among Cambrian primitive molluscs, but not in "lophophorates", and thus strongly support very close relationships and similar biomineralizing mechanism between them. We propose that hyoliths and molluscs inherit their mineralized skeletons from a very similar non-mineralized common ancestor, but phylogenetically divergent from each other very early during the Cambrian explosion.



<sup>&</sup>lt;sup>°</sup> Speaker

#### Assessing the fossil evidence for the 'biomineralization toolkit'

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The Ediacaran-Cambrian transition was a dramatic event in the history of animal life on Earth, yet the processes underlying it are poorly understood not least the role of biomineralization in driving this fundamental evolutionary episode. One explanation for this event, based on observations on the developmental and molecular biology of modern organisms, is that all animals inherited a common 'toolkit' of genes, independently co-opted to similar tasks, including building skeletons. This initially imprecise 'toolkit' was subsequently honed by the acquisition of more and more complex gene regulatory networks. Here I review the evidence for the biomineralization toolkit from the fossil record and provide direct evidence to test the importance of the genetic basis of the skeleton in the origin of the animals. I have compiled together our current knowledge of the distribution of different mineral systems, skeletal tissues and their organic frameworks in both a phylogenetic and temporal context, across animals. This supports multiple, independent, origins of biomineralized skeletons through the Ediacaran- Cambrian transition, with a repeated pattern of initial mineralization of a pre-existing organic skeleton with loose control, utilizing common ancestral genes and regulatory networks, followed by increased control via the accumulation of lineage specific secretory mechanisms, and skeletal fabrics. Suggesting a key role for the biomineralization toolkit in the origin and assembly of animal body plans.

Speaker

# Exceptional preservation of organic matrix and shell microstructure in a Cretaceous *Pinna* fossil

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PhotoEmission Electron spectroMicroscopy (PEEM) was used to observe exceptional preservation in organic matrix components and shell microstructure in a 66 Ma bivalve shell. PEEM is a novel method to detect, *in situ*, preservation quality, and provides a noninvasive, non destructive, and spatially explicit map of prismatic and nacre tablet microstructure, mineralogy, crystal orientations, and organic compounds. This technique was used to compare Cretaceous and modern bivalves in the genus *Pinna;* results demonstrate that the 66 Ma shell: (1) preserves original aragonite and calcite crystals in nacre and prismatic layers, respectively, (2) maintains nearly identical nacre tablet and prism microstructure and crystal orientations, and (3) preserves components of interprismatic proteins. Remarkably, interprismatic proteins are preserved with intact peptide bonds and show an abundance of glycine, an important amino acid for protein folding and mechanical flexibility. Preservation of glycine chains in a 66 Ma shell supports the exceptional quality of protein preservation documented here. This quality of preservation may not be uncommon among fossil shells with nacre, reflecting the entrapment and subsequent preservation of the molecular matrix by shell minerals. Thus, PEEM analysis provides new insight into the taphonomic processes influencing shell and molecular fossils, including the effects of molluscan diagenesis, physiology, biomineralization, and evolution.



Speaker

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# Hypercalcification in Permian circumpolar seas: Not what you expect

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Ever since Robert Etheridge, Jr. and W. S. Dun carried out the first in-depth study of the iconic Gondwanan bivalve Eurydesma, its massively thickened shells have seemed anomalous for circumpolar conditions: "The umbonal region of the valves in Eurydesma is of extraordinary thickness, and it is interesting to note, as Mr. Charles Hedley has pointed out, that all recent bivalves comparable in valve thickness occur in tropical waters" (Etheridge and Dun, 1910, p. ix). In addition, several species of eastern Australian bivalves (including Eurydesma), some gastropods, and many brachiopods are relative giants for Paleozoic seas, even at lower latitudes. *Eurydesma* grew to a maximum size of 15 cm, with umbones up to 6 cm thick. The unrelated but co-occurring anomalodesmatan bivalve Myonia corrugata achieved similar sizes and valve thicknesses. One specimen of the inoceramiform pteriomorph, Aphanaia de Koninck, is 41.5 cm in length, and 18 species of bivalves, gastropods and brachiopods were larger than 10 cm in size. Modern polar bivalves tend to be small and thin-shelled (e.g., www.arcodiv.org/seabottom/Bivalves.html). If body size is expressed as LOG(SQRT(L\*H), 2), where L and H are shell lengths and heights, then 23 eastern Australian Permian shells (bivalves, brachiopods, gastropods) exceeded a log2 size of 6, compared with only a single extant species of Antarctic bivalve. Likewise, modern polar taxa are drab in color, whereas at least three of the Australasian Permian species, including *E. cordatum*, were brightly colored. To the degree that temperature is responsible for the differences in size and color, these observations suggest that the early Permian high southern latitudes were not as cold as they are today. Indeed, the Miocene may represent a reasonable analog, as some Miocene Antarctic bivalves are strikingly similar to common Permian ones (e.g., the Miocene scallop Australochlamys and erssoni and the similar Permian one, Deltopecten mitchelli). These conundrums are explored using paleoenvironmental information obtained from sedimentology and sclerochronology. Of added interest is the observation that cold conditions may promote individual and taxonomic longevity.



Speaker

# Shell microstructural evolution of protobranch bivalves; with a focus on the nacre-loss event

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Shell microstructure can be potentially preserved in fossils, and therefore is considered as a clue for inference on evolution and phylogeny of the past life. Presenter have evaluated stability and reliability of shell microstructures as characters for protobranch higher systematics by reconstructing a molecular phylogeny of the group. Mapping of shell-microstructure characters on the phylogenetic tree confirmed that the composition of shell microstructures is conservative at the superfamily level and can be divided into three major groups; RESP (radially elongate simple prismatic structure) group, homogeneous group and nacreous group. However, this trend is not necessarily applied to that of fossil protobranchs. Previous studies shown that the ancestral taxon of each protobranch superfamily possessed primitive nacreous structure (i.e. nacreous group). Here I report shell microstructures of fossil protobranchs mainly from the Late Mesozoic. I revealed that several taxa changed their shell microstructural composition from homogeneous to nacreous group around the Jurassic-Cretaceous boundary. This drastic morphological change seems to be related to a high production cost of the nacreous structure. Also, shell microstructural composition classified into non-nacreous group can be regarded as homoplasy in Recent protobranchs.



#### Protein fossilization in vertebrate hard tissues

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Vertebrate hard tissues consist of mineral crystallites within a proteinaceous scaffold which normally degrades postmortem. However, decalcification of Mesozoic hard tissues preserved in oxidative settings released brownish stained extracellular matrix, cells, blood vessels, and nerve projections. Raman Microspectroscopy showed that these fossil soft tissues are a product of diagenetic transformation to Advanced Glycoxidation and Lipoxidation End Products generated via oxidative crosslinking of proteinaceous scaffolds. Reducing environments, in contrast, lacked soft tissue preservation. Comparison of fossil soft tissues with modern and experimentally matured samples reveals how proteinaceous tissues undergo diagenesis and explains biases in their preservation in the rock record. This provides a target, focused on oxidative depositional environments, for finding cellular-to-subcellular soft tissue morphology in fossils and validates its use in phylogenetic and other evolutionary studies.

Speaker

## The effect of ocean acidification on the shell microstructure in the recent brachiopod *Magellania venosa* (Dixon, 1789): lessons for the past and future

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Due to the threat of ocean acidification in the last century and in the immediate future, more research has focused on the study of the potential impact of low pH conditions on calcifying organisms. Brachiopods are considered one of the best archive to record how calcite-shelled animals respond to ocean acidification. However, little is known about the relationship between their biomineralization processes and environmental conditions specifically different pH conditions. Here, we cultured six adult individuals of Magellania venosa (Dixon, 1789) from Chile under different pH conditions (7.35 to 8.15 ±0.05) over different time intervals. These were subjected to detailed microstructural investigation by using SEM. Different features of the microstructure of the brachiopod shell were measured, such as size and shape of the basic structural unit (fibres), thickness of the primary layer and density of punctae, and finally a comprehensive dataset was created for morphometric evaluation. Normal ontogenetic variation of fibre morphometry is generally consistent with the trend already observed in that the fibres become wider and flatter with age. In addition, along the growth direction the primary layer progressively thickens and the density of punctae increases. The objective was to ascertain whether the general microstructural patterns will be maintained by specimens cultured in different pH conditions. We observed the following morphometric variations under low pH condition, the produced fibres were smaller, the primary layer increased rapidly in thickness and the density of punctae was higher. Furthermore, our results suggest that M. venosa produced shells with more organic-rich matrix when settled in low pH conditions for an interval of about one year.



S6 // Oral

Speaker

## Sclerite microstructure and aragonite biomineralization in problematic Cambrian chancelloriids

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Sclerite microstructure of the extinct Cambrian animal chancelloriids is detailed based on well preserved, abundant collections of isolated sclerites from lower Cambrian (Stages 2 to 3) rocks of South Australia and North China. More than 1500 specimens including 5 genera and 8 species are analyzed. They are Chancelloria cf. eros Walcott, 1920, C. racemifundis Bengtson in Bengtson et al. 1990, C. sp., Archiasterella hirundo Bengtson in Bengtson et al. 1990, Ar. pentactina Sdzuy, 1969, Allonnia tripodophora Doré and Reid, 1965, Eremactis mawsoni Bengtson and Conway Morris in Bengtson et al. 1990 and Paracambrothyra guttaia gen. nov. sp. nov. The sclerite microstructure consists of two distinctive layers: an outer organic layer and an inner aragonitic fibrous layer. The organic layer is relatively thin ( $^{2} \mu$ m) and continuous over the entire sclerite, ornamented by tubercles, fine granules and ridges. The aragonitic layer is composed of remarkably preserved bundles of longitudinal, tangential and irregular aragonite fibres. Biomineralization of sclerites is proposed to occur as a two-step process. Firstly, the organic layer forms as a template delimiting an enclosed compartment. Secondly, in the compartment, calcium and bicarbonate ions and organic matter released by calcifying epithelium precipitate on the inner surfaces of the organic layer, arranged in specific patterns of orientation. Therefore, chancelloriids are suggested to be able to control the arrangement and orientation of aragonite minerals in a relatively higher level, indicating that this animal was well adapted to exploit aragonitic saturated marine conditions.



S6 // Ora

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# The carrier shell *Xenophora crispa* (König, 1825): microstructure and agglutination process

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The genus Xenophora comprises species of marine gastropods, known from the Cretaceous and still living today, which have the ability to form their shells agglutinating various kinds of objects, from other shells to bio/lithoclasts. The shell microstructure of species of Xenophora and the mechanisms of agglutination, as well as its functional meaning, are still poorly known; also, no data is available on the nature of the cement used to agglutinate fragments to the shell. Species of Xenophora show different agglutination potentials, from species lacking attachments to others completely covered by agglutinated materials, as the case of the Mediterranean Xenophora crispa (König, 1825). To better understand the mechanisms leading to agglutination of shells and bio/lithoclasts in X. crispa, we analyzed shell sections of fossil (early Pleistocene, Arda and Stirone Rivers, Italy) and Recent specimens (Mediterranean Sea, Spain) at the Scanning Electron Microscope (SEM) and powders, collected from different parts of the shell, at X-Ray Diffraction (XRD). SEM analyses showed the occurrence of a thin prismatic layer ( $^{5}\mu$ m) below the agglutinated fragments, whereas the bulk of the shell is made of a typical aragonitic microstructure (crossed lamellar fabric), with the exception of prismatic/spherulitic layers present in the thickest part of the shell (columella and peripheral edge). XRD analyses indicated aragonite as the major mineral component of the shell; however, calcite, usually uncommon in gastropod shells, sporadically occurred in both fossil and recent specimens, mainly in the thickest parts of the shell.

Our results point out that: 1) shells and bio/lithoclast attachment in *X. crispa* occur on a prismatic microstructure, which thus represents a highly functional fabric for attachment (e.g., muscle attachment in bivalves), 2) *X. crispa* shells are composed by both aragonite and calcite, but the latter occurring only in traces and probably limited to thin prismatic/spherulitic layers in the columella and peripheral edge.



S6 // Poster

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## A combined proteomic and transcriptomic analysis of shell matrix proteins in the pond snail *Lymnaea* stagnalis

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Acquisition of hard tissues is one of the most important events in biological evolution. Hard tissues such as bones, teeth and shells are often preserved as fossils. Molluscan shells show a continuous and abundant fossil record throughout the Phanerozoic, providing us with an excellent target of investigation on the origin and evolutionary history of hard tissues. To this end, understanding of the molecular mechanisms of biomineralization is essential. Shell matrix proteins (SMPs) have been believed important in molluscan shell formation, and their amino acid sequences have been characterized for a number of species. However, we still do not know the in vivo functions of those SMPs nor detailed mechanisms of shell biomineralization. In order to setup a platform for a systematic functional analysis of shell matrix proteins, we performed a combined transcriptome and proteomic analysis for the shell matrix proteins of the pond snail Lymnaea stagnalis. We identified a total of 207 proteins from the shell matrix of L. stagnalis. A total of 165 of them showed similarities to known proteins. We searched for conserved domains in those proteins to infer their possible functions, and classified the proteins into six categories: extracellular protein, enzyme, cation-interaction, polysaccharide interaction, proteinase inhibitor, and others. In order to identify SMPs which may promote shell precipitation, we compared the expression levels of the genes encoding SMPs between the right side and the left side of the mantle tissue. Underlying assumption is that the genes for functional shell matrix proteins promoting shell precipitation would be more strongly expressed in the right hand side of the mantle in the dextral snail, while there would be no such differential expression pattern for the proteins which were accidentally trapped within the shells. A total of 17 proteins indicated statistically higher gene expression in the right side than in the left, and 11 proteins out of them, including calcium-binding proteins such as C-type lectin and EF- hand proteins, turned out to be mantle specific proteins. Further characterization of proteins identified in this study, especially those inferred to be promoting shell precipitation, would help us better understand the mechanisms and evolution of hard tissue formation.



<sup>&</sup>lt;sup>°</sup> Speaker

## Which is the optimal shell-part to sample for geochemical analyses? Trace element and stable isotope compositions of five recent brachiopod species

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Recent and fossil brachiopod shells are excellent biomineral archives for (palaeo)climatic and (palaeo)environmental reconstructions. They precipitate their calcite shells in isotopic equilibrium with ambient seawater mostly with no or limited vital effect; also, their low-magnesium calcite shell is generally quite resistant to diagenetic alteration. Despite this, only few studies address the issue of identifying the best part of the shell to sample for geochemical analyses. Here, we investigated the link between shell ontogeny, microstructure and geochemical signatures recorded in different parts of the shell. To reach this aim, we analyzed the elemental (Mg, Sr, Na) and stable isotope ( $\delta^{18}$ O,  $\delta^{13}$ C) compositions of five recent brachiopod species (Magellania venosa, Liothyrella uva, Aerothyris kerguelensis, Liothyrella neozelanica and Gryphus vitreus). Specimens were collected from different latitudes and different environments (Chile, Antarctica, Indian Ocean, New Zealand and Italy) and had different shell layer successions (two-layer and three-layer shells). Besides the different trends shown by the two- and three-layer shells in their trace element and stable isotope records, a similar patterns in the ventral and dorsal valves of these two groups was observed, suggesting that both valves can be used for geochemical and isotope analyses. The present investigation of recent brachiopods indicates that the best region to sample is the middle part of the midsection of the shell, and that the primary layer, the posterior and anterior parts as well as the outermost part of the secondary layer should be avoided. Also, in fossil shells, the outermost and innermost layers should be discarded as they may be the first parts to be diagenetically altered. Finally, among all proxies,  $\delta$ 180 values seem to be least affected by different microstructures and shell ontogeny, thus, making it a most powerful and important recorder of (palaeo)climatic and (palaeo)environmental changes.



Speaker

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#### Reading the age of an ammonite from its jaws

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Assessing ammonite lifespan is a challenge for macroevolutionary studies. Age estimations based on growth features and chemical compositions of the low Sr aragonitic shell have been attempted on few exceptionally preserved specimens, but remain questionable. Compared to the aragonitic shell, the calcitic covering of the lower jaw (called aptychus) is poorly investigated although in Recent cephalopods, chitinous beaks are considered relevant proxies for the age of the animal. Sclerochonological studies carried out on recent and fossil mollusks have provided a methodological framework that could be applied to ammonite lower jaws. Following these studies, well-preserved aptychi from the Campanian of Alabama (Mooreville Chalk Formation) were investigated to assess its potential for sclerochonological studies. Microstructural observations indicate that fine growth features (up to  $2\mu$ m thick) are well preserved and that a part of paleobiological information is preserved. We analyzed growth lines spacing-out, microstructure, and variation of the chemical composition along the growth direction ( $\partial^{18}$ O and trace elements) in order to provide the first age estimations for ammonites obtained from non-shell structures.

### **S7- Bird in the past environments**

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#### Ontogenetic change in the giant bird Gastornis

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The genus *Gastornis* includes large terrestrial herbivorous birds known from Europe, North America and China during the Paleocene and the Eocene. The Thanetian Mont-de-Berru site in north-eastern France has yielded remains referred to two species, *G. parisiensis* and *G. russelli*. While many specimens of *G. parisiensis* are known, including post-cranial as well as cranial material, the species *G. russelli* Martin, 1992 is based on a single left tarsometatarsus (the holotype), and a referred fragmentary beak, both in the collections of the Paris Natural History Museum. Martin (1992) briefly described this beak and provided a drawing, in which the missing tip is reconstructed as forming a distinct hook, for which there is no factual evidence.

A new preparation and reexamination of this beak leads to a new interpretation. The specimen (R2583) corresponds to the fused premaxillae and maxillae showing a very large naris which is much larger and anteriorly placed than the naris observed on the known *Gastornis* beaks, in which it is clearly very small and posterodorsally located. This significant difference at first sight challenges the attribution of this beak to *Gastornis*. However, an examination of the skull bones of both juvenile and adult specimens of *Sylviornis neocaledoniae* shows that in this bird both the position and size of the naris changed during ontogeny, from a large and anterior naris in juveniles to a small and posterodorsal naris in the adults. Assuming that the same kind of allometric growth occurred in *Gastornis*, we interpret the beak R2583 as a juvenile, not an adult, specimen.

The attribution of this beak to a juvenile therefore challenges the referral of this specimen to the species *Gastornis russelli*. The holotype tarsometatarsus of *G. russelli* belonged to an adult, to judge from the complete fusion of its bony components. The beak is too large to consider it as a juvenile of *G. russelli*, but is consistent with *G. parisiensis*, the other *Gastornis* species known from the same site. Therefore, we suggest that specimen R2583 belongs to a juvenile of *G. parisiensis*. The type tarsometatarsus of *G. russelli* differs from that of *G. parisiensis* only in its smaller size. A revision is required to establish if *G. russelli* is a valid species or should be included in *G. parisiensis*, in which case the small size of the tarsometatarsus currently attributed to *G. russelli* would imply significant size variation or sexual dimorphism in *G. parisiensis*.



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## What is a long neck? The effects of scaling relationships between skeletal dimensions and body size in living and fossils birds

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Birds constitute a classic example of modern vertebrates with highly variable neck lengths ranging from short necks in songbirds to extremely long, serpentine necks in herons. Since this includes a wide array of small to very large species, this raises the question of how neck length relates to body size. Furthermore, neck length is not necessarily an indicator of the number of cervical vertebrae since a few elongated vertebrae may form an equally long neck as do many short vertebrae.

We sampled the skeletons of a diversity of bird species (including fossil taxa) and compiled quantitative data of body proportions. We tested the length of the cervical vertebrae in relation to body size in order to reveal if the avian neck is subject to allometry. Next, we analyzed the relationship between vertebral length and the length of other body parts such as pelvic limb bones. This enables to reveal trends in proportion between the neck and other parts of the skeleton.

Our results show that neck length shows an isometric scaling in relation to body size in the majority of taxa. Pelagic specialists and birds that forage below or around the water surface tend to have a relatively long neck, whereas many birds that forage on the ground have a relatively short neck. The length of the central vertebra shows moderate negative allometry in relation to femur length and tibiotarsus length. It scales with strong negative allometry in relation to tarsometatarsus length. The vertebral length decreases relatively as tarsometatarsus length increases.

Variation in neck length appears to be related to functional differentiation in terms of foraging. The neck in birds serves many demanding tasks and is of particular importance for feeding. The association between vertebral length and tarsometatarsus length may support a reported trade-off between quantitative design (i.e., relative volumes of bone) and maximum rates of avian posthatching growth. Since the tarsometatarsus bone is one of the longest and fastest growing in the body of birds, this pattern of development may limit the relative growth of the vertebrae resulting in shorter vertebrae.

The present study, as the first large scale analysis of the scaling patterns of the cervical vertebral column in living and extinct birds, provides new information on the function and development of the avian neck. Next, we aim to include non-avian theropods in order to reveal if the growth trade-off occurred after the theropod-bird transition.



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## How large was the Pleistocene 'giant ostrich' of China? Mass estimates for *Struthio anderssoni* and their implications

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Large ostrich eggs have been known from Quaternary deposits (especially Pleistocene loess) in northern China since the 1890s. The egg-based taxon Struthio anderssoni was erected for them by Lowe in 1931, and a few skeletal remains have also been referred to it. The large sizes of these eggs and bones, exceeding those of the living Struthio camelus, have often been emphasized, and the term ?giant ostrich' has frequently been used. However, no quantitative estimates have so far been provided for Struthio anderssoni. We have estimated the mass of that bird using two distinct approaches. A mass estimate of 270 kg, which is considerably above the maximum weight for S. camelus (mass range: 100-156 kg for males, 90-110 kg for females), has been obtained from the minimum circumference of an incomplete femur from the Late Pleistocene of the Upper Cave at Zhoukoudian, using Campbell and Marcus's method. Using Hoyt's equations based on the transverse and longitudinal diameters of the shell, we have estimated the volume and mass of eggs from various Pleistocene localities in northern China, on the basis of measurements available in the literature. Volumes range from 1542.9 cm<sup>3</sup> to 2399.9 cm<sup>3</sup> and masses from 1.7 kg to 2.6 kg. This again is more than the values for wild S. camelus (volume: 1082 - 1425 cm<sup>3</sup>; mass: 1.1 - 1.5 kg). Dyke and Kaiser's equations linking egg mass to femur length and body mass of the female bird indicate a femur length range of 304.8 - 371.9 mm (mean: 338.35; range in S. camelus: 249 - 330 mm, mean: 289.5) and a mass range of 176.9 ?350.8 kg (mean: 263.85 kg). A S. anderssoni femur from the Upper Cave had a length of 355 mm, within the estimated range, and the above-mentioned femur-based mass estimate of 270 kg is also within the range of masses estimated from egg measurements. Our results show that S. anderssoni was indeed a giant ostrich, with a mass that could be more than 150 % that of S. camelus, and within the range of other very large extinct birds, such as the giant moa, Dinornis robustus. Since S. anderssoni lived in northern China during cold periods of the Pleistocene, its large size could be interpreted as an adaptation to a cold climate, following Bergmann's rule. However, very large ostriches from the Miocene (e.g. Ukraine) and the Early Pleistocene (e.g. Hungary, Georgia, Tanzania) did not live under cold climates, which suggests that other reasons must be sought for the very large size of *S. anderssoni*.



S7 // Ora

Speaker

### An exceptional bone bed of Enantiornithine birds in the late Cretaceous of Brazil

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Despite abundant discoveries of Mesozoic birds in the last few decades, knowledge of their evolution during the last 20 million years of the Cretaceous remains scant. However, this time interval is vital for understanding the rise of modern birds as well as the pattern of avifaunal turnover during the Cretaceous-Paleogene transition. We report on a remarkably rich site (William's Quarry; discovered in 2004 by WN) contained in the Upper Cretaceous Adamantina Formation (Bauru Group) of southeastern Brazil (Presidente Prudente, western São Paulo State). Excavations at this site have produced hundreds of partially articulated and isolated remains of small to medium-sized enantiornithine birds concentrated in a very small area (approximately 6 m<sup>2</sup>) of red-pink fluvial sandstones and claystones. The remains include numerous postcranial elements as well as many skull portions (isolated rostra, mandibles, and crania) preserved in three-dimensions and representing at least three taxa. This site constitutes the most abundant avian Mesozoic locality in the Americas and the richest site of Late Cretaceous age in the world. As such, this site provides key information for contrasting hypotheses of avian diversification during the K-Pg transition and the earliest divergences of modern birds. Together with other Late Cretaceous localities from Gondwana, the information revealed at this site indicates a clear abundance of enantiornithine bird species during the ~80-70 mya interval. Such a record is difficult to reconcile with hypotheses arguing that modern (neornithine) birds originated in the southern hemisphere during the Late Cretaceous.



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## Life history of the basal pygostylian, Confuciusornis sanctus

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Hundreds of specimens of Confuciusornis sanctus have been recovered from the Early Cretaceous Jehol Group of Northeastern China. Here we investigate the bone microstructure of 22 long bones sampled from ten different sized Confuciusornis specimens to assess life history patterns of this basal pygostylian bird. Analysis of the bone histology of the various bones revealed differences in the histological structure of their bone walls. By comparing the histology of the Confuciusornis bones to ontogenetic changes in modern bird bone histology we were able to separate the Confuciusornis material into different age classes representing, juvenile, subadult and adult sizes. When the histology "age-assigned" specimens were plotted on a graph obtained from "morphometric" analyses, the histology correlated with different sized birds. Our findings suggest that Confuciusornis took several years to attain skeletal maturity and that the "clusters" reflect ontogeny i.e. "age cohorts" rather than sexual dimorphism or interspecific differences. This supports the earlier hypothesis that like Archaeopteryx and several other basal birds, Confuciusornis experienced a slower growth rate than most extant birds. Considering recent identification of a reproductive female Confuciusornis specimen (without tail feathers), we have been able to ascertain when sexual dimorphic traits became evident in the species. Our findings suggest that males exhibited long tail feathers early in ontogeny, suggesting that these early birds were able to reproduce well before they were adult body size.



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# Selection on avian ecology structured the dawn of the crown bird radiation

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The fossil record and recent molecular phylogenies support an extraordinary early Cenozoic radiation of crown birds (Neornithes) following the Cretaceous-Paleogene (K-Pg) mass extinction. However, questions remain regarding the mechanisms underlying the survival of the deepest lineages within crown birds across the K–Pg boundary, particularly since this global catastrophe eliminated even the closest stem group relatives of Neornithes. Here, ancestral state reconstructions of neornithine ecology reveal a strong bias toward taxa exhibiting predominantly non-arboreal lifestyles across the K-Pg, with multiple convergent transitions toward predominantly arboreal ecologies later in the Paleocene and Eocene. By contrast, ecomorphological inferences indicate predominantly arboreal lifestyles among enantiornithines, the most diverse and widespread Mesozoic avialans. Global paleobotanical and palynological data show that the K-Pg Chicxulub impact triggered widespread destruction of forests. We suggest that ecological filtering due to the temporary loss of significant plant cover across the K-Pg boundary selected against any flying dinosaurs (Avialae) committed to arboreal ecologies, resulting in a predominantly non-arboreal postextinction neornithine avifauna composed of total-clade Palaeognathae, Galloanserae, and terrestrial totalclade Neoaves that rapidly diversified into the broad range of avian ecologies familiar today. The explanation proposed here provides a unifying hypothesis for the K-Pg-associated mass extinction of arboreal stem birds, as well as for the post-K-Pg radiation of arboreal crown birds. It also provides a baseline hypothesis to be further refined pending the discovery of additional neornithine fossils from the Latest Cretaceous and earliest Paleogene.



Speaker

## Taphonomic implications of a thanatocoenosis dominated by avifauna exhibiting opisthotonic postures, around lethal CO<sub>2</sub>-emanating thermal springs in the Danakil Depression, Afar, Ethiopia

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The Danakil Depression (Afar, Ethiopia) lies 120 m below sea level, and consists of a windswept saline flat, floored by a 2 km layer of salt, in which rise low mounds with active volcanoes, including Erta 'Ale. The area is a hot desert, but sheetfloods from the highlands course over the saltflats, percolating down fractures into the subsurface, where they become heated by the high heat flow. The resulting thermal waters well up as multicolored salt thermal springs at Dallol, Black Lake, and Gaet'ale.

At least 10 dead birds were seen around the circular spring-fed lake at Gaet'ale. All of them were well-preserved, having effectively been pickled by the hypersaline brine of the lake. The largest bird was a Black-headed Heron (*Ardea melanocephala*), which was partly covered in salt. The other birds, which were in various states of entombment by the surrounding salt, included the Eurasian Kestrel (*Falco tinnunculus*), Painted Snipe (*Rostratula benghalensis*), and possible ravens and swifts. Two dead birds have also been noted around the Black Water spring, while a dead Isabeline Wheatear (*Oenanthe isabellina*) has been recorded from Dallol. The dead birds around these thermal springs were most probably killed by CO<sub>2</sub> emanations, such as were observed coming out of the Dallol crater in 2011. Almost all the birds examined showed signs of opisthotonia or post- or perimortem convulsions. The Black-headed Heron displays classic opisthotonic posture, also known as "dead bird" or "dead dinosaur" posture, with a strongly recurved neck and head arched backwards through muscular contractions. The Painted Snipe lies with its long beak pointed upward and slightly backwards, and with one extended leg in an awkward, unnatural position, indicating possible perimortem convulsions. The Eurasian Kestrel, although with a short neck, displays extreme opisthotonia, with its head hyperextended right back, so that its beak points backwards.

This avifauna-dominated thanatocoenosis, involving several different species of birds, all displaying opisthotonia, is a potential key to solving riddles from the fossil record, where multispecies sudden-death assemblages have been recorded, showing similar opisthotonic postures and perimortal convulsions, related to the death throes of dying animals. Death by CO<sub>2</sub> poisoning around thermal springs can now be added to other postulated causes of death for such thanatocoenoses- such as droughts, lethal red algal blooms, poisonous waters, and flash floods.



<sup>&</sup>lt;sup>°</sup> Speaker

# New Zealand's *Platydyptes* old penguins with a new view: significance of the genus

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New Zealand is home to a magnificent record of fossil penguins (Sphenisciformes). Uniquely adapted to aquatic life, their dense, ballasting bones predispose penguins to fossilise. Platydyptes, first described by B.J. Marples in 1952, is one of the most crownward of the stem (basal) penguins and one of a few described Late Oligocene genera. This position within penguin history shows Platydyptes as a precursor for the "modern" or crown radiation of penguins, with importance for understanding functional morphology. Despite the potential value of the genus, the last published work on *Platydyptes* was by Simpson in 1971, on taxonomy but not including phylogeny or function. Platydyptes penguins are robust, adding to their preservation potential; while there is some variation in size, the three currently described species P. novaezealandiae, P. amiesi, and P. marplesi can be considered medium-sized ancient penguins (the smallest described species P. marplesi is closer in size to a king penguin, ~95cm height, than to a crested penguin, ~50-70cm height). A redescription of the genus is planned, to include new potentially diagnostic features from the P. novaezealandiae holotype, and the description of undescribed specimens from Hakataramea. For instance, a semi-articulated partial skeleton from the Otekaike Limestone of Hakataramea (OU 22804) varies from other Platydyptes. This fossil preserves the taxonomically diagnostic humerus as well as rarer elements such as the mandible, quadrate, a semi-complete sternum, and pelvis. While showing characteristics of *Platydyptes*, OU 22804 does not fall into the currently described species. Further ahead a phylogenetic study is also planned.



Speaker

#### Pygostyle formation in early birds

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The pygostyle, a compound element formed through fusion of the distal caudal vertebrae, is one of the most definitive characteristics of living birds but is absent in the most basal known taxon, the Late Jurassic Archaeopteryx whose elongate tail resembles that of its non-avian dinosaurian close relatives. In the Early Cretaceous, birds with bony tails even longer than that of Archaeopteryx co-exist with the basalmost pygostylians, birds whose abbreviated tails end in a pygostyle. With no obvious transition apparent from the fossil record, the evolution of this compound element has remained largely mysterious. The vast collections of Early Cretaceous birds from the Jehol deposits in northeastern China are dominated by subadult material and these fossils shed light on the formation and development of the pygostyle in individual lineages of early birds. Most informative are numerous specimens of young juvenile enantiornithines, which in particular show unusual allometric growth in the tail with this part of the skeleton being proportionately much longer in the youngest individuals. Osteohistological sampling and advanced scanning technologies applied to juvenile and subadult specimens further elucidates details of the formation of this element in individual lineages. The greater overall length of the pygostyle in the Confuciusornithiformes and Enantiornithes appears to correspond with a greater number of co-ossified vertebrae relative to the shorter pygostyles present in the Sapeornithiformes and Ornithuromorpha. Apparent differences in the number of caudal vertebrae forming the pygostyle in these clades may suggest multiple originations of this element or that the primitive pygostylian condition consisted of a pygostyle formed by at least twice the number of vertebrae observed in extant neornithines. As in living birds, the formation of the pygostyle is a post-hatching event but the time it takes for complete fusion to occur varies between basal lineages.



## Laser-Stimulated Fluorescence reveals preserved soft tissues which unravel the complexity of avian flight evolution

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Fossils of exceptionally preserved theropod dinosaurs have pushed back the origins of important anatomies related to avian flight. The unique anatomical configurations they possess indicate a highly diverse road to modern flight capabilities. Whilst less flight proficient lineages went extinct, rare evidence exists of unusual adaptive trends towards improved flight proficiency. For example, our work with Laser-Stimulated Fluorescence produced a quantitative body outline of the basal bird *Anchiornis*, from the extinct anchiornithid clade. This revealed a narrow, extended wing form with undifferentiated feathering. Additional data is therefore paramount to understanding the full range of early avian flight development.

Using Laser-Stimulated Fluorescence we discovered that the short-tailed early bird *Confuciusornis* (Pygostylia: Confuciusornithidae) had extensively muscled shoulders in contrast to reduced breast muscles. This evolved along the confuciusornithid lineage through incremental development of the deltopectoral crest of the humerus in the absence of a keeled sternum - opposite to the keel-dominated configuration of modern birds.

We provide the first direct soft tissue evidence of an alternative musculoskeletal framework among early pygostylian birds, which led to novel, improved flight proficiency. These findings indicate that the transition to more modern crown birds during the Cretaceous included the elimination of lineages that had differentially improved flight proficiency, suggesting that this process of elimination was more nuanced than previously supposed. Such parallelism evident here presents a valuable opportunity to further explore the role of parallel evolution in shaping the development of avian flight.



S7 // Ora

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## Multiple origins of powered flight among paravian theropod dinosaurs: constraints from new phylogenetic, aerodynamic and anatomical data

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The evolution of birds from paravian theropod dinosaurs is a classic evolutionary radiation. Unfortunately, there is a lack of consensus on the geneology of birds and their very closest relatives. This has made it difficult to understand the timing and sequence of evolutionary changes along the line of descent to modern birds, particularly those involved with flight.

We have addressed this issue through a larger, more resolved phylogeny produced by analysing a revised dataset using an automated pipeline of analysis tailored to large morphological datasets. The enhanced automation and newly developed techniques of this analytical pipeline should greatly increase access to more in-depth analyses using parsimony as a criterion for phylogenetic inference.

We corroborate the grouping of dromaeosaurids and troodontids (Deinonychosauria) as the sister group to birds. We also recover the basal 'Jianchang' paravians as the basalmost avialans (Anchiornithidae e.g. *Anchiornis*), instead of troodontids. Wing loading and specific lift (theoretical and *in vivo* based criteria devised to discern volant from flightless avians) were calculated for taxa with vanned feathers and interpreted in the context of the improved phylogeny. This provided upper and lower bounds for flapping-based locomotor evolution, especially powered flight. Our results show that theropod powered flight appears to be limited to paravians and originated multiple times. The dromaeosaurids *Microraptor* and *Rahonavis* are especially strong non-avialan candidates for this behaviour.

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#### A new caudipterid dinosaur from the Lower Cretaceous Jehol Group of China

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Caudipteridae is a primitive group of oviraptorsauria only found in the Early Cretaceous Jehol Group of western Liaoning, China. It is one of the first true feathered dinosaur that avian-like pennaceous remiges and rectrices present. Its discovery reduces both skeletal and soft tissue gap between small theropod dinosaurs and birds. Here we describe a new caudipterid species from the Lower Cretaceous Yixian Formation from Yixian County, Liaoning Province. This turkey-sized specimen is an adult individual based on fusion between neural arch and centrum on all preserved vertebrae. It is assigned to caudipteridae by a combination of following characters: relative short tail with few caudals; humerus about 50% of the femoral length; the metacarpal I shorter than half length of the metacarpal II; slightly concave proximal articular surface of manus phalanx I-1; proximal portion of metatarsal III compressed transversely. While it can be distinguished from known caudipterids Caudipteryx and Similicaudipteryx by small oval pleurocoel near the dorsal margin of the centrum, scapula shorter than the humerus, ulna subequal to humerus, relative small radiale angle, extremely short metacarpal I less than 40% length of metacarpal II. Phylogenetic analyses using both coelurosaurian and oviraptorosaurid matrix support the new species belong to caudipteridae. The new species exhibits a mosaic morphology. The features of its manus, such as slender digit III with full phalanges, ligament pit dorsally located, are more similar to other oviraptorosaurids rather than caudipteridae. We conclude that the manus of oviraptorosaurids show a complex evolution, different group has its own evolutionary trend. Its radiale gives new understanding of evolution of radiale angle along coelurosauria.



Speaker

## Soaring like a vulture in the Cretaceous: Sapeornis and the evolution of energy-saving aerial strategies in early birds

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Interpretations of the avian fossil record suggest that strategies to save cost of flight might have evolved by the Early Cretaceous, long before the origin of modern birds. In this study, we use a combination of computational modelling and morphofunctional analyses to infer the flight properties of the raven-sized, 125-million-years-old bird Sapeornis chaoyangensis. Specifically, lever theory as applied to the well-developed DPC of the humerus of this bird, and multivariate and computational models of modern neornithines, evidence that S. chaoyangensis would have had energetic limitations for prolonged flapping flights and suggest a flight behaviour comparable to that of modern soarers. Our results also indicate that the high-lift wings of S. chaoyangensis would have enabled this bird to soar in continental thermals. Aerodynamic modelling (slow gliding speeds with low lift-to-drag ratios and circling pattern during soaring) further evidences that S. chaoyangensis would have had an aerial behaviour similar to thermal soarers such as vultures and storks. Combined to known paleobiological evidences of herbivory and grasping feet, our results indicate that S. chaoyangensis was a thermal soarer with an ecology similar to that of living South American screamers. In summary, our results provide evidence documenting that thermal soaring, a strategy to reduce aerial costs observed in many medium-to-large modern birds, had evolved by at least 125 Ma among large early birds. This conclusion highlights once again the significant breadth of ecological, functional and behavioral diversity reached during the earliest avian evolutionary radiation of the Mesozoic.



Speaker

#### Bone fusions in manus and pelvis in the early evolution of birds in light of new discovery

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The skeleton of birds show remarkable modifications pertaining to powered flight. The most noticeable feature is bone fusion in the hand, feet and pelvis, which enhances the strength and rigidity of the body. However, the historical origin of avian bone fusions remains allusive. This is largely because of the lack of transitional fossils and developmental studies on modern birds. Recently, we reported one of the earliest avian records that has a fully fused alular-major metacarpals and pelvis from the 120 million years old horizon from the Jehol Biota, northeast China. We traced the degree of fusion in manus and pelvis across Paravian phylogeny, and demonstrate that these features evolved independently in non-avian theropods, Enantiornithes, and Ornithuromorpha. The fusions of these bones are rare in known non-avian theropods and Early Cretaceous birds, but are well established in Late Cretaceous and crown birds, revealing a complicated evolution trajectory not appreciated previously. We suggest that the developments of bone fusion were polymorphic close to the origin of birds, resulting in the varying degrees of fusion in Paraves. However, that development polymorphism appear to be fundamentally restricted along the line to modern birds by the Late Cretaceous, where all birds have a completely fused manus and pelvis, suggesting developmental plasticity. Alternatively, the degree of bone fusion in this primitive bird may have been induced by modifications in genes or developmental paths (e.g., Hox). Future studies and fossil discoveries are required to clarify these hypotheses and pinpoint the developmental pathways involving the bone fusions in early avian evolution through to their modern pattern.



Speaker

# New Ichthyornis specimens: shedding new light on a classic taxon

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The Late Cretaceous toothed bird *Ichthyornis dispar* was one of the first known Mesozoic avialans, and is recognized today as one of the closest relatives of crown birds among Mesozoic stem birds. As such, the skeletal morphology of *Ichthyornis* may be more representative of the ancestral condition of crown birds than that of any other known Mesozoic avialan, and its study has crucial implications for understanding the origins and early evolution of crown birds. Previous work on *Ichthyornis* has largely been based on limited fossil material discovered over a century ago.

Here we present high-resolution scans of new, exquisitely preserved three- dimensional specimens of *lchthyornis* from the Late Cretaceous of Kansas, focusing on the pectoral girdle and wing elements. The new specimens are more complete and in better condition than the classic material, and include some previously unrepresented elements, as well as better preserved examples of several bones. These include a complete, three-dimensionally preserved sternum, including robust caudolateral processes and relatively developed sternal incisures. The coracoid exhibits very large and recurved acrocoracoid and procoracoid processes, and the scapula preserves a robust, pointed and hook-shaped acromion process, differing from previously referred specimens. This last character is of particular interest, as it represents a previously described autapomorphy of *lchthyornis dispar*. Thus, the new material may represent a previously unknown species, or this putative autapomorphy may be more variable among *l. dispar* than previously appreciated. Wing bones, carpals and hand elements are well preserved as well, and include the first complete radiale known from *lchthyornis*.

Ongoing work on these and other new *Ichthyornis* specimens will shed new light on morphological evolution across the proximal-most portion of the stem-bird phylogenetic tree.



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#### Shining a light on nightbird relationships: A totalevidence phylogeny of strisores

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Strisores is a clade of largely insectivorous crown-group birds that includes highly specialized fliers such as the Apodiformes (swifts and hummingbirds), as well as the nocturnal Caprimulgidae (nightjars), Steatornithidae (oilbird), Nyctibiidae (potoos), Podargidae (frogmouths), and Aegothelidae (owletnightjars). Recent molecular and morphological phylogenetic analyses have uniformly recovered the nocturnal strisorians as a paraphyletic grade with respect to Apodiformes. However, despite the use of large-scale molecular datasets, the precise phylogenetic relationships between the nocturnal strisorians have been resolved inconsistently by different studies and remain controversial.

Given the lack of consensus between results based on molecular data, we examined the possibility that incorporating morphological data from fossils might improve resolution of this phylogenetic problem. Putative stem-members of nearly all major strisorian lineages have been described from Eocene fossil deposits, potentially providing critical information on ancestral character states within Strisores. We adopted a total-evidence approach combining both molecular and morphological data, which has hitherto only been applied to strisorian phylogeny to a limited extent. Our phylogenetic dataset includes 117 morphological characters scored for 24 strisorian taxa (of which 14 were fossil taxa) as well as DNA sequences from the extant taxa. This dataset was analyzed using Bayesian phylogenetic methods in MrBayes, resulting in a novel phylogenetic topology of Strisores that is nonetheless largely congruent with the findings of a comprehensive recent molecular phylogenetic analysis of modern birds.

Our results suggest that total-evidence approaches are promising in their potential to help resolve outstanding questions in crown-bird systematics. In future work, we aim to further clarify the early evolution of Strisores by performing a tip-dating analysis on our dataset to generate a time-calibrated phylogeny of these specialized birds.



Speaker

## An exceptional perinate Enantiornithes from the Lower Cretaceous of Spain and its implications for ossification pattern in early birds

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The evolutionary diversification of birds has resulted in a marked variation of locomotory adaptations in perinates, a wide range of developmental strategies of hatchlings, and important differences in their growth rates. Discoveries of fossil remains of juvenile birds from the Creta- ceous have furthered our understanding of the developmental pathways of some of the earliest branching avian lineages. Indeed, the analysis of the timing of ossification in these primitive birds can address uncertainties in the foundations of avian comparative developmental biology and the group's morphological evolution. Using a wide range of analytical and imaging tech- niques (including propagation phase contrast synchrotron microtomography and synchrotron rapid scanning X-ray fluorescence elemental imaging) we explored in depth and non-invasively a unique, nearly complete skeleton of an early juvenile Enantiornithes from the Early Cretaceous (c. 127 Ma) Konservat-lagerstätte of Las Hoyas (Spain), MPCM-IH-26189. The specimen clearly belongs to Enantiornithes, the most species-rich clade of Mesozoic birds, but its early ontogenetic stage makes it impossible to know whether it represents a new species. Irrespective, of the three enantiornithine taxa described from Las Hoyas MPCM-IH-26189 appears closer to Iberomesornis than to Eoalulavis and Concornis, in both skeletal proportions and morphology. This specimen is amongst the smallest known Mesozoic avians, representing post-hatching stages of development. The fossil sheds light on Enantiornithes' osteogenesis. A complex ossification pattern is present in the sternum, in which both the fan-shaped caudomedial xiphial ossification and the two parasagittal strap-like trabeculae are present, while the craniomedial bony discoid has not ossified yet. At least ten free caudal vertebrae are present, which is an unusually high number. Comparisons between this new specimen and other known early juvenile enantior- nithines support an asynchronous pattern in the sequence of ossification of the sternum and the vertebral column across some of the earliest avians. Our work indicates that the tempo of skeletal maturation and the developmental strategies of the hatchlings of basal birds was more diverse than previously thought, approximating the situation in neognaths.



<sup>&</sup>lt;sup>°</sup> Speaker

#### Vocal specialization through tracheal elongation in an extinct Miocene pheasant from China

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Modifications to the upper vocal tract involving hyper-elongated tracheae have evolved many times within crown birds, and their evolution has been linked to a ?size exaggeration' hypothesis in acoustic signaling and communication, whereby smaller-sized birds can produce louder sounds. A fossil skeleton of a new extinct species of wildfowl (Galliformes: Phasianidae) from the late Miocene of China, preserves an elongated, coiled trachea that represents the oldest fossil record of this vocal modification in birds and the first documentation of its evolution within pheasants. The phylogenetic position of this species within Phasianidae has not been fully resolved, but appears to document a separate independent origination of this vocal modification within Galliformes. The fossil preserves a coiled section of the trachea and other remains supporting a tracheal length longer than the bird's body. This extinct species likely produced vocalizations with a lower fundamental frequency and reduced harmonics compare to similarly-sized pheasants. The independent evolution of this vocal feature in galliforms living in both open and closed habitats does not appear to be correlated with other factors of biology or its open savanna-like habitat. Features present in the fossil that are typically associated with sexual dimorphism suggest that sexual selection may have resulted in the evolution of both the morphology and vocalization mechanism in this extinct species.



S7 // Poster

Speaker

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#### Colour patterns in the stem upupiform Messelirrisor

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The Eocene age deposits of Messel have yielded an important array of bird taxa, many of which represent stem members of extant clades. One of these birds is the stem upupiform *Messelirrisor*. Like many of the Messel birds, specimens of *Messelirrisor* have exceptional soft tissue preservation including feathers, with some even showing original colour patterns. Thanks to the discovery that integumentary structures such as feathers are preserved due to the retention of the pigment melanin, original colouration can be predicted through quantitative comparison to modern bird melanosomes. Here, we analyse multiple specimens of *Messelirrisor* and predict a likely colouration of mixed blacks and greys, as well as a striped black and white tail. The extant members of Upupiformes, the hoopoes and wood hoopoes, show strikingly different colouration to one another which is likely related to their respective feeding habitats. Of the two extant clades, *Messelirrisor* shows more similarity to the wood hoopoes which are specialist arboreal feeders. The colour predictions therefore match the presumed forested environment of Messel and the predicted perching habit of *Messelirrisor*, although there is no evidence that the distinctive iridescence of wood hoopoes was present in *Messelirrisor*, which has implications for behavioural adaptations related to signalling.



Speaker

# Tooth reduction in Mesozoic birds had a negligible effect on body mass

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Tooth reduction and loss was an important evolutionary process in Mesozoic birds. Analysis of evolutionary trends in the total mass of the dentition, a function of tooth size and tooth number, has the potential to shed light on the evolutionary pattern of tooth reduction and loss, and on the causes of this pattern. Because modern birds lack teeth, however, they cannot provide the basis for a model that would allow estimation of tooth masses in their Mesozoic counterparts. We selected the teeth of crocodilians as analogues of those in Mesozoic birds because the latter are the closest living relatives of the former, and because the two groups are similar in tooth morphology, tooth implantation, and tooth replacement pattern. To estimate tooth masses in Mesozoic birds, we formulated four regression equations relating tooth mass to various linear dimensions, which were measured in 31 intact isolated teeth from eight individual crocodiles (*Crocodylus siamensis*). The results for Mesozoic birds show that dental mass as a proportion of body mass was negligible, at least from the perspective of flight performance, suggesting that selection pressure favoring body mass reduction was probably not the primary driver of tooth reduction or loss. Variations in dental mass among Mesozoic birds may reflect the different foods they ate, and the different types of feeding behavior they displayed.



S7 // Poster

Speaker

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## S9 - Coevolution of life and environments: integrating the palaeoecological, sedimentological and geochemical records

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## Unusual microbial mat-related structural diversity at 2.1 billion years old and implications for the Francevillian biota

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Microbial life in the Paleoproterozoic remains poorly described despite existing paleontological and biogeochemical evidence pointing towards the existence of significant microbial diversity since the Archean. The 2.1-billion-years-old (Ga) Francevillian sedimentary rocks in Gabon have been intensively studied because of economic interests in their uranium and manganese ore deposits but also due to the oldest reported macroscopic fossils of various sizes and shapes. A large diversity of exceptionally preserved mat-related structures comprising 'elephant-skin' textures, putative macro-tufted microbial mats, domal buildups, flat pyritized structures, discoidal microbial colonies, horizontal mat growth patterns, wrinkle structures, 'kinneyia' structures, linear patterns and nodule-like structures have been reported in a 20 m thick interval of both sandstone and black shales. Petrographic analyses, scanning electron microscopy, Raman spectroscopy and organic elemental analyses of carbon-rich laminae and microtexture provide strong evidence in favour of mat-colonized sediments. The microtextural composition of bacterial mats encompasses floating grains of silt-sized quartz and concentrated heavy minerals, as well as wavy-crinkly laminae and pyritized structures. Comparisons with modern analogues, and a  $\delta^{13}C_{org}$  composition of -30.67 to -41.26, indicate a paleo-marine setting typical of the modern euphotic zone, colonized by benthic photoautotrophic microorganisms. The low  $\delta^{13}C_{org}$  signatures suggest the coexistence of multiple trophic levels involved in the cycling of photosynthetically derived Corg, including phototrophy, heterotrophy and methanotrophy. The relatively close association of the oldest colonial macroorganisms to the microbial mats may imply that bacterial communities acted as potential benthic  $O_2$  oases linked to oxyphototrophic cyanobacterial mats. In addition, their presence most likely improved the preservation of the macroscopic specimens, as bacterial mats are known to strongly biostabilize sediments. The Francevillian series host the oldest community assemblage of microscopic and macroscopic biota, providing a new window into the Paleoproterozoic microbial life and widening our understanding of biological organization at that time.



Speaker

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# Iron ooid forming environments in the aftermath of the End-Triassic mass extinction

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Iron ooid deposits are relatively common during some periods of the Phanerozoic, but their depositional environment often lacks a modern analogue. To understand the formation and context of iron ooids, they must be documented in a sedimentary and sequence stratigraphic context. The Ferguson Hill Member of the Early Jurassic Sunrise Formation of western Nevada, USA was examined to contextualize one of the earliest Mesozoic occurrences of iron ooids in the Panthalassa, following the Triassic/Jurassic boundary. A detailed facies model and sequence stratigraphic framework was developed for deposits from New York Canyon, NV, and lithologic samples underwent detailed thin section and SEM microscopy to determine facies as well as the distribution and nature of iron ooids.

The Ferguson Hill Member of the Sunrise Formation was deposited on a northwestward-dipping carbonate ramp, with facies including shallow-subtidal skeletal – peloidal wackestone to packstone, ooid-skeletal packstone to grainstone shoal, and lower ramp carbonate shales and turbidites. Iron ooids appear in ooid-skeletal packstones to grainstones just above flooding surfaces in columns across the study area. SEM imaging of iron ooids revealed the laminations are irregular and mottled at the sub-micron scale. The chemical composition of the iron ooid laminations showed areas rich in silicon and oxygen- interpreted as silica, and areas rich in iron, manganese, silicon, aluminum, and oxygen- interpreted as chamosite.

This increase in the abundance of iron ooids up section New York Canyon indicate the presence of a condensed section where prolonged low oxygen conditions allowed chamosite to accumulate at the sediment water interface. The condensed low- oxygen section is recognized in other columns as an accumulation of authigenic iron and little to no bioturbation. Owing to the deposition of chamosite in anoxic environments, iron ooids found in the Early Jurassic may be used as a potential indicator of low-oxygen conditions during the biotic recovery following the End-Triassic extinction.



S9 // Oral

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# Integrating microfacies and sedimentology in a modern Caribbean fringing reef (Puerto Morelos, Mexico)

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The occurrence and abundance of skeletal grains types in carbonate sediments, especially benthic foraminifera, are widely used as facies indicators and enviromental proxies, such as water depth. Here, we investigate sediment composition of a Mesoamerican fringing reef off Puerto Morelos, (Quintana Roo, Mexico), where microfacies distribution can serve as an analogue for reconstructing the development of Holocene and Pleistocene fringing reefs. Representative biogeomorphic zones were sampled and photographed by Scuba diving or snorkeling along a transect perpendicular to the reef crest. For each sample we determined: a) particle size distribution of 150 grams of sediment; b) composition of 150 major non-skeletal and skeletal grain types (bivalve, echinoderms, sponge spicules, Halimeda, gastropod, foraminifera, coral, octocoral, Polychaete, ostracods, red algae, tunicata spicules, pellets/aggregates); c) foraminifera in Reef Assessment and Monitoring, which is an indicator of the biological condition of the reef environment). The research shows that each reef zone has a characteristic biofacies (inner and outer lagoon, back-reef, reef crest, fore-reef and sand terrace). Furthermore, some taphonomic features of the foram species are directly related to the reef environment. The Foram index average is 2,73 (3



S9 // Ora

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## Habitat shift during the Middle Miocene Climatic Optimum of Southern Patagonia recorded in phytolith assemblages

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High global temperature and pCO<sub>2</sub> characterized the Middle Miocene Climatic Optimum (MMCO; ca. 17-14.5 Ma) and are thought to have promoted highly diverse ecosystems in warm and wet climates at high latitudes. However, only sparse observations inform interpretations of regional climate and biotas outside the northern hemisphere. The Santa Cruz Formation (SCF; 47-52°S) of coastal Patagonia (ca. 17.8– 16.6 Ma) represents the southernmost sedimentary sequence in the world recording the onset of the MMCO. SCF fossiliferous horizons yield one of the most species-rich and well-preserved vertebrate assemblages on Earth. Plant macrofossils and well preserved phytolith assemblages also occur in the SCF within the same strata as the faunas. These linked fossil records allow us, for the first time, to compare in detail animal and plant paleoecology and vegetation structure through the onset of the MMCO in southern South America. Here we present results from analysis of phytolith assemblage composition (% plant functional types) documenting vegetation change during the early part of the MMCO, and interpret it in light of our current climate proxy data. Stable isotope ratios from fossil enamel and bones from the same strata further allow us to reconstruct local Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) to test for potential climatic drivers of biotic change. Our preliminary results show high values for forest:open-habitat indicator ratios (indicating dominance of woody vegetation) in most phytolith assemblages, excepting the oldest assemblage. While there is no clear trend in overall forest:open-habitat ratio through time, the dominant forest indicators do vary across assemblages - palm phytoliths decrease through time while other forest indicators increase. This pattern could be explained by vegetation shifts through time, spatial heterogeneity, or both. Both phytolith and isotopic data indicate that grass communities consisted mainly of C3 pooid grasses. Interestingly, grass phytoliths display a considerable decrease in size from older to younger strata, which may reflect the onset of a dryer and warmer climate. While isotopic data further support this climatic trend, our data suggest that drying did not result in an expansion of open-habitat grasses.

**S9 // Oral** 

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#### Palaeoenvironmental and palaeoclimatic evolution of the lower Pleistocene Arda River succession (Italy): a multidisciplinary approach

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The geological record provides a unique archive to apply a multi-proxy approach to document the long-term fluctuations of environmental variables for palaeoclimatic and palaeoenvironmental reconstructions. The lower Pleistocene Arda River marine succession (Italy) represents an excellent site to perform an integrated investigation, combining sedimentological, palaeoecological (body and trace fossils) and geochemical tools, to unravel the evolution of a complex marine setting in the frame of early Pleistocene climate change and tectonic activity.

Here, we pursue 1) facies analyses and a palaeoecological investigation of the rich macrobenthic and trace fossils, to reconstruct the palaeoenvironments of the Arda succession, and 2) whole- shell and sclerochemical stable isotope analyses ( $\delta^{18}$ O,  $\delta^{13}$ C) on bivalve shells (*Arctica islandica, Glycymeris* spp. and *Aequipecten* spp.) to scrutinize the palaeoclimatic changes approaching the Early-Middle Pleistocene Transition and the beginning of precession-driven Quaternary-style glacial–interglacial cycles.

Based upon biosedimentary insights the Arda River succession represents a subaqueous extension of a fluvial system, originated during phases of advance of fan deltas affected by high-density flows triggered by river floods, which are an expression of early Pleistocene climate changes. At the top of the succession clast supported conglomerates indicate a major sea level drop and the establishment of a continental environment. Sclerochemical analyses undertaken on bivalve shells indicate that seawater temperature seasonality was the main variable of climate change within the study area during the early Pleistocene. In particular, strong seasonality (14.4–16.0 °C range) and low winter palaeotemperatures were assumed to be the main drivers for the widespread establishment of "northern guests" (i.e., cold water taxa) populations in the Palaeo- Adriatic Sea around 1.80 Ma. This is confirmed also by trace fossils, recording the presence of the cold-water ichnotaxon *Macaronichnus*. This study highlights the importance of multidisciplinary analyses based on the integration of different tools to greatly improve the resolution of palaeoenvironmental and palaeoclimatic reconstructions, which should be applied to other geological sites and different time intervals.

<sup>&</sup>lt;sup>°</sup> Speaker

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#### **Ediacaran extinction and Cambrian explosion**

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The the past bill disappearand 'Cambrian E: subsequent

The Ediacaran-Cambrian transition marks possibly the most important geobiological revolution of the past billion years, including both the Earth's first biotic crisis of macroscopic eukaryotic life - the disappearance of the enigmatic 'Ediacara biota' - and its most spectacular evolutionary radiation - the 'Cambrian Explosion'. Understanding the cause(s) behind this extinction event and its relationship to the subsequent Cambrian radiation is thus key to understanding the origins of the modern biosphere. Here, we collate recent research on this interval from a wide range of scientific fields, describe competing models ('catastrophe' and 'biotic replacement'), and outline several key questions which will help drive research on this critical interval in Earth History. These include: 1) What do the large perturbations to the Ediacaran carbon cycle (the Shuram and 'BACE') represent? 2) For either the 'catastrophe' and 'biotic replacement' models, can we identify plausible extinction drivers? And, 3) what role did the end-Ediacaran extinction play in the Cambrian explosion that followed? Finally, we argue that the biggest step-change in organismal and ecological complexity arrives at the White-Sea Nama boundary, rather than at the Ediacaran-Cambrian boundary itself. This would in turn suggest that the latest Ediacaran Nama interval (ca. 548-539 Ma) may represent the earliest phase of the dramatic metazoan radiation commonly referred to as the 'Cambrian Explosion'.



## Incorporating palaeoecological, sedimentary and geochemical data to revisit the End-Ordovician mass extinction event

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The end-Ordovician Hirnantian interval coincides with one of the largest mass extinctions in Earth history, with one of the three largest Phanerozoic glaciations, and with large isotopic excursions (C, S, O, N, Nd). The Late Ordovician Mass Extinction (LOME) eradicated ~85% of marine species and occurred in two discrete pulses, one at the beginning of the Hirnantian and the other later near the end of the Hirnantian. The current view is that the rapid expansion of ice sheets resulted in glacioeustatic sea-level fall and decreased temperatures and caused the first pulse of the LOME while the second pulse of the LOME occurred as glaciers melted, oceans warmed, and anoxic seawater transgressed onto the shelves. Here, we argue that some of these remarkable claims arise from the undersampling of incomplete geological sections that led to apparent temporal correlations within the relatively coarse resolution capability of early Palaeozoic biochronostratigraphy. We examine two exceptionally thick and complete sedimentary records spanning the Ordovician-Silurian boundary from two, low and high, palaeolatitude settings (Anticosti Island in Canada and Anti-Atlas of Morocco respectively). This correlation reveals a Cenozoic-style scenario including three main Hirnantian glacial-interglacial cycles punctuated by numerous multi-order sea level changes. In addition, the Anticosti neritic carbonate section permits direct temporal comparisons among several proxy records including glacio-eustasy, carbon budget changes, and LOME faunal diversity changes. We envisage a more complex situation than the previous LOME scenario associated with a single, major glacial event. In our newly proposed scenario, the first pulse of the LOME is tied to an early phase of melting, not to initial cooling, and the largest  $\delta^{13}$ C excursion associated with the second pulse of the LOME occurs during final deglaciation, not at the glacial apex as typically interpreted. We have also tested the end Ordovician neritic carbonates of Anticosti Island with relatively novel tracers of continental weathering and oceanic anoxia in order to gain more insight into this dynamic time interval.



Speaker

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#### δ<sup>18</sup>O values of Late Cretaceous Western Interior Seaway deep water marine bivalves

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The North American Western Interior Seaway (WIS) was an epicontinental marine system that connected the southern Tethys Sea to the northern Boreal Sea during the Late Cretaceous (ca. 100 Ma to ca. 66 Ma). It hosted a varied invertebrate and vertebrate fauna including ammonites, baculites, inoceramids, sharks and large marine reptiles (e.g., plesiosaurs and mosasaurs). The amount of seawater input from the Tethys Sea and Boreal Sea and the amount of freshwater input from runoff, precipitation, and aquifers into the WIS complicate the WIS's oxygen isotopic composition ( $\delta^{18}$ O) of seawater and thus reconstructed temperatures. In this study, we measure Campanian (ca. 83 Ma to ca. 72 Ma) and Maastrichtian (ca. 72 Ma to ca. 66 Ma) well preserved calcitic and aragonitic deep water marine bivalves from the WIS across numerous genera (i.e. Inoceramus, Mactra, Cucullaea, Ostrea and Lucina) and that span a wide geographic range across the western United States. The deep water marine bivalves' bulk  $\delta$ 180 values can be used as a paleoclimate indicator and to assess how much diagenesis has altered the original oxygen isotope composition. Whereas marine bivalves  $\delta^{18}$ O values range from +0.19 to -13.62, the majority of  $\delta^{18}$ O values group between -1 to -4 (vs. PDB). Higher values most likely represent unaltered oxygen isotope compositions, as this study's calculated paleotemperatures are in agreement with other proxies of the Campanian and Maastrichtian climate. Lower values are most likely diagenetically altered. Interestingly, the measured  $\delta^{18}$ O values do not show a latitudinal temperature gradient, however, we cannot rule out this gradient because the oxygen isotope values of the seawater could be lower at higher latitudes as predicted by models. In addition, we measured well preserved inoceramids across growth axis to determine if annual cycles are preserved. Our results revealed cyclicity similar to annual patterns measured in modern samples. Surprisingly, one inoceramid specimen with very low  $\delta^{18}$ O values (-12 to -13) that strongly suggest digenetic alteration still preserves observable cyclicity. Our data suggest that conservative diagenesis may preserve seasonal cycles and shift original  $\delta$ 180 values lower instead of completely resetting the oxygen isotope composition.

**S9 // Oral** 

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#### Decreasing environmental influence on the Phanerozoic success of marine calcifiers

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The vast Phanerozoic fossil record of marine calcifiers allows for quantitative assessment of environmental influences on past life. Calcifying organisms build their skeletons from calcite and/or aragonite, and the metabolic cost of shell secretion is influenced by the interplay of mineralogy and environment. Mg:Ca ratio and temperature control whether abiotic calcium carbonate is precipitated as calcite or aragonite, and variations in those conditions are likely to have affected calcifying organisms throughout Earth history. Here, we combine a model of seawater Mg:Ca ratio with  $\delta^{18}$ O temperature reconstructions to quantify calcite-aragonite sea conditions from the Ordovician – Pleistocene. We correlate calcite-aragonite sea conditions with the ecological success of aragonitic taxa at stage resolution, calculated as Summed Common species Occurrence Rate (SCOR) based on genus-level occurrences from the Paleobiology Database. Calcite-aragonite sea conditions significantly co-vary with the ecological success of aragonitic taxa in the Palaeozoic, but correlation ceases in the Mesozoic. We attribute this to the consequences of the end-Permian mass extinction: The prevalence of physiologically buffered taxa rose sharply across the Permian-Triassic boundary. Mobile, predatory and metabolically active taxa increased in importance after the end-Permian extinction and during the Mesozoic. This transition marked the end of a dominantly environmental control on ecological success in the marine realm.



Speaker

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### Facies selectivity of benthic invertebrates in microbialites: implications for the "Microbialite Refuge" hypothesis

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Oxygenic photosynthesis by cyanobacteria in thrombolite and stromatolite habitats is becoming increasingly recognized as an important oxygenated refuge for invertebrates throughout the Phanerozoic. The discovery of oxygen-dependent invertebrates in microbial habitats from the aftermath of the latest Permian mass extinction, has led to the proposal that these microbial habitats provided an oxygenated refuge in otherwise anoxic settings. Here we investigated the distribution of ca. 35,000 benthic individuals found in ca. 100 samples from a post-extinction microbialite succession on the 'Great Bank of Guizhou' (South China) representing thrombolite, stromatolite, and non-microbial facies. The investigated habitats are all interpreted to have been deposited above storm weather wave base. The recorded benthic community from the microbialite succession is the most species-rich currently known from the Early Triassic, and does not record a temporal dynamic due to persistent environmental stress inferred from the palaeontological and geochemical records. The stromatolites were, however, the least diverse, and thrombolites also recorded significantly lower diversities when compared to the non-microbial facies. We also found that bioclasts within the thrombolites and stromatolites were transported and concentrated in the non-microbial fabrics, i.e., cavities around the microbial framework. Therefore, many of the identified metazoans from the post-extinction microbialites are not observed to have been living within a microbial mat. Furthermore, the lifestyle of many of the taxa identified from the microbialites is not suited for, or even amenable to life, within a benthic microbial mat. The high diversity of oxygen dependent metazoans in the non-microbial facies on the 'Great Bank of Guizhou', and inferences from geochemical records, suggests that the microbialites and benthic communities developed in oxygenated environments, and negates the role of microbialites as an oxygenated refuge.



Speaker

#### Size matters in the Ediacara biota

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The phylogenetic affinities of fossils of the Ediacara biota have long been debated. In 1957, the discovery of small-sized taxa of Ediacara fossils in South Australia, like *Spriggina, Parvancorina* and *Tribrachidium*, led to broad acceptance of the significance of this biota. However, the existence of Ediacaran bilaterians is still debated. Specialists that dismiss the Ediacara biota as a "failed experiment" in the history of life, leave un-answered the origins of the trace fossil taxa that are used worldwide to define the base of the Cambrian.

The recent discovery and attention given to new, small-sized taxa, in the late Ediacaran strata of South Australia, as well as emphasis on Ediacaran trace fossils, including both trackways and feeding traces, confirms that the Ediacara biota includes stem-group bilaterians.

A record of organic-walled microfossils of increasing complexity and size, in south China and central Australia, characterizes the early part of the Ediacaran Period. By the late Ediacaran, the Mistaken Point assemblage of large, benthic marine organisms, exhibiting self-similar growth, had populated the deep seafloors of Newfoundland and England. The younger White Sea and Nama assemblages of South Australia, Russia, Namibia, South China and NW Canada, record the advent of more diverse benthic communities of soft bodied organisms, together with some of their feeding and locomotive traces, in shallower seas. The Ediacaran ended with the first evidence of mineralized tubes and frameworks in carbonate sediment, along with clear traces of scavenging and mat-mining by almost overlooked, small-scale metameric organisms in the Ediacara biota preserved in fine-grained siliciclastic sediment.

The origins of bioturbation, for purposes of scavenging in the late Ediacaran, saw an escalation in the Early Cambrian, both in intensity and scale, reflecting the onset of the Cambrian explosion. Arguably, tiny unmineralized Ediacarans gave rise to larger, appendage bearing, benthic bilaterian animals recorded by sharp sets of bilobed furrows and biramous appendage traces, such as *Didymaulichnus* and *Rusophycus* in the earliest Cambrian siliciclastic sediments in the Uratanna and Mt Terrible formations of South Australia, the Chapel Island Formation of eastern Newfoundland, and the Ingta and Backbone Range formations of NW Canada. These trace fossils are the first evidence of the evolution of cuticular integuments that heralded the mineralized body-fossil record by the end of the Fortunian Stage of the Early Cambrian, and the effective loss of laminated sandy mat grounds.



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#### Integrated paleontological analysis aimed to the characterization of a shallow-water platform system (Alicante province, Southern Spain)

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Tortonian and Thyrrenian deposits were studied in the Cabo de la Huerta section (Alicante Province, Southern Spain), which for its exposure is an area where numerous didactic and outreach geological activities are developed. Taphonomic, taxonomic and ichnological analyses were carried out to establish the paleoenvironmental setting were these materials deposited. Tortonian deposits are characterized by interbedded coarse- and fine-grained calcarenites. In the fine grained calcarenites, bioclasts are represented by well preserved irregular echinoids, pectinid bivalves and scarce terebratulid brachiopods. The coarse-grained calcarenites show intense bioturbation by Ophiomorpha nodosa; as for bioclasts, gastropods, bivalves and red algae are common and intensively fragmented. These beds were interpreted as deposited by storm events in an open marine platform, which background sedimentation is represented by the fine-grained calcarenites. Thyrrenian material overlies the Tortonian unit after an angular unconformity. In the Thyrrenian unit, four levels were recognized, organized in a regressive sequence. The first level shows cross lamination and tiny fragmented bioclasts, in some occasions oriented on the laminae. Red algae, corals, bryozoans, vermetids, bivalves and gastropods are present, some of them belonging to the so called "Senegalese Fauna", indicative of warm/subtropical climate. In level 2, fossil content is the same as in level 1 but with a completely different kind of preservation. Bioclasts are only coarsely fragmented, some of them are unbroken although never preserved in life position. Very differently preserved bioclasts from the same taxa are present in this level, from perfectly preserved in shape and ornamentation to bioeroded, fractured and completely abraded, this pointing out mixing of shells with very different residence time on the substrate. Levels 1 and 2 have been considered as deposited in a beach environment, level 1 during normal conditions, while level 2 during major storms mixing the shells (possibly also of living animals) present in and on the substrate. Large fragments of vermetid reefs are also present in level 2, destroyed and transported landward by the intense waves. The section is capped by lutitic interval, where only continental gastropods were recorded, and convex-shaped, cross-bedded rhizolith-rich sandy bodies, representing a freshwater/brackish lagoon and the migration of the dunes of the backshore, respectively.



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#### Disappearance of orbitolinids in upper Cretaceous shallow marine successions of southeast France: relationships with the Mid Cenomanian Event 1?

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The "Mid Cenomanian Event 1" (MCE 1) is a major perturbation of the carbon cycle, characterized by two  $\delta^{13}$ C positive peaks: 1a and 1b. It was recognized in the Vocontian Basin (Blieux section). There, the onset of MCE 1 has been associated with major relative sea-level fall, arid climatic and oligotrophic conditions. In order to give further support to these environmental and climatic interpretations, three shallow-marine sections (Caussols, Col des Abbesses, and Le Bourguet) were studied; they are located on the northern part of the Durancian Isthmus. Field, facies, carbon isotope, and clay mineral assemblage analyses, ammonite and calcareous nannofossil biostratigraphy, sequence stratigraphy, and correlation of these mixed carbonate- siliciclastic sections were performed. The MCE 1 was identified in both Caussols and Col des Abbesses sections. Le Bourguet which is the most siliciclastic studied section, is not suitable for stable isotope analyses. All these sections are characterized by the presence of orbitolinids, but their stratigraphic distribution is constrained. The preliminary correlation of these sections shows that orbitolinids occurrence and disappearance are not related to a specific sedimentary facies. However, their first occurrence in Caussols and Le Bourguet sections is associated with a change in clay mineral assemblages. In the Col des Abbesses section, orbitolinids occur in the lower part where clay mineral assemblages have not yet been analyzed. Their disappearance occurs in all the studied sections around the Early-late Cenomanian Boundary, which coincides with the MCE 1 onset and there again with a change in clay mineral assemblages. In the Aquitaine Basin (southwest France), orbitolinids also disappear around the Early-late Cenomanian Boundary. Does the orbitolinid disappearance result from particular environmental conditions? Are these conditions related to the relative sea level and/or climate changes corresponding to the MCE 1 onset? High-resolution sequence stratigraphy and clay mineral assemblage analyses are in progress in view to specify these conditions.



Speaker

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# Effects of the Late Paleozoic climate transition on soil ecosystems of the Appalachian Basin: evidence from ichnofossils

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The Late Paleozoic transition is a critical interval in Earth history in terms of tectonics, climate, and life. The Upper Pennsylvanian to Lower Permian Monongahela and Dunkard groups of the western Appalachian Basin (U.S.A.) contain abundant paleosols possessing varying suites of ichnofossils. Through comparison to modern analogs, these ichnofossils serve as indicators of soil moisture, soil organic content, water table level, precipitation, evapotranspiration, and landscape stability. As a result, ichnofossils of soil organisms are excellent indicators of fluctuations in biological activity in response to changes in environment and climate through time. Analysis of ichnofossil assemblages in these paleosols can, therefore, be used to refine the details of the changing Late Paleozoic terrestrial landscapes.

A study along a 50 km long, north-south transect of multiple 30-50 m high sections of the Monongahela and Dunkard groups through southeast Ohio and West Virginia resulted in the recognition of 12 pedotypes with distinct ichnocoenoses. Ichnofossils included rhizoliths, *Planolites, Palaeophychus, Taenidium, Camborygma, Skolithos, Thalassinoides, Psilonichnus,* plant-feeding traces, and coprolites produced by various plants, larval and adult arthropods, and vertebrates. Soil-forming environments included palustrine, levee, proximal to distal floodplain, interfluve, backswamp, marsh, and fen settings. In general, ichnocoenoses were less diverse and comprised of shallow and simple ichnofossils in poorly drained Entisols and Inceptisols of the lower part of the studied sections. Ichnocoenoses became more diverse and comprised of deeper and more complex ichnofossils in well-drained Vertisols in the middle portion of the section. Near the top of the studied section, diversity and abundance of traces decreased again, but maintained their depth in calcareous Vertisols. The ichnocoenoses indicate an upward decrease in precipitation and an increase in seasonality. In addition to this trend through time, however, the nature of the ichnocoenoses varied within each interval recording short-term oscillations in soil properties and precipitation.

Terrestrial ichnocoenoses serve as an important archive of environmental data not otherwise preserved in the sedimentary record. Analysis of these suites of ichnofossils is critical to evaluating climatic conditions in deep time and their effects on soil ecosystems.



Speaker

## Decaying process of marine vertebrates: how are the whale- and sea turtle-fall communities established?

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Decaying whale carcass on the seafloor creates a unique biological community, the so called whalefall community, similar to communities around vents and seeps in the deep-sea. Studies on bathymodiolin bivalves and siboglinid polychaetes living in such places suggested progressive adaptation of those organisms to seep and vent environments through the decaying vertebrate- falls. In this point of view, the marine reptile-falls would be more important than whales because of thier longer fossil record; however, the decaying process of marine reptiles have not been investigated in detail. In addition, a vertebrate-falldependent biological community is sustained for multiple years even after removal of soft tissue. At that stage, organic matter within the bones would be an energy source, but it is still unknown how the organic matter in the bone is used. We deployed several sea turtle carcasses and pieces of whale bones on a shallow sea floor (11 to 14m in depth) in Tsukumo Bay, Noto Peninsula, Japan, to reveal decaying processes of sea turtle-fall and transportation process of organic matter from inside of the bones to the outside. The carcasses were observed by scuba, and some bones were recovered and maintained in aquarium to observe in detail. Beggiatoa microbial mats, Zoomthamnium sp. which has chemosymbiotic bacteria, and dorvilleid polychaetes in/on the bones appeared before ca. 30 days after deployment of the both sea turtle and whale carcasses. It is noteworthy that the sea turtle-fall sustained a chemosynthetic community similar to whale-falls. Observations of recovered bones in aquarium revealed accumulation of fecal excretions around the whale bones and ejection of the fecal excretions from the bones. There were many polychaeates and copepods in the bones and those animals ejected the feces from the bones. Higher total organic content of sediments with shorter distance from the bone were observed, and the growing microbial mat on the sediment accumulated from feces indicate that the transportation of organic matter from inside to outside of the bones by polycheates and copepods are an important factor to establish and sustain the vertebrate-fall dependent biological community.



S9 // Oral

<sup>&</sup>lt;sup>'</sup> Speaker

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## Late Quaternary relative sea-level changes and evolution of the Lacepede Shelf, southern Australia

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The River Murray of the Murray-Darling Basin is the largest river system in Australia to reach the sea (1,060,000 km2) where it debouches on the Lacepede Shelf, in SE South Australia. The Lacepede is a wide (180 km), shallow (≤150 m), tectonically stable shelf, part of the largest modern temperate coolwater carbonate depositional province in the modern world. During the Quaternary, the dominant geomorphological changes within the region have directly resulted from transgressive/regressive events with minimal isostatic effects in this far-field environment. At times of lower sea-level in the Middle and Late Pleistocene (> 120 m BPSL, Penultimate and Last Glacial Maxima; ca. 130 ka and ca. 20 ka, respectively) much of the shelf was subaerially exposed, allowing the former River to extend ~200 km farther south relative to the modern coastline. The Lacepede Shelf provides an excellent record of the history of the River Murray during the last glacial cycle as well as the history of sea-level changes and the evolution of the former shorelines. Preliminary results based on taxonomy, taphonomy and dating (14C-AMS and AAR) of foraminifers, as well as sedimentological and geocheminal data from three cores located within the palaeo-channels of the ancient river system, show sea-level at 40-50 m BPSL during the Pleistocene-Holocene transition (~12 ka) and 55-60 m BPSL at ~45 ka. In environmental terms, the river mouth represented an estuarine-lagoonal environment during colder/drier conditions in which the river flow was minor (end of MIS 3 and MIS 2). This is shown by an assemblage dominated by A. beccarii -E. excavatum, a predominance of Ammonia over Elphidium and taphonomical signals of oxidation with reduced sedimentation. During the transition to milder conditions and the beginning of the sea-level rise (end of MIS 2), the estuarine/lagoon system prevailed under relatively saltier conditions, dominated by an assemblage of A. beccarii -E. advenum, with higher abundances of Elphidium over Ammonia. Finally, following the marine transgression after the LGM, conditions became more open marine in character, showing coarser grain, higher carbonates and quartz levels, higher abundance, richness and diversity of foraminifers, with B. translucens, C. refulgens, E. excavatum, R. globularis, T. oblonga, Q. incisa becoming the dominant taxa. During the LGM, the ancient River Murray was restricted to a narrow palaeo-channel, transporting minimal terrigenous sediment to the shelf edge.



**S9 // Oral** 

<sup>&</sup>lt;sup>\*</sup> Speaker

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## Biotic interactions and food chain/web reconstruction of a community from Cretaceous Interior Seaway (CIS), Manitoba, Canada: local and beyond

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The Upper Cretaceous Millwood Member (Campanian) is well exposed in Russell area of SW Manitoba. Bulk sampling along a fossiliferous horizon near the middle part of the member revealed a diverse time-averaged community dominated by mollusks. Over 900 macrofossil specimens are assigned to: Scaphopoda: Dentalium gracile; Gastropoda: Euspira obliquata; Anomalofusus sp.; Graphidula culbertson; Graphidula cretacea?; ?Mesalia sp.; Oligoptycha concinna?; fasciolariid gen. et sp. indet.; Pelecypoda: Astarte sp.; ?Inoceramus sp.; Cephalopoda: Baculites scotti, Hoploscaphites sp.; and Decapoda (a crab): Cretacocarcinus smithi. Previous study recovered Foraminifera (e.g.: Bathysiphon, Ammodiscus, Glomosspira, Haplophragmoides) from similar horizon at a nearby site, it is feasible to include these microorganisms in the community. Trace fossils help uncover some other components. Abundant bioerosion traces on Dentalium, Euspira, and Astarte are assigned to Maeandropolydora sulcans, whose maker is generally believed to be spinoid polychaetes. They are the unpreserved elements of the community. Well preserved and commonly presented predatory drilling traces Oichnus paraboloides on Dentalium, ?Mesalia, Euspira, Astarte, and fasciolariid gen. et sp. indet. are interpreted to be made by Euspira, the only naticid gastropod in the community. Crushing/peeling predation traces and repaired scars on Dentalium, Euspira, Graphidula are interpreted to be caused by Cretacocarcinus. On the basis of these biotic interactions within the benthic community and the feeding habit of living Dentalium, reconstruction of the local food chain/web is attempted: Foraminifera > Dentalium > Euspira > Cretacocarcinus; Foraminifera > Dentalium > Cretacocarcinus; ?Mesalia, Euspira, Astarte, and fasciolariid gen. et sp. indet. > Euspira > Cretacocarcinus. A diverse Campanian vertebrate fauna has been reported in CIS, including fish, mosasaurs, plesiosaurs, sharks etc. Based on previous studies on the food remains in the body chambers of ammonites, durophagous predation on scaphitids, tooth marks on an ammonite, gut contents of mosasaur and plesiosaur specimens, the food chain above Cretacocarcinus in the CIS is proposed as: Cretacocarcinus > Hoploscaphites/Baculites > Fish (e.g.: Enchodus) > Plesiosaur (e.g.: Polycotylus) / Mosasaur (e.g.: Tylosaurus)/Shark. The extended food chain and complex food web may represent a mature and stable marine ecosystem of CIS during Campanian.



<sup>&</sup>lt;sup>°</sup> Speaker

## Belowground rhizomes and roots in waterlogged paleosols from the Middle Jurassic of Beijing, China

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Plant rhizomes and roots have existed in terrestrial ecosystems since at least the Devonian, but the documentation of belowground plant tissues is sparse in the fossil record. In this study, fossils representing belowground rhizomes and roots are described from the top of the Upper Yaopo Formation (Middle Jurassic), at the Yuejiapo section, Mentougou District, Beijing, China. Morphological studies of the plant fossils, together with lithofacies analyses, provide new information on plant-soil interactions during the Jurassic period. Three types of rooting systems are recognized from two fossiliferous beds. The Bed-1 Flora is interpreted as representing a *Cladophlebis* -dominated community, where abundant foliage remains mainly of *Cladophlebis* cf. *C. scariosa* and *Cladophlebis delicatula* are associated with Type-A rooting system. The Bed-2 Flora includes Type-B and Type-C rooting systems, although the floristic composition is unknown due to the absence of identifiable foliage specimens. The Type-A and Type-B rooting systems consist of abundant *in situ* vertical rhizomes, fine shoot-borne roots and lateral roots, and are consistent with those of some extant ferns. The Type-C rooting system shows a thick central taproot and at least three orders of lateral roots, an architecture typical of diverse (pro)gymnosperms, from the Late Devonian to the Recent. The *in situ* rooting systems, as well as sedimentary evidence, contribute to the recognition of stacked, reworked Entisols in a dynamic waterlogged environment.



Speaker

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## Oldest petee ridges, produced by desiccated microbial mats, in c. 3 Ga peritidal Pongola quartzites, South Africa

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Southern Africa has the most continuous record of relatively little deformed and weakly metamorphosed Palaeoarchaean to Palaeoproterozoic supracrustal rocks. These rocks also host the best preserved record of early life spanning the time period from c. 3.5 to 2.0 Ga. The fossil record consists of microbial body fossils, trace fossils in the form of microborings; stromatolites, oolites, oncoids and microbial mats in carbonate rocks; silica-iron oxide oncolites; and microbially-induced sedimentary structures in siliciclastic rocks. In the Chobeni Fm, Nsuze Gp, the basal part of the c. 2.98-2.95 Ga Pongola Supergroup, guartzites and carbonate rocks, with well developed columnar stromatolites, microbial mats, and oolites, are interbedded with mafic volcanic rocks. The carbonates were deposited in shallow water intertidal to subtidal settings, while the interbedded planar crossbedded quartzites were deposited in subtidal sand dunes. They grade upwards into rippled tidal sandstones, and often contain silicified rip-up clasts of carbonate microbial mats. In the quartzite overlying the Main Carbonate, there is a trough crossbedded facies, possibly formed in a fluvial, or flood tidal, channel. A bedding plane of the quartzite is covered with a polygonal network of what appear to be suncracks in mudstone. However, the cracks appear in relief, standing 1-2 mm high, in quartzite, with no mudstone present at all. The cracked surface occupies an area of 20 cm by 40 cm. The cracks are hierarchical, and form three orders, with decreasing thickness. The primary cracks are c. 2-3 mm wide and c. 15 mm long; the secondary cracks are c. 1.5-2 mm wide and c. 10 mm long, and the rare tertiary cracks are c. 1 mm wide and c. 8 mm long. The cracks are mainly straight-edged, but some cracks are slightly to highly curved. These cracks are interpreted as petee ridges, formed when a coherent microbial mat formed on the guartz-rich sandstone surface, had become subaerially exposed and desiccated, perhaps during an extended period of exposure such as during a neap tide. The desiccated microbial mat then was buried under more sand during a renewed period of sedimentation. The microbial mat decayed, and only the sandy infillings of the desiccation cracks survived. More prominently developed petee ridges occur in the c. 2.1 Ga Magaliesberg Quartzite Fm of the Pretoria Gp, but this occurrence in the c. 3 Ga Chobeni Fm is the oldest example of petee ridges reported from anywhere on earth.



Speaker

# Polar wildfires and fire-adapted seed dispersal during the Cretaceous global hothouse

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Several highly effective fire-adaptive traits first evolved among modern plants during the mid-Cretaceous, in response to the widespread wildfires promoted by anomalously high atmospheric oxygen (O2) and extreme temperatures. Serotiny, or long-term canopy seed storage, is a fire- adaptive strategy common among plants living in fire-prone areas today, but evidence of this strategy has been lacking from the fossil record. Deposits of abundant fossil charcoal from sedimentary successions of the Chatham Islands, New Zealand, record wildfires in the south polar regions (75°–80°S) during the mid-Cretaceous (ca 99–90 Ma). A new species of fossil conifer reproductive structure, *Protodammara reimatamoriori*, was consistently associated with these charcoal-rich deposits. Neutron tomography revealed the morphology and internal anatomy of these fossils, which exhibit a range of serotiny-associated characters. Fouriertransform infrared spectroscopy has chemotaxonomically constrained the phylogenetic placement of these fossils, demonstrating that fire adaptations evolved independently in at least two conifer families during the mid-Cretaceous. Numerous fossils from similar, contemporaneous deposits of the Northern Hemisphere suggest that serotiny was a key adaptive strategy during the high-fire world of the Cretaceous.



Speaker

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#### Possible characteristics of the Cambrian SPICE event on the North China Platform

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The Steptoean Positive Carbon Isotope Excursion (SPICE) event is a well-known geochemical excursion episode in geologic history with many reports from around the world. Nevertheless, the North China paleocontinent (Sino-Korean Craton) was a little left out from the very beginning, probably due to the scarcity of deeper marine deposits and the lack of biozonal defining agnostids.

In the last decade or so, several works on the North China SPICE event had helped to bridge this gap, and the results had been rather fruitful. To date, at least seven sections were published with the SPICE signal on the North China Platform – five from northern China and two from South Korea; all shallow marine setting, except one deep marine setting from the latter. Lately, we had added another new SPICE record from Liaoning Province, northern China. It provides the highest resolution stable carbon isotope data (average sampling interval ~0.2 m, n=119) ever reported from this shallow marine carbonate platform.

The SPICE curves on the North China Platform seem to have reduced peak  $\delta^{13}$ C and difference values ( $\Delta^{13}$ C). Some of the previous studies perhaps failed to sample the higher peak value as their sampling intervals are rather widely separated. However, the peak  $\delta^{13}$ C values of the North China SPICE curves are consistently lower than the global average. The maximum values are slightly more than +4 in North China, while the global average is about +5 to +6 . For  $\Delta^{13}$ C, the North China numbers are between 1.7 to 3.8, compared to the global 4. This may not be easily explained by the difference between shallow and deep marine setting, as all the latest SPICE data indicate that the peak and difference values are reduced on the Sino-Korean Craton, including the deep-water South Korea section. This may actually imply certain paleoenvironmental uniqueness of the North China Platform, and its relationships to the trilobite mass extinction events do require further investigation.

IPC 5

Speaker

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## The pioneering role of Precambrian bioturbators preceding the Cambrian fauna: a sedimentological and paleontological case study from the western United States

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Subsurface bioturbation during the late Precambrian (555-542Ma) expanded and restructured available niche space, pushing the existing marine fauna to adapt and evolve. The late Ediacaran infaunal ecosystem expansion led to major changes in the sedimentology and structure of the substrate and drove the marine realm towards the Cambrian Explosion. The lower Member of the Wood Canyon Formation of the western United States preserves traces left by vermiform (worm-like) animals within two largely complete sections (and an additional stratigraphically reduced section) that span the Precambrian-Cambrian boundary. From these deposits, we present a hypothesized trajectory of changes in density and diversity of bioturbation leading up to and across the boundary. These trends will be used in conjunction with temporally congruent body fossil assemblages from the Dengying Formation of South China and the Deep Spring Formation of the western United States. Body fossil data from China indicates a potential shift in the vermiform populations, from rigid upright-growing individuals to one dominated by flat-lying flexible individuals. This shift is followed closely by the evolution of macrobiomineralization and reef-building behaviors often associated with the onset of the Cambrian Explosion. Through correlation of late Precambrian body fossil assemblages and the trace fossils of the Wood Canyon Formation, we can deduce the increasing influence of burrowing density on the substrate dwelling communities. We can also infer the degree to which changes in burrowing behaviors drove the early Cambrian marine fauna to diversify and take on life modes that reflected the changing substrate conditions.



S9 // Oral

Speaker

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#### The ichnological record in Iceland – unusual finds in unexpected landscape

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Iceland represents the classical example of an area fully formed by volcanic activity. Its geological history goes back to the Lower Palaeogene, when the northern part of the Mid-Atlantic Ridge activated in an area of hotspot expression. North American and Eurasian Plate divergence started consequently. The primarily undersea volcanism continuously verged into surface extrusion, whereas four main periods of volcanic activity, creating volcano-stratigraphic units 16 Ma–Recent, can be defined.

The geological structure of Iceland is created mainly by volcanic rocks or materials of volcaniclastic origin. Sediments are not abundant here; however, they are represented by varied range of lithotypes in relation to the character of its palaeoenvironment. Clays, siltstones and conglomerates were originated mostly in an area of lagoons, lakes, river basins and deltas. Shales, mudstones and siltstones of lacustrine origin are less abundant. As far as marshy areas are concerned, mudstones with high amount of organic compound, sporadically with thin lignite beds, were formed. Diatomites were originated in shallow lakes.

The sediments, mostly those that are associated to marine environment, often contain abundant macrofossil records. There were many scientific works dedicated to marine fauna assemblages, especially Bivalvia, Gastropoda, Scaphopoda, Cirripedia, Annelida etc. The freshwater and terrestrial animals are much rarer.

In the sedimentary formations in Iceland, it is possible to observe much evidence of ecologic relationships within former palaeo-assemblages based on the trace fossils. The fossil record of animal activities have not been yet studied here; however their information potential is very large. At this moment, we identified varied bioerosion signs of Weichselian age, which remained after mechanic damages on shells, caused by the activity of predators; or after mechanic attachment of epibiotic organisms (e.g. *Anellusichnus, Caulostrepsis, Centrichnus, Clionolithes, Finichnus* and *Oichnus*), a lot of traces after locomotion on the surface or inside sediment, resting traces and escape traces were also found here (Miocene-Pleistocene). The interesting aspect is that the marine ichnoassemblages have worldwide geographic range (e.g. *Arenicolites, Helminthopis, Lockeia, Planolites, Rosselia* and *Teichichnus*); in constrast, the lacustrine trace fossils are mostly endemic (*Helminthoidichnites, Mammillichnis, Thorichnus* igen. nov. and *Vatnaspor* igen. nov.).



Speaker

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# Trace fossil infill: a tool to interpret bottom-current deposits

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In the last years, infilling of trace fossils has been revealed as a very useful tool to evidence lost sedimentary record. The sedimentary record is preserved exclusively in the burrow infill; the fill was emplaced deep within the sediment avoiding mixing by bioturbation or later erosion. In the middle Lefkara Formation at Petra Tou Romiou section, Cyprus, the Chalk Unit shows regular alternance of calcilutites and thin calcarenite beds. Most of the fine-grained calcarenite beds are associated to calcilutites in biogradational sequences. Nevetheless, coarser and other fine-grained calcarenite beds show clear normal grading changing upward to parallel and wave laminations. Some of these coarser-grained beds are very continuous but other display lateral changes in thickness, and even disappearance and the exclusive record of a suttle pressure dissolution seam. Calcilutites are best interpreted as pelagic sediment, while coarser-grained calcarenite beds with normal grading correspond with distal turbidites and fine-grained with biogradational sequences are associated to bioclastic sandy bottom-current deposits. For a correct interpretation of the involved processes, a detailed analysis of the transition between types of facies is essential, with attention to the registered trace fossils.

We have been focused on calcilutites and its transition with coarser-grained calcarenite beds. Ichnological analysis allows the differentiation between two trace fossil assemblages, located in the calcilutites, according to the infilling material: a) light trace fossils with calcilutite infilling similar to the host sediment, and b) conspicuous dark trace fossils with calcarenite infilling similar to the calcarenite beds. A variable relationship between calcarenite beds and conspicuous dark traces is observed, from two extremes, as conspicuous trace fossils coming down from a well-preserved calcarenite bed, to absence of conspicuous trace fossils but only presence of a pressure dissolution seam into the calcilutite interval. Detailed analysis of this variability allows interpret progressive grades of erosion affecting the turbidite calcarenite beds, including its total remobilization and the record of the "missing" sediments as the infilling of the trace fossils. Ichnological anaysis reveals as a proxy for a correct interpretation of the deep-water sedimentary processes and the influence of the reworking and erosion on turbidites.



Speaker

#### Co-evolution of marine and terrestrial biodiversification: links to producer stoichiometry and the leaf economics spectrum

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The broad patterns of marine and terrestrial faunal and floral biodiversity parallel one another, especially through the Meso-Cenozoic. This suggests a common factor underlying the diversification of the biosphere in general: the stoichiometry of food. The succession of increasingly phosphorus-rich major phytoplankton taxa through the Phanerozoic has been previously implicated in the diversification of the marine biosphere. Phosphorus is critical for cellular nucleic acid and cell membrane synthesis, energy storage and transfer, and bone construction. According to the theory of ecological stoichiometry, stoichiometrically-imbalanced food exhibits high carbon-to-phosphorus (C:P) ratios and consumers must therefore initially expend more energy upfront to respire carbon and obtain inorganic nutrients like phosphorus, whereas stoichiometrically-balanced food is characterized by much lowered C:P ratios. Increasing food quality (low C:P ratios) would leave more energy for biosphere "energetics" of metabolism, reproduction, and presumably micro- and macro-evolution that require increasing amounts of nutrient-rich food. Nutrients are originally derived from land via orogeny and volcanism.

The diversification of terrestrial floras parallels the successive dominance of vertebrate faunas. According to the leaf economics spectrum, certain plant traits are considered to be broadly universal and applicable to macroevolutionary timescales. Angiosperms tend to lie toward the "fast-return" end of the spectrum of rapid resource acquisition, short leaf lifespans, low leaf dry mass per area, and high concentrations of phosphorus whereas gymnosperms tend to lie at the opposite "slow-return" end. The dramatic increase of vertebrate diversity during the Cenozoic, as exemplified by fish, would therefore seem related to the spread of angiosperms and the availability of phosphorus for bone construction. The parallel evolution of diatoms and angiosperms and the explosive evolution of the Acanthomorpha (especially the Percomorpha) though the Cenozoic suggests a linkage between continents and oceans, possibly via enhanced decay of angiosperm leaf litter and the uptake of phosphorus by diatoms. The "chondrostean" and "holostean" radiations of fish are similarly paralleled by dominance of pteridophytes (Devonian to Triassic) and gymnosperms (Triassic into Cretaceous), respectively. These inferences are assessed against recent biogeochemical models.



Speaker

## Integrative study of the Angeac-Charente bonebed (Berriasian, Lower Cretaceous, Charente, France): vertebrate paleoecology and paleobehaviour implications

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Opportunity to study ecology and behavior of extinct vertebrates within their past ecosystem is exceedingly rare. Moreover, Lower Cretaceous terrestrial ecosystems of Europe are poorly known. The Berriasian (Lower Cretaceous) French paleontological site of Angeac-Charente, have fossilized a rich Mesozoic terrestrial swampy ecosystem. From 2010, 8 excavation campaigns have yielded a high diversity, richness and quality of fossils usually not found associated in a single chronostratigraphic unit. They include 7100 identified isolated vertebrate macroremains wearing abundant biological and mechanical marks, 64000 unidentified bone fragments, numerous identified vertebrate microremains, 130 natural casts of dinosaur tracks, 3320 vertebrate coprolites containing many plant and vertebrate inclusions, 140 Mollusca casts and numerous plant remains. Here we present our in progress results of an integrative multiproxy study based on taphonomy, sedimentology and ichnology of the Angeac vertebrate macroremains.

About 120 natural casts of true dinosaur tracks of various sizes have been found in a single bedding plane and could be associated, suggesting a social behavior for a same dinosaur trackmaker, interpreted as stegosaur. Few sauropod tracks of 1 meter diameter have been also identified, including one showing grooves created by the dinosaur skin scales of the moving foot in mud. Such dinoturbation explains most of sediments and bone modifications, as displacements, *in-situ* breakage and trample marks. The bonebed is mixed, multitaxic, monodominant and present a high taxonomic vertebrate diversity (39 taxa). Ornithomimosaur remains dominate the bonebed and belongs to at least 43 individuals, present a "catastrophic" age profile, are localized, not sorted and unabraded, indicating a mass mortality occurrence of a juvenile-dominated multiyear group. A complete turtle shell and most of 730 isolated plates, previously identified as *Pleurosternon bullockii* turtle remains, show bite marks. The *in-situ* position of the complete shell and the presence of hook marks, bisected pits and pits on the edges of the shell indicate the use of the "nutcracker" technique by a crocodiliform, Goniopholididae.

These taphonomical, paleoecological, paleobehavioural and paleoenvironmental informations indicate that Angeac site was the environment of life for the vertebrates and provide a unique opportunity to reach the landscape of a Lower Cretaceous European Ecosystem.



<sup>&</sup>lt;sup>\*</sup> Speaker

## The structure of rodent and lagomorph communities across the Cenozoic of North America: the importance of regional topography and climatic differences

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Several recent studies have demonstrated dramatic changes in North American rodent and lagomorph communities through the Cenozoic, with open-habitat specialists becoming common as open and arid habitats spread. Increased crown heights and burrowing, jumping, and cursorial adaptations appeared in rodents and lagomorphs millions of years before parallel changes in ungulate communities. To date, studies have primarily focused on continental scale analyses, but summation of geographically widespread faunas obscures how changes occurred in individual communities. Thus, comparison of regional and local scale changes are key to understanding how individual communities have changed, which is expected to be strongly influenced by topography and local climate conditions. Here we use a database of all fossil rodents and lagomorphs in North America to compare small mammal communities through time from eight distinct regions, and examine whether changes were synchronous across the continent or differed as a consequence of differences in topography and vegetational history. The earliest mammals with hypselodont (ever-growing) cheek teeth appeared in the late Eocene of the Northern and Central Great Plains. Hypselodont taxa appeared later in other regions, in the early Oligocene of the Pacific Northwest, early Miocene of the Great Basin and California Coast, and late Miocene of the Gulf Coast. The timing of shifts to communities dominated by taxa with high-crowned teeth was similarly regionally variable, starting in the early Oligocene in the Northern Great Plains and Pacific Northwest, early Miocene of the Central Great Plains and California Coast, middle Miocene of the Great Basin, and late Miocene of the Gulf Coast. Multiple regions showed increases in low-crowned taxa and simultaneous declines in hypselodont taxa at the time of the Middle Miocene Climatic Optimum. In the Pliocene, both the Pacific Northwest and Northern Great Basin shifted to faunas dominated by hypselodont taxa. Burrowing and cursorial species became common in the late Oligocene of the Pacific Northwest and Northern and Central Great Plains, but not until the middle Miocene in the Great Basin and late Miocene on the Gulf Coast. These results help to reveal important regional differences in the nature and timing of shifts within rodent and lagomorph communities through the Cenozoic.



Speaker

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## The use of ostracods in palaeoecological reconstructions on the example of the Callovian and lower Oxfordian of the Mikhailovcement (Ryazan Region, Russia)

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The Mikhaylovcement section (Ryazan region) is the key section for the Callovian and lower Oxfordian of the Moscow Synecline (MS).

Here 2436 individuals representing over 50 ostracod species were studied and grouped by various methods of the ostracod analysis, including the species diversity and abundance per sampling unit, size clusters of ostracods, and cosmopolitan to endemic species ratio. Also, palaeodepths and palaeotemperatures were inferred from the ratio of index-species restricted to peculiar environmental conditions.

These data allow us to establish five successive ostracod assemblages in the section representing an alternation of relatively deeper water and shallower water palaeoenvironments, which, possibly, are indicative for transgressive-regressive events in this area. The events in ascending order correspond to the intervals representing by the ostracod beds with *Cytherella*, with *Lophocythere* sp. A, with *Lophocythere sp. B- Neurocythere flexicosta labyrinthos*, and by the *Neurocythere dulcis* and *Sabacythere attalicata-Eucytherura costaeirregularis* ostracod zones. The earliest four of these events, probably, reflect the pan-European transgressive-regressive cycles, while the latest one is difficult to correlate directly with any event beyond the MS. The ostracod assemblage representing the later interval has no analogues in Western Europe despite the fact that it corresponds to the beginning of the most widespread Oxfordian transgression. Perhaps, this difference was related to the fact that at the beginning of the Oxfordian, the depths in the MS exceeded the lower limit of the macrophyte distribution (within 30-40 m below sea level) and, thus, prevented the migration of ostracods, which were coenotically associated with macrophytes in Western Europe, to the Russian Platform. During all the earliest transgressive events the palaeodepths here hardly did exceed this ecological barrier allowing West European ostracods to migrate to the MS and adjacent areas.

In general, during relatively deeper water phase of all the transgressive events, the boreal index was increased, while relatively shallower water ostracod assemblages were mostly formed under only the Tethys watermass influence.

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Speaker

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#### Molecular characterization of preserved tissues in a Cretaceous ankylosaur

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Pyrolysis-gas chromatography-mass spectroscopy (py-GC-MS) was conducted on a range of tissues from an exceptionally preserved nodosaurid ankylosaur, Borealopelta markmitchelli from the Early Cretaceous of Alberta. These experiments afforded pyrolysates dominated by n - alkane/alkene couplets with up to 32 carbon atoms. These couplets result from the breakdown of aliphatic biopolymers that are the dominant component of kerogens and have been formed when lipids polymerize and replace protein and other poorly-recalcitrant biopolymers [1,2]. Notably, the n -alkane/alkene couplets are absent from the concretion and the sediment surrounding the ankylosaur. Epidermis and horn tissues also contain assemblages of small nitrogen-, oxygen- and sulfur-containing heterocyclic and aromatic molecules characteristic of eumelanin (e.g. pyrrole, indole, N-methylpyrrole and methylphenol). Of special note, is the presence of significant amounts of benzothiazole which is diagnostic for pheomelanin. Sulfur may be incorporated into melanin during diagenesis to yield thiophenes, alkylthiophenes and benzothiophenes, which are also observed and could similarly be derived from phaeomelanin. As far as is known, however, diagenetic sulfurization is not known to give rise to benzothiazoles. Gastroliths and stomach contents each had characteristic pyrograms. The former contained an abundance of small aromatic components including alkyl benzenes and phenols with low contents of heterocyclics and n-alkane/alkene couplets. The stomach contents had a strong signal for aliphatic biopolymer in addition to a distinctive pattern of  $C_{27}$  and  $C_{29}$ steranes.

[1] Gupta *et al.* (2008) Molecular taphonomy of macrofossils from the Cretaceous Las Hoyas Formation, Spain. Cretaceous Research 29, 1-8.

[2] Stankiewicz et al. (2000) Alternative origin of aliphatic polymer in kerogen. Geology 28, 559-562.



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## Spatial gradient of pyrite sulfur isotope in early and middle Ediacaran successions of South China

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The amount of sulfate in the early and middle Ediacaran ocean was tied directly to oxygen levels in the atmosphere and the deep ocean. Isotope fractionation between sulfate ( $\delta^{34}S_{CAS}$ ) and pyrite ( $\delta^{34}S_{pyr}$ ) can express the environmentally diagnostic biogeochemical pathways of the sulfur cycle, thus can indicate the sea-water sulfate level. High-resolution sulfur isotopes complied with inorganic and organic carbon isotopic stratigraphy were obtained from early and middle Ediacaran successions of western Zhejiang and southern Anhui provinces, South China. The results show that Ediacaran  $\delta^{34}S_{CAS}$  values almost keep consistent, on the contrary,  $\delta^{34}S_{pyr}$  values display spatial gradient through the shallow water facies and deep water facies of Yangtze Block of South China.  $\delta^{34}S_{pyr}$  values in platform facies are significantly higher than those in slope and deep-water facies, but comparable with those in the deepest water facies. The most distinctive spatial pattern is an overall decrease in  $\delta^{34}S_{pyr}$  values from shallow to deep facies, following by an increasing trend in deepest facies. The observed spatial pattern of  $\delta^{34}S_{pvr}$  is best interpreted as evidence for oceanic redox stratification with euxinic deep waters and relatively oxic shallow waters. When pyrite precipitation occurs in euxinic deep waters, lower  $\delta^{34}S_{pyr}$  values are expected because sulfate reducing microbes have full access to marine sulfate, which was already a few mM in Ediacaran oceans, and maximum sulfur isotope fractionation is possible. In contrast, when pyrite precipitation occurs within sediments in shallow-water facies, sulfate availability is limited by diffusion and high  $\delta^{34}S_{pvr}$  values are expected. It is possibly inferred that Doushantuo sediments in inner and outer shelf facies were mostly deposited in relatively oxic conditions, whereas euxinic conditions frequented deeper waters in intra shelf, slope, and basinal facies. The research offers a first-order framework of stratified ocean in early and middle Ediacaran ocean immediately after the end of Snowball event.



S9 // Oral

Speaker

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#### Distribution and evolution of Carboniferous reefs from the shelves around the South China and North China blocks

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After the collapse and disappearance of reef ecosystem during the Frasnian-Famennian and Hangenberg mass extinction events, the Carboniferous reefs on the shelves around the South China and North China blocks underwent evolutionary episodes of recovery, decline, and turnover. In early Tournaisian times, microbial biostromes composed of stromatolites were present in Pingchuan, Gansu, North China. In the late Tournaisian, Waulsortian-like mud mounds developed in Liuzhou, Guangxi, South China. However, no skeletal bioconstructions have been reported from the Tournaisian. They first appeared in the middle Visean as low- height coral biostrome in Huishui, Guizhou, South China. The abundance and diversity of skeletal bioconstructions increased distinctly during late Visean times, as evidenced by coral organic reefs and biostromes, coral-microbial-bryozoan organic reefs, and microbial reef mounds and biostromes. The reef abundance declined strongly in Serpukhovian times, with only few coral biostromes exposed in Alashan, Inner Mongolia, North China. A distinct change in reef types occurred after the Mississippian-Pennsylvanian boundary, when phylloid algae and red algae reefs known at Ziyun, Guizhou and Beibuwan, Guangxi, replaced metazoan reefs and became dominant in the reef ecosystem. The evolution of Carboniferous reefs on the shelves around South China and North China blocks, was controlled mainly by the changes in reef-builder abundance, sedimentary facies, relative sea level, and even global climate. During times, such as Visean and late Bashkirian to middle Kasimovian, when reef-building metazoan flourished, carbonate facies was wide-spread ascribed to relative sea-level rise, metazoan reefs developed abundantly. On the contrary, when reef-building metazoan declined and non-carbonate facies became more abundant due to relative sea-level fall, metazoan reefs were suppressed as during the Tournaisian and Serpukhovian. From the Mississippian to Pennsylvanian, the changes from metazoan reefs into algal reefs were caused primarily by the development of shallow-water carbonate facies resulting from relative sea-level fall. In addition, global climate cooling and warming, resulted from the waxing and waning of Gondwana glaciation, may also influence the reef evolution, as evidenced from the consistent transgression and regression events and global reef evolutionary pattern during the Carboniferous.



S9 // Ora

Speaker

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## Recovery scenario of the benthic biota in the aftermath of the latest Ordovician events: cases from a near-shoal belt of the Upper Yangtze Platform, South China Block

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In reconstructions of behavioral aspects and diversification, ecological types of the marine facies during the glaciation episode of the earliest Silurian are quite different due to the diachronous of environmental shift after the extinction events. Oceangraphic parameters were diverse on the Upper Yangtze Epicontinental Sea, South China Block. Typical black shales of the Lungmachi Formation are favorable for the records of graptolitic sequences from deeper off-shoal and shelf belts which maintained stagnant and anoxic marine seafloors. However, the shallower near-shoal belts along coastline of the Dian-Qian-Gui Oldland were more oxic and thus idealized settings for the inhabitation of benthic fauna in Rhuddanian (basal Silurian). Two types of ecological assemblages are recognized. The Niuchang Formation at the Dongkala, Fenggang is about 8m in thickness, and composed of grey and greyish yellow silts and marls. Monotonous Helminthoides (ichnofossil) occur with high abundance; in contrast, other body fossils are extremely sparse. Such a case indicates low diversity of tracemakers. The Rhuddanian unit at the Xiangshuyuan section, Shiqian is 3.3m thick yellow and yellowish-green silty shales intercalated with 6 thinbedded units and lenses of bioclastic limestones. Highly diverse and abundant benthic taxa including stromatolites, sponge spicules, tabulate and rugose corals, trilobites, ostracods, brachiopods, and crinoids are identified from microfacies of the limestones. This bioclastic facies records the highest biodiversity of the shelly fauna when compared to equivalent units elsewhere on the South China Block. It provides a remarkable association of the metazoan marine life of the earliest Silurian, more than two-fold the number of taxa than the former taxonomic records. Owing to its unique lithological and biotic components, we formally name this units the Kuzhuyuan Formation. Recovery of the earliest Silurian diverse shelly fauna was limited, and occurred in the near-shoal belt in Shigian where the marine water was higher clarity.

S9 // Oral

Speaker

#### Mid to late Pleistocene productivity changes in the east equatorial Pacific from benthic foraminiferal assemblages

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The East Equatorial Pacific (EEP) accounts for 5-10% of the global marine production while representing only 10% of the global ocean. Evaluating glacial-interglacial changes in the past productivity is relevant for the general understanding of the Earth's climate system. Reconstructions of paleoproductivity from different proxies in the EEP reveal complex spatial and temporal patterns. In this study we qualitatively evaluate the strength and mode (episodic versus sustained) of the organic carbon flux to the seafloor using absolute and relative abundances of benthic foraminifera for the last one million years in the EEP. Foraminiferal assemblages are analyzed in IODP Hole 1381C (2064 m water depth) and ODP Site 1242 (1364 m water depth) located offshore the Costa Rica margin. The Hole U1381C spans the last 700 kyr and the Site 1242 records the period from 0.7 to 1 Ma. The foraminiferal faunas show significant glacialinterglacial changes in abundance and species composition. We interpret that the assemblages respond to changes in the seasonality of the productivity and therefore to the organic carbon arriving to the sea floor together with variable oxygenation levels in the bottom waters and the sediment. Those changes are likely linked to global oceanographic and atmospheric organizations occurring during mid to late Pleistocene abrupt climate changes. Acknowledgements: This study is a contribution to project "Reconstruction of the organic carbon flux to the sea-floor in the East Equatorial Pacific during the Mid Pleistocene Transition: implications of the ocean in climate changes". CGL2016-79878-R.



S9 // Poster

Speaker

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#### Facies characterization and sedimentological scenario of the Messinian stromatolites from Western Mediterranean (Northern Bajo Segura Basin)

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The Messinian stromatolites intimately related to the Messinian Salinity Crisis (Terminal Carbonate Complex unit) from the northern sector of the Bajo Segura Basin (Cam section, Sierra del Colmenar, SE Spain) have been studied. To understand the direct relationship between the morphologies of the stromatolites and their depositional context in order to reconstruct the paleoenvironmental conditions for their growth, a detailed study of their architecture, external morphology, and internal morphology (macrofabric/general internal structure and microfabric) was carried out. The studied sequence presents a highly developed stromatolitic level whose macrostructure consists of domical and interdome forms arranged parallel to the coast and acting as a palaeogeographic barrier. The analysis of facies relationships enable us to infer that the stromatolites were formed in a restricted, subtidal-intertidal to supratidal environment. The variation in internal morphology over vertical stromatolite growth provides evidence of minor changes in the physical environment during the development of each stromatolitic subfacies. The upper part of subfacies 1 marks the beginning of a subtidal environment with conditions of constant humidity and low hydrodynamic energy, which is maintained throughout the development of subfacies 2. Subfacies 3 represents a sudden loss of depth and an increase in hydrodynamic wave energy, and the transition to subfacies 4 indicates the begins of a progressive increase of depth begins that continues until reaching its maximum in subfacies 5. The transition from subfacies 5 to 6 indicates a gradual decrease in depth and during the formation of subfacies 7, shallowing continued and puts an end to stromatolite growth. Finally, domes and interdome filling material undergo sub-aerial exposure and are shaped by an erosive process, as represented by the late-Messinian unconformity.



S9 // Poster

Speaker

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#### Microinclusions (palynomorphs and paleoparasites) recovered from a Late Pleistocene carnivore coprolite from southern Brazil

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A unique, cylindrical coprolite (MCPU-PV-141; 180 mm long, 40 mm diameter) was collected in the Upper Pleistocene Touro Passo Formation of southern Brazil and has a diverse array of inclusions. The macroremains include plant fragments and undigested bones, some of which were identified as ground sloth osteoderms preliminarily assigned to an indeterminate Mylodontidae. Additionally, through standard palynological methodology, different palynomorphs were also found. The most common palynomorphs were grass pollens (Poaceae and Cyperaceae), followed by a small amount of tree pollens (Arecaceae, Myrsinaceae and Myrtaceae) and less representative Pteridophyta and Bryophyta spores. This pollen diversity can be interpreted as a landscape with small groves, formed by trees, which provided shadow and air humidity for the pteridophytes and bryophytes. The grasses were the most common vegetation, which must have covered the land as in a savanna. Large water bodies were not so common, as demonstrated by the lack of aquatic plant palynomorphs. As the total amount and pollen diversity was not so large, the presence of palynomorphs inside the coprolite is interpreted as being derived from an accidental ingestion trough the water or food, not by feeding directly the vegetation. The preliminary paleoparasitological analysis of the coprolite revealed the presence of 14 specimens (11.9  $\pm$  1.1  $\mu m$  long, 11.5  $\pm$  1.2  $\mu m$  wide) with morphological and morphometric characteristics compatible with oocysts of protozoans belonging to Eucoccidiorida. In addition to protozoans, were also observed three specimens (60.8  $\pm$  1.4  $\mu$ m long, 30.8  $\pm$ 1.4 µm wide) with size and shape similar to Spirurida nematodes. Currently, both taxa have species known by parasitize carnivorous mammals and are also acquired through the predation of other vertebrates. Although it is not possible to determine the host only by the morphological and morphometric study of the paleoparasites found, molecular analyzes are being conducted with the purpose of detecting the specific DNA of certain protozoans, which show narrower specificity with some species of carnivores, in an attempt to elucidate the animal that produced this coprolite. Therefore, it is expected that the analyses of microremains (palynomorphs and paleoparasites) in the specimen MCPU-PV-141 provide significant information about this large-sized carnivore that inhabited the Late Pleistocene Touro Passo paleoenvironment.



<sup>&</sup>lt;sup>°</sup> Speaker

#### Pleistocene palaeoenvironmental changes in the Western Iberian margin: integrative ichnological and TOC analysis

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Site U1385 (Shackleton Site) was drilled in the Western Iberian Peninsula by IODP Expedition 339, with the aim to generate a marine reference section of sub-Milankovitch climate variability during the Pleistocene. Here we present the study of a selected Pleistocene record to evaluate the integrative ichnological and Total Organic Carbon (TOC) analysis as a proxy for palaeoenvironmental reconstructions. Ichnological analysis reveals a trace fossils assemblage composed of seven ichnotaxa, such as *Chondrites, Nereites, Palaeophycus, Planolites, Thalassinoides, Thalassinoides* -like traces, and *Zoophycos*, belonging to *Zoophycos* ichnofacies, as well as a variable degree of bioturbation. Four ichnofabrics have been differentiated, *Planolites* ichnofabric, *Thalassinoides* ichnofabric, *Zoophycos* ichnofabric and *Chondrites* ichnofabric, showing a variable distribution through the studied interval. Ichnological features reveal generalized favourable environmental conditions for the macrobenthic trace maker community, in terms of oxygen and nutrients, although is recognized the existence of punctual impoverishment indicating to lower oxygen levels and food supply. TOC data vary between 0.6 and 1.43 wt % with no significant fluctuations, pointing to generally good oxygen, nutrients and productivity conditions. Changes in palaeoenvironmental conditions during the studied interval, interpreted from the integrative TOC/ichnological analysis, can be related with climatic variations associated to glacial-interglacial cycles.



Speaker

# Metabolic Time Machine: an emerging field of geogenomics

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"Metabolic Time Machine" is a forthcoming project aiming at elucidation of the nature of adaptation of life to secular changes of earth environments, especially focusing on arguably the most drastic environmental change in geohistory, viz., the rise of atmospheric oxygen. To this end, we attempt to integrate earth and life sciences with the help of metallomics, information science, as well as the key concept of geogenomics. Recent development of DNA sequencing technologies has resulted in producing complete genome data for an increasing number of living organisms. Just like humans did not evolve from a chimpanzee, however, those genome data, be they from a sponge or a bacterium, do not represent the genomes that our ancestors possessed. The ancestral genomes (coding and non-coding sequences, gene set, synteny, gene orders, etc.) should be (and shall in this project be) reconstructed for each node of the phylogenetic tree through comparisons of genome data of living organisms. The reconstructed genomes, in turn, will support us to infer the biochemistry and physiology of the common ancestor at each node through molecular cloning of the genes encoding an ancestral sequence (gene resurrection) and reconstruction of metabolic pathways based on the set of enzyme genes contained in the genome, respectively. In this context, we focus on the proteins and biomolecules that utilize a metal element such as Fe, Cu, Zn, Co, Mg, Mn, Ni, Mo, W, etc., or a non-metal element such as Se, as an integral component for two reasons. One is that the availability of these elements in the environments for organisms is expected to have changed depending on the oxidative state of the environments throughout the geohistory. The other is that the secular changes of the abundance for each of those elements can be (and shall in this project be) quantified using the state-of- the-art analyses of the samples preserved in the geological record. The resulting hypotheses of interactions between life and environments shall be tested through mathematical models. All the data obtained in this project shall be interconnected and be released to the public through the "integrated geogenomics database". Although this project is to be supported by a national source, ample schemes of international exchanges shall be offered. We thus seek for international partners who are willing to collaborate with us.



Speaker

#### Transfer functions derived from planktonic microfossils and their use to reconstruct past seasurface conditions: strengths and limits?

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Planktonic microfossils constitute key material for paleoceanographers for which they are, since nearly one century, basic tools for stratigraphic and paleontological reconstructions. Approaches relying on the compilation of modern eco-biogeographical databases, derived from the analysis of recently fossilized populations in the topmost oceanic sediment layers, provide comprehensive sets which have considerably improved our bioclimatic knowledges on modern microfossil assemblages. These modern sedimentary spectra, analysed for their contents/ relative abundances in planktonic microfossils, offer the advantage of integrating regional taphonomic processes, and can furthermore be statistically tested and exploited to provide proxies of oceanic conditions, as done for instance with transfer functions *sensu lato* (e.g. Kucera *et al.* **//** 2005; Telford and Kucera, 2013). Here we test the robustness of the Modern Analog Technique (MAT), thanks to the coupling of two databases compiling complementary microfossil training sets, i.e. planktonic foraminifera and dinoflagellate cysts. We focus our tests on the North Atlantic Ocean (and its border seas), and on several time scales over the Quaternary. Those sets were extensively tested in the last decade, providing very coherent paleoceanographic reconstructions along the western European margin. A selection of these results is presented here.



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# Characterizing traces of predation and parasitism on fossil echinoids

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Living echinoids are observed interacting with various predators and parasites, producing a range of distinct traces that are found on Recent and fossil echinoids. However, descriptions of the morphology and ecology of drill holes on echinoid tests vary, and identifying trace-makers on fossil echinoids remains contentious due to the paucity of diagnostic criteria. Rigorous characterizations and descriptions of a broad range of traces observed on echinoid tests could improve our ability to identify and interpret ecological interactions between echinoids and their predators and parasites in the fossil record.

Here we describe and characterize traces of biotic interactions found on fossil echinoid tests from the southeastern U.S. using museum collections and recent field work in the region. 13 species were targeted based on their abundance in the collections, and all specimens were examined for traces inferred to be biological in origin using light-microscopy. A total of 2,550 specimens were examined, and 341 traces were observed. The following morphological characteristics were recorded for each trace: trace outline, maximum diameter, edge characteristics, and trace location on the test. Using these descriptive variables made it possible to group traces with comparable morphological descriptions into 8 general categories: circular, figure-eight, irregular, linear, notched circle, oblong, rectangular, and subcircular. A total of 46 representative example traces from each category were then selected for SEM imaging to create highresolution images of each morphological class to enhance trace characterizations.

Circular traces were most common (n=158), followed by subcircular (n=58) and oblong (n=51) traces, interpreted as being produced by either predation or parasitism. These traces had a wide range of outline characterizations, including smooth, rounded, beveled, irregular, and jagged. In rare cases, circular and subcircular traces were surrounded by a dissolution halo (n=25), interpreted as the product of acid etching during gastropod predation.

These categorizations contribute to a growing literature on echinoid associated traces, and ecological interpretations of interactions with echinoids. A thorough classification of trace types may promote the identification of traces on fossil echinoids, and enhance our ability to identify evolutionary trends in interaction intensity and diversity in the fossil record.



Speaker

## Lipid biomarkers and invertebrates reveal that microbialites on the Neotethyan platform formed in oxygenated environments following the latest Permian mass extinction

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After the latest Permian mass extinction event, microbial mats filled the ecological niche previously occupied by metazoan reefs, resulting in widespread microbialites. We aim to identify the lipid biomarker (molecular fossil) and invertebrate fossil records from Neotethyan platform margin sections to understand the conditions that led to the formation of widespread microbial- metazoan bioherms. Here, we find that thrombolitic and stromatolitic microbialites from Çürük Dag (Turkey) and Kuh e Surmeh (Iran) contain abundant lipid biomarkers (molecular fossils), representing input from cyanobacteria, anoxygenic phototrophic bacteria, sulfate-reducing bacteria, and halophilic archaea. The biomarker inventory suggests that the microbialites were constructed by cyanobacteria-dominated microbial mats. Biomarkers of halophilic archaea are interpreted to reflect input from the water column, suggesting that the Neotethys experienced at least episodically hypersaline conditions. We also demonstrate that bacteria, possible keratose sponges, and microconchids lived synergistically to form microbial-metazoan bioherms in the immediate aftermath of the extinction along the western margin of the Neotethys. Abundant fossils of oxygen-dependent invertebrates (i.e. microconchids, bivalves, gastropods, brachiopods, and ostracods) and foraminifers were also found within these bioherms. The presence of invertebrates in conjunction with abundant molecular fossils of cyanobacteria indicates an oxygenated water column. The proliferation of post-extinction microbialites is, therefore, attributed to a relaxation of ecological constraints caused by the magnitude of the extinction.



<sup>&</sup>lt;sup>\*</sup> Speaker

## Ichnofabric analysis of deep-sea calcilutites affected by turbidites and bottom currents at the Eocene of Cyprus: macrobenthic response to palaeoenvironmental conditions

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The Chalk Unit at the middle Lefkara Formation at Petra Tou Romiou section, Cyprus, shows regular alternance of calcilutites and thin calcarenite beds. Calcilutites are best interpreted as pelagic sediment, while calcarenite beds correspond to distal turbidites or bioclastic sandy bottom-current deposits. Here we present the ichnofabric analysis (trace fossil composition, density of bioturbation, and tiering complexity) of calcilutite intervals to characterize the trace maker community structure, its evolution during calcilutite deposition, and the relationship with the associated palaeoenvironmental parameters. A composite chalky ichnofabric with profuse bioturbation is recognized, consisting of abundant Planolites, Chondrites, and Zoophycos, common Thalassinoides, and rare Taenidium. Background mottling generated by biogenic activity in the soup-ground mixed layer, corresponding to the uppermost tier, is rarely observed. The upper tier assemblage is composed by Thalassinoides, Taenidium and Planolites, the middle tier is constituted by Zoophycos and large-Chondrites, and the deeper tier consists, exclusively, of small-Chondrites. This ichnofabric shows an autocomposite character, associated to bioturbation by a single ichnocoenosis and gradual upward migration of the tiered macrobenthic community as the slowly calcilutite sedimentation progress. Abundant, diverse, and persistent, bioturbation, reveals maintenance of favorable palaeoenvironmental conditions for macrobenthic trace maker community during pelagic sedimentation of individual calcilutite intervals between calcarenite beds. The differentiated composite ichnofabric is observed as a general pattern in the calcilutites through the section, regardless the particular calcilutite interval between the calcarenite beds, with only punctual variations. This fact allows interpreting an equivalent response of the trace maker community after turbidites and bottom-current processes evidencing a similar reestablishment of background palaeoenviromental conditions related to calcilutite deposition. Minor variations in this pattern can be related to taphonomic processes associated to calcarenite deposition. We can conclude that calcarenite deposition processes didn't disturb a wellestablished calcilutite macrobenthic trace maker community probably due to a relatively rapid reestablishment of background palaeoenvironmental conditions.



<sup>°</sup> Speaker

## Vast Holocene diatom mat deposits and their relationship to rapid sinking of diatom blooms by downslope shelf water off the northwestern Weddell Sea, Antarctica

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The Southern Ocean is very important for the oceanic sequestration for atmospheric  $CO_2$  in the world's ocean and one of the major mechanisms by which carbon is sequestered to the deep ocean is diatom-dominated phytoplankton blooms accompanied by mass sinking of bloom biomass. However, the fate of the sinking from the surface to the deep-sea floor has not been adequately resolved. Here, we report an extensive mat deposit as proof of rapid export of huge diatom blooms in the seasonal sea ice zones on Antarctic shelf to deep-sea sediments off the northwestern Weddell Sea. We present new evidence that these diatom mats formed from mass sinking of diatom blooms off the shelf break aided by northward advection and subsequent sinking of plankton-rich cold shelf water in the sea ice zones, resulted from isopycnal mixing of Weddell Sea shelf water with Modified Circumpolar Deep Water. The mass accumulation of diatom blooms on a scale that is recorded in the sediments, however, may require major cooling conditions; such a cooling condition may facilitate the continuous drawdown of diatom blooms driven by the intensification of the downslope shelf water. The carbon export from the diatom blooms at the seasonal ice on the Antarctic shelf might have significantly influenced the biogeochemical cycling in the glacial Southern Ocean, especially when downslope shelf-water formation following the Antarctic Slope Front markedly increases along the circum-Antarctic continental margin during glacial periods. Moreover, our results show that the mass sinking of shelf bloom diatoms by downslope flow along Antarctic continental margin may partly explain the "enigma" of rapid biomass decline following spring biomass maximum of the Antarctic phytoplankton.



Speaker

# S10 - Conservation palaeobiology and historical ecology of marine ecosystems

#### Keynote

Jeremy Jackson // Where is the conservation in conservation paleobiology?
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# Where is the conservation in conservation paleobiology?

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Paleobiological data contribute importantly to basic understanding of the timing and extent of human impacts on the environment. But beyond greater refinements to this obituary for nature, it remains unclear how paleobiology can contribute useful insights for achieving concrete conservation targets. A major complication is that both natural and anthropogenic disturbances have complex cascading effects on biological interactions among species due to differences among species' life histories, habitat preferences, and diet. For example, changes in Caribbean ecosystem structure and species extinction lagged over 1 myr after oceanographic changes following emergence of the Central American Isthmus because of the drawn out shift from predominantly soft sediment to biogenic coastal habitats. These changes in habit further set off changes in food webs due to more intense rates on predation. These effects were again further compounded by megafuanal extinction in response to intensified Pleistocene climate variability and sea level fluctuations in addition to decreased productivity. Such complex ecological shifts underlie the increasingly ominous phenomenon of extinction debt and highlight the importance of the changing composition of keystone species in response to anthropogenic pollution and climate change. For example, increasing nutrient pollution is degrading seagrass and coral reef habitat along the Florida coast with concomitant losses of associated species; in effect reversing the changes millions of years before due to Caribbean isolation from the Pacific. But when pollution was reduced in Tampa Bay, seagrass meadows were fully restored. Conservation paleobiology needs to sharpen its focus on the past responses of such keystone species in relation to their trophic position and life histories. In doing so, we can provide powerful long-term insights for ecosystem restoration.



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#### Lessepsian fish invaders caused major assemblage shift on the Israeli shelf: evidence from a live-dead agreement study

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The eastern Mediterannean is one of the regions most impacted by the the establishment of alien fish species from the Red Sea (Lessepsian invasion). However, despite important recent studies, lack of data on the marine fish fauna in this area before the Suez Canal opening severely hinders accurate predictions on the progress and impacts of this phenomenon. We investigate the impact of the establishment of alien fish species by comparing the marine fish death assemblages (DAs) in the surficial sediments along the Israeli coast with the living assemblages (LAs). Such a comparison can quantify the magnitude of major assemblage shifts in recent times, because the death assemblage retains a strong signal of the taxonomic composition and community structure of pre-impact assemblages. Our DAs are based on identified otoliths from grab sediment samples collected at 10-40 m water depth. The LAs includes data from 1990-2012 trawl surveys. Assemblage shifts were quantified by comparing the DAs with the LAs in terms of species richness, evenness, taxonomic similarity, and rank-order in species abundance. Moreover, we compared the relative species abundances; the contributions of alien versus native species; the relative abundances of tropical, subtropical, and temperate species; and the community composition by multidimensional scaling plots. The DAs are dominated by species native to the Mediterranean: the conger Ariosoma balearicum in 10 m depth and the anchovy Engraulis encrasicolus at 20-40 m. In contrast, the LAs are dominated by alien species. The taxonomic similarity is low (< 0.5), that is, the species which constitute the LA are different from those of the DA. The rank order of species abundance also differs between LAs and Das, showing that alien species are more abundant in the LAs than in the DAs, whereas the native species show decreased abundance with time. The DAs are characterized by a higher species richness and evenness, well within the expectations of the effects of time-averaging. Thus, our live-dead agreement confirms the occurrence of a massive shift in the composition and structure of fish assemblages.



Speaker

# The historical ecology of the Lessepsian invasion: perspectives from sediment cores

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Since its opening in 1869, hundreds of tropical species entered the Mediterranean Sea via the Suez Canal. This so-called "Lessepsian invasion" is the single largest marine biological invasion. Yet, quantitative data of its spatial and temporal extent and that of the native communities is available only for the last few decades. This brief historical perspective hinders our understanding on how the invasion progressed since its beginning and how factors such as the progressive enlargement of the Canal, the changes due to the Aswan dams on the Nile discharge, the decline of the saltwater barrier of the Bitter Lakes and seawater warming affected the process.

To overcome this impediment, we reconstructed the onset of the Lessepsian invasion and the changes in the native community by studying molluscan shells in two 1.4-meter-long sediment cores collected at 30 and 40 m water depth off Ashqelon in southern Israel.

At 30 m depth, non-native species were present in the sandy upper 50 cm of the coreand at the sandy sediment at its bottom, but were absent from the muddy sediment at its middle 60 cm. In non-metric multidimensional scaling (NMDS) plots, the molluscan community is structured in different assemblages down-core, with a more distinct separation of the uppermost 25 cm suggesting that the most modern assemblages have experienced a stronger directional change than those along the time interval captured by the rest of the core.

At 40 m depth, very few non-native species were present and limited to the upper 55 cm of the core, again with an apparent greater richness in less muddy intervals. In NMDS plots, there is poor structuring of the assemblage down-core. Because the analysis of living and death assemblages from grab samples suggests a major ongoing change of the community, the lack of a strong signal in this core may indicate that this change is a very recent phenomenon at this depth.



Speaker

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#### Trematode dynamics through time and space in Holocene sedimentary successions of the Po Basin, Italy

Michele Azzarone \*+<sup>1</sup>, Daniele Scarponi <sup>1</sup>, John Huntley <sup>2</sup>, Rafal Nawrot <sup>3</sup>, Alessandro Amorosi <sup>1</sup>, Monica Caffara <sup>4</sup>, Andrea Gustinelli <sup>4</sup>, Michał Kowalewski <sup>3</sup>

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Holocene brackish succession (core 204S7) of the Po Plain revealed a recurrent association between increases in parasite prevalence (trematodes traces on the valves of Abra segmentum) and parasequence bounding surfaces. Here we expand the investigation of trematode parasitism in bivalve species to a ~25km down-dip cored transect in the Po Plain, which crosses different paleo-environments: brackish (core 204S7), nearshore (core 205S6), and nearshore to proximal marine (core 205S14). Non-Metric multidimensional scaling (nMDS) is applied to investigate main drivers of mollusk turnover and highlight the primary Holocene sedimentary packages of Po plain stratigraphic architecture. The faunal turnover along the nMDS major axis expresses the combined effect of salinity and bathymetry, highlighting alternating periods of rapid flooding and gradual shallowing (i.e., meter-thick parasequences). The results are generally consistent with previous interpretations and largely invariant to spatial and taxonomic scales of the analysis. Parasite prevalence in individual samples displays a high temporal variability across all the investigated cores and an overall decreasing trend seaward. Single-sample values in A. segmentum range from 7% to 70% in core 204S7 and 8% to 53%, in core 205S6. Along core 205S14, Donax semistriatus prevalence ranges from 17% to 33%. Four flooding surfaces highlighted by fossil ordination outputs have been recognized in core 204S7. Three of them are associated with significant peaks in prevalence (i.e. outside the 95% randomization confidence interval) for A. segmentum (at 12.3m, 10.3m and 9.3m core depth) and Loripes orbiculatus (at 12.3m core depth). Along the core 205S6, statistically significant prevalence peaks for Lentidium mediterraneum (18.0m and 10.9m core depth) and Chamelea gallina (13.2m core depth) coincide with three of the six centennial-scale flooding surfaces recognized. Along core 205S14 mollusc turnover highlights three flooding surfaces only (28.0m, 25.6m and 25.1m core depth), which are not associated with statistically significant prevalence peaks among the investigated samples. In conclusion, the recurrent association between flooding events and surges in trematodes infestation appears restricted to brackish and nearshore settings. Nevertheless, these evidences suggest that anthropogenic sea-level rise may have led to significant alterations in host-parasite interactions along a wide spectrum of coastal ecosystems.

IPC 5

Speaker

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# Conservation paleobiology and the psychological distance of climate change: A perspective from construal level theory

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The field of conservation paleobiology holds great promise in providing a long-term perspective on biotic responses to the major environmental stressors-climate change, habitat change, invasive species, pollution and overexploitation of wild species-acting on biodiversity today. Despite this potential, results from a recent survey of marine conservation biologists aimed at characterizing their conception of "longterm" indicated that they tend to think data on time scales of centuries and longer (e.g., paleontological data) are needed to address conservation issues related to climate change, but not the other four environmental stressors. Here, we propose a hypothesis to explain this result based on the construal level theory of psychological distance. This theory posits that an event that is psychologically distant from a person in one or more dimensions, including temporal, spatial, social, and hypotheticality distance dimensions, will be construed by the person in a "higher," more abstract way than an event that is closer to the person. Specifically, we propose that because climate change is perceived as a long-term environmental stressor that is psychologically distant (i.e., the longer temporal scales of climate change involve higher level, more abstract construals) data derived from the fossil record are more likely to be perceived as useful for addressing this phenomenon. In contrast, the other environmental stressors might be perceived as psychologically closer (i.e., easily observed, with lower level, more concrete construals), so paleontological data are not likely to be perceived as necessary to address these stressors. Psychological distance presents a previously unrecognized obstacle to the full application of paleontological data in conservation science. Recognizing this psychological bias may help develop targeted communication strategies to increase peoples' motivation to use paleontological data in conservation efforts.



Speaker

## Exploring the utility of dermal denticle assemblages to reconstruct shark communities on coral reefs

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Historical accounts often depict high shark densities that sharply juxtapose contemporary reports in the same regions, but without quantitative shark baselines, we are unable to estimate true declines and understand how reef ecosystems functioned before major human impact. We are exploring the utility of shark dermal denticles, the tiny tooth-like scales covering elasmobranch skin which accumulate and are well-preserved in coral reef sediments, to reconstruct historical shark communities. In this study, we assessed the fidelity and resolution of the modern denticle record on Palmyra Atoll (central Pacific), where sharks are famously numerous and well-studied. We compared denticles accumulating in the carbonate sediments of several reefs on the atoll with previously collected shark abundance data from four different ecological survey methods: underwater visual census, baited remote underwater video stations, tagrecapture studies, and catch per unit effort (CPUE) during scientific fishing. We found a strong correlation between denticle abundance per kilogram of reef sediment and underwater visual census data collected from the same reefs. We also found that denticle types reflected the known shark taxa on the atoll. Comparing denticle assemblages with the outputs of these traditional survey methods helps standardize the denticle record and explore its limitations, enabling comparisons between denticle assemblages in congruent habitats across space and over time. When applied to fossil denticles, this new tool could provide insight into shark communities before industrial fishing, facilitate assessments of the magnitude and ecological consequences of shark declines, and help set more appropriate, region-specific management targets.



Speaker

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## Complexity and stability of marine paleocommunities during escalation and restructuring

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Anthropogenically-driven biological change is currently resulting in catastrophic losses of biodiversity. To anticipate ecosystem responses and effectively manage resources, we must understand how ecosystems respond to extreme changes; yet there are no precedents in human experience to guide us. Accordingly, the assessment and reconstruction of ecosystem dynamics during previous intervals of environmental stress and climate change in deep time has garnered increasing attention. The nature of the fossil record, however, raises questions about the accuracy of reconstructing paleocommunity and paleoecosystem-level dynamics. Here, we present the results of two studies, the first of which assesses the reliability of such reconstructions by simulating the fossilization of a highly threatened and disturbed modern ecosystem, a Caribbean coral reef. System structures of the modern and simulated fossil reef food webs were evaluated and compared, including guild richness and evenness, trophic level distribution, predator dietary breadth, food chain lengths, and modularity. Second, we present a large deep-time marine food web from the early Mesozoic (Anisian) of western Tethys and consider how ecosystem resilience may differ from modern ecosystems. We find that fossil marine communities can successfully be used to understand community dynamics during past regimes of environmental change. Despite the loss of species, guilds, and trophospecies interactions, particularly soft-bodied organisms, the overall guild diversity, structure, and modularity of the fossil ecosystem remained intact. This has important implications for the early Mesozoic food web, as our results indicate that ecosystem complexity was low and resilience was relatively high, though these likely changed through time due to rapid diversification and increasing predation. These factors appear to affect community structure and stability and are thus important drivers of evolutionary change.



Speaker

#### Superficial deposition of palynomorphs in continental shelf as the evidence on continent and ocean communication (southernmost Brazil)

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Actuopalinogical and sedimentological studies in continental shelfs are important tools to comprehend the coastal dynamics and their relationships with continental areas. These studies are useful in paleo environmental and paleo climatic reconstructions. The main objective of this work was to describe the superficial depositions of sediments and palinomorphs at the inner continental shelf of Rio Grande do Sul. A total of 48 samples were collected between 2 and 22 m, nearby Balneário Hermenegildo. Linear Models were used to verify the relations between frequencies of palinomorphs/sediments and depth. To carry out Cluster Analysis and DCA, published data from Patos's lagoon were used in order to verify the similarity between palinomorphs content of lagoon and platform environments. The sediments deposited on continental shelf presented high skewness and low sorting, with prevalence of silt and clay particles size nearby coastal areas. These characteristics point to a continental (silt and clay) and relicts (sand) deposits influence. A substantial palinomorphs diversity were observed, including 44 taxa of plants, 5 algal taxa, besides Foraminifera, Porifera, Ochrophyta, Fungi and Scolecodonts. Among these, Poaceae, Cyperaceae, Amaranthaceae and Compositae/Asteraceae were more frequent. Some areas inside Patos's lagoon showed greater palynological similarity with the continental shelf due the marine influence. Despite this similarity, we observed a gradation between lagoon and continental shelf palynological contents. The pollen assemblage described here reflected the natural vegetation of Rio Grande do Sul coastal areas, beyond cultivars influences (Oryza e Pinus). This emphasizes the importance of palynological studies to understand anthropic changes at the landscape.



Speaker

# Microgastropods as potential proxies for past hypoxic events

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Coastal hypoxia is a growing global problem responsible for the formation of "dead zones". Hypoxic events have caused widespread damage to fringing coral reef ecosystems in Bocas del Toro, Caribbean Panama. However, because environmental monitoring of these reefs only began less than ten years ago, we do not know if these hypoxic events are part of a natural process or exacerbated by human impacts such as eutrophication and global warming. We explore the utility of micrograstropods to reconstruct changes in hypoxia over millennia. Abundant, diverse and well-preserved microgastropod assemblages were extracted from two reefs with different hypoxia intensities in Bocas del Toro using four 3 m long reef matrix cores, which recovered the last ~400 years. The majority of the microgastropod diversity was represented by families with diverse and specialised lifestyles such as Caecidae (microphagous feeders), Cerithiopsidae (sponge-feeders), Eulimidae (echinoderm parasites) and Pyramidellidae (invertebrate ectopar- asites). Interpretation of the data will be facilitated through the use of oxygen and carbon isotopes to categorize environmental conditions related to hypoxia such as freshwater input, temperature and human-derived sources of nutrients. This study will help reveal the historic precedence of hypoxia in this area and the most appropriate microgastropod taxa as proxies for environmental disturbances.

Speaker

#### Deep marine environments: a potential refuge during times of severe environmental stress

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Evidence suggests that eruption of the Siberian Traps triggered environmental stresses that facilitated a dramatic reorganization of marine communities and resulted in the largest Phanerozoic extinction event at 251.94 Ma. Echinoids underwent a severe loss of diversity during the end-Permian mass extinction (EPME). It was proposed that a single echinoid lineage survived the extinction event, but new findings suggest that stem group echinoids did in fact survive, but exhibited the Lazarus effect. Fossil echinoids are rare during the earliest Triassic with only three published localities recording articulated specimens. Preservation bias fails to explain the rarity of echinoids following the EPME, as dissociated skeletal parts are largely resistant to taphonomic constraints. Thus, it is speculated that echinoids were restricted to refugia (i.e., ecosystems that act as sanctuaries during times of environmental stress). Ecological studies on modern marine environments have suggested that deep-sea communities are more resilient than shallow-water communities as they are more immune to sea surface temperature change. It is hypothesized that deep-marine environments could serve as a refuge in response to future climate change trends. There is growing evidence in the rock record to support this hypothesis. The Shangsi section is one of the three localities with earliest Triassic articulated echinoids, preserved in an upper slope environment adjacent to a tropical to subtropical intracratonic platform on the South China microcontinent. A new species of cidaroid echinoid was found along bed surface 28d, which consists of a calcimicrobial limestone deposited ~50 Ka after the extinction at water depths of ~150-200 m. Paleotemperature calculations from Shangsi indicate a rapid increase to 34 . Surface temperatures of this magnitude would dramatically affect the development of most modern tropical to subtropical cidaroid echinoids. However, modeling of the earliest Triassic Paleotethys Ocean suggests that temperatures at 150-200 m water depth were 5-10 cooler than the surface ocean. Therefore, this deep-marine community could have been more resilient to temperature stresses associated with the EPME. The discovery of a new earliest Triassic cidaroid echinoid at Shangsi increases our understanding of echinoid evolution across the PTB and highlights the importance of deep-marine environments toward the survival of marine biota during major environmental perturbation.



S10 // Oral

<sup>&</sup>lt;sup>'</sup> Speaker

#### Foraminifera in the estuaries of South-West England: maerl, sea grass and conservation

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The estuaries and near-shore marine environments of South-West England were an important location for the early investigations of foraminifera. George Montagu, Fortescue Millett, Edward Heron-Allen and Arthur Earland have all left an important 200-year legacy in our understanding of both the species present and their (palaeo)ecology.

The Fal & Helford Estuaries, Plymouth Sound & Estuaries and the Exe Estuary have all been given EU designations as Special Areas of Conservation (SAC). Following UK legislation in 2009, Marine Conservation Zones (MCZ) have been created around the UK, especially in South-West England, where a number of important MCZ are located, including the sea grass meadows of Tor Bay MCZ. If marine conservation is to be successful it must be underpinned by up-to-date science and, in the case of foraminifera, this relies on work by palaeontologists rather than marine biologists, w ho tend to avoid such groups.

Foraminifera are important constituents of marine and estuarine ecosystems, being present in both large numbers and with high levels of species diversity. Saltmarsh, mudflats and sea grass meadows contain distinctive assembl ages of foraminifera, which often show intimate relationships with other fauna and flora. This is particularly true in the maerl beds of the Fal Estuary. Maerl is a collective name for calcareous seaweeds (*Rhodophyta*) that provide an important habitat for many vertebrate and invertebrate species. Our investigation s have found that the high diversity fo raminiferal assemblages present in the samples associated with the maerl are largely the result of sediment 'trapping' rather than in-situ, high diversity assemblages. Many of the species found within the beds of maerl are associated with sea grass communities, while others come from assemblages known to exist on both the higher mudflats and the saltmarsh environments present in the area. Understanding both modern ecology and post-mortem transport of foraminifera is, therefore, an important part of estuarine and near-shore marine research and our interpretations of such environments in the fossil record. As many of the estuaries in Devon and Cornwall have catchments with a long history of mining (especially in the 19th century) the relationship between test deformity in foraminifera and metal pollution can also be demonstrated.



Speaker

## Comparative fidelity of higher taxa in benthic marine assemblages of coastal North Carolina, USA: implications for conservation paleobiology and paleoecology

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Studies assessing the mismatch between living communities, and concurrently accumulating death assemblages represent a key theme of conservation paleobiology, and have been fruitful in gaging the scale of human induced faunal changes, and conducting more informed analyses of fossil data. However, past research has primarily focused on single higher taxa with hard parts (e.g., mollusks, corals, diatoms). In contrast, few studies have included multiple phyla, and we lack analyses intended to simultaneously evaluate all phyla. Thus, we know little about multi-taxon fidelity patterns or variation in fidelity across classes and phyla.

To evaluate higher-taxon fidelity and taphonomic biases within and across higher taxa, we sampled live and death assemblages by dredging in coastal North Carolina (USA). A total of 53 localities representing a wide range of depths and habitats were sampled. Samples yielded specimens representing 7 higher taxa with variable skeletal types (arthropods, annelids, brachiopods, cnidarians, echinoids, mollusks, and sponges). Species richness and relative abundance for live and sympatric death assemblages were examined within and across higher taxa and relative fossilization potential was estimated for each major taxonomic group.

Samples included 12,981 live and 58,548 dead individuals that represented 247 species from the 7 phyla. Locality richness was moderately correlated between live and dead samples (R2 = 0.4). Preservation potential was elevated for more heavily biomineralized taxa with fewer skeletal components (e.g., mollusks) and depressed for phyla with multiple skeletal elements and limited or no biomineralization (e.g., echinoderms, arthropods, and annelids).

These results indicated low levels of multi-taxic faunal fidelity. That is, class and phylum level composition of live and death assemblages differed considerably, regardless of water depth, habitat type, and proximity to local anthropogenic stressors. Not surprisingly, within-taxon fidelity appeared to be much higher for mollusks comparing with other taxa, which generally displayed very low compositional fidelity. Whereas a single case study cannot provide reliable generalizations, the results reported here can serve as a starting point toward developing numerically- grounded strategies for considering taphonomic overprints in multi-taxic analyses, both in the context of conservation paleobiology and deep-time paleoecology.



<sup>&</sup>lt;sup>°</sup> Speaker

# Tracking trends in the historical ecology of Florida's freshwater springs and rivers using fossil and recent mollusks

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The aquatic communities of Florida's freshwater ecosystems have been studied by ecologists for over 50 years. In contrast, the death and fossil assemblages, which preserve molluscan- components of past communities and can provide unique historical and ecological perspectives, have received limited attention. However, historical data on faunal composition, biodiversity, and spatial structuring of regional faunal associations, which predate the industrial revolution, can be potentially invaluable: they can help us to quantify the ongoing ecosystem shifts driven by recent environmental and anthropogenic changes. The multi-millennial perspective afforded by the most recent fossil record may also improve conservation planning and assist in developing restoration goals for Florida's freshwater systems under threat.

To address these issues, three types of samples were collected from Florida's Silver, Ocklawaha, and Wakulla Rivers: living mollusks (life assemblages), surficial shell accumulations (death assemblages), and *in situ* river bank sediments (fossil assemblages). One hundred and eleven samples collected so far yielded 28,082 specimens representing 20 species of mollusks.

Quantitative analyses indicate that diversity is highest in death assemblages, intermediate in fossil assemblages, and lowest in life assemblages. Many live and dead samples are dominated by recent invasive taxa, such as *Corbicula fluminea* and *Melanoides tuberculata*, while fossil samples include species that are rare or absent in life and death assemblages, suggesting changes in these mollusk communities that predate modern ecological research. Nonmetric multidimensional scaling and PERMANOVA tests indicate that fossil assemblages are similar in faunal composition across all studied river systems (depressed beta diversity), whereas life assemblages are more variable (i.e., life assemblages from the adjacent Silver and Ocklawaha Rivers are similar to one another, but distinct from those of Wakulla River) and display elevated beta diversity.

These results tentatively indicate that, when compared to past ecosystems, present-day mollusk associations shifted notably in faunal composition, display depressed diversity, and are more heterogenous regionally. A potential cause of this increased heterogeneity may be the uneven regional success of recent invasive taxa that can alter the underlying, endemic molluscan communities. As previously demonstrated for marine systems, comparisons of live, dead, and fossil mollusks may be used to quantify recent shifts in biodiversity, composition, and spatial structuring of freshwater communities.



<sup>.</sup> Speaker

#### Fossil foraminifera in conservation paleobiology

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Shelled foraminifera occur in all marine and marginal marine environments usually in great abundance. Their small size makes them easily sampled in statistically valid abundances with almost any sampling technique. In shelf, marsh, lagoon, bay, and estuarine environments, foraminifera occur in cores dating back thousands of years, providing a detailed record of biotic and habitat changes in areas of conservation. Species of foraminifera are variably sensitive to changes in temperature, salinity, oxygen, productivity, pollution, nutrient input from agriculture and sewage, and increased flooding.

In San Francisco Bay, California, forams from cores penetrating the previous inundation of the sea at 125 ka indicate a fauna undisturbed by humans at all. In the Bay today, an invasive Japanese species from ship bilge waters now dominates the foraminiferal assemblages. Comparison to the fossil assemblages indicates that the invasive species moved in but did not out-compete or replace that assemblage but rather just grew enormous populations over the existing biota.

In coastal marine habitats in New Zealand, foraminifera provide a clear history extending back to before Polynesians first inhabited the area, through the immigration of Europeans and their agricultural activities, to modern populations that impact the environments with fertilizers, sewage, wastes of other kinds, fishing and agriculture. Of major importance, early European logging activities and later urban growth increased freshwater runoff that decreased salinity in the estuaries and impacted the macrobiota, all of which the forams recorded. Forams also indicate natural changes in these environments induced by faulting, tsunamis, flooding, and sedimentation that have import in marine conservation.

Fossil forams have successfully documented changes in marine environments caused by natural and human impacts in many places in the world. Their small size, enormous numbers and environmental sensitivity make them especially useful in conservation paleobiology.



**S10 // Oral** 

#### Murky waters in benthic quarters – the dynamic distribution of Hong Kong foraminifera, a reflection of coastal ecosystems in Anthropocene Asia

Briony Mamo \*+<sup>1,2</sup>, Moriaki Yasuhara <sup>1,2</sup>, Jonathan Cybulski <sup>1,2</sup>, David Baker <sup>1,2</sup>

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Perched on the main drainage outlet for the Pearl River Delta Metropolitan Region, one of the most densely populated areas in the world supporting 1.2 billion people, is Hong Kong. Over recent millennia, this region has undergone sea-level rise, alternating salinities, delta progradation, monsoonal onset, and anthropogenic shoreline development and advancement. During this time, the marine communities of Hong Kong have endured substantial alteration and they've increased exponentially since the 19th century. Hong Kong has hosted some of the most polluted waters in the world and aggressive clean-up measures are increasingly being implemented, yet we have little information regarding both their past and present benthic communities. Recent research has established a stark water quality gradient stretching from more pristine eastern Hong Kong heading west to the increasingly polluted Pearl River Estuary, strongly influencing local corral community distribution, diversity and abundance. In 2016, cores (3 m) and surface sediment samples were collected to assess modern and palaeobenthic foraminiferal communities. Preliminary results reveal, surprisingly, flourishing modern communities that are distinctly controlled by strong local environmental parameters, generating very different assemblages across relatively small distances. When compared to palaeoassemblages, we can gauge benthic community change through these ecosystem upheavals and subsequent recovery, alteration or decimation. This work and ongoing analyses not only enables historical understanding of the area's marine ecosystem development but comparing results to the last foraminiferal study some 30 years previous informs us regarding current environmental management protocols and their effectiveness since implementation



S10 // Ora

Speaker

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# Historical voyages, tourist souvenirs and the fate of the endemic mollusc fauna of Rapa Nui

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Rapa Nui, also known as Easter Island, is the most geographically isolated island on Earth. This isolation has led to high endemism, which is 35-40% for molluscs. In addition to its biological uniqueness, Rapa Nui has a unique human history, as it has been inhabited for over 1000 years. During this time, populations have oscillated between about 15,000 to a few hundred inhabitants in the late 1800s. Close to 8,000 people now live on the island where tourism provides the majority of the population's income. As a result, benthic resources such as molluscs are intensively harvested (at least since the 1970s) to be sold as souvenirs. The presence of endemic molluscs from Rapa Nui has been documented by naturalists on historical voyages since the early 1900s. However, our recent sampling of shell assemblages from six sites around the island revealed that some of these species (e.g. Cypraea caputdraconis or 'pure') are missing from current communities. The only trace we found of them was as jewelry in souvenir markets. To understand if the absence of these species from assemblages is due to overharvesting, we hypothesized that the molluscs from dead shell assemblages would be significantly smaller than the ones collected during historical voyages when the human population was much smaller. We measured the size of 13 species of gastropods abundant both in our samples and in the collections at the National Museum of Natural History (Smithsonian Institution). Half of these species are currently used for jewelry and the other half do not seem to be exploited. Our results will allow us to determine if harvesting pressure from the local souvenir industry is affecting the size of shells, making them smaller than they were in the past. These findings will also inform natural resource managers of Rapa Nui about the current state of the endemic mollusc fauna, hopefully leading to education of the local community on the importance of protecting their unique resources.

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Speaker

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#### Fossil assemblages help define historic variation in Caribbean coral reefs, revealing a possible modern bright spot

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An 8-hectare exposure of a suite of Holocene coral reefs in Caribbean Panama provides an opportunity to quantify the Historical Range of Variation (HRV) that existed on these reefs before human impact. We compare the composition of fossil and modern death coral assemblages, and survey data of living coral communities. Results reinforce the conclusion that most reefs in the region today have transitioned to alternative stable states, driven by declines in the staghorn coral Acropora cervicornis and other coral components. Contradicting this region-wide shift, however, we discover one modern reef whose coral assemblage is contained within the fossil- defined HRV, identifying it as a potential vestigial reef community. We use these findings to explore how fossil-defined HRV can help better define pre-human baselines, identify conservation bright spots and develop critical thinking of processes governing the trajectory of reefs into the future.

Speaker

### MEGACENE: The fate and function of marine megafauna from the Pliocene to the Anthropocene

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The marine megafauna includes the largest organisms on Earth. Today, human over- exploitation and habitat degradation threaten these animals, many of which modulate marine food webs and ecosystem processes. We used to think that the threats that marine megafuauna are experiencing in the Anthropocene had no precedent. Our research overturns this assumption. Based on a new analysis of the fossil record, we identify a previously unrecognized extinction event among marine megafauna during the late Pliocene, a period of great climatic variability and sea-level oscillations. We found that extinction rates were three times higher during this time than in the rest of the Cenozoic, with 36% of Pliocene genera failing to survive into the Pleistocene. To gauge the potential consequences of this event for ecosystem functioning, we evaluated its impacts on functional diversity. Seven (14%) functional entities (unique trait combinations) disappeared, along with 17% of functional richness (volume of the functional space). The origination of new genera during the Pleistocene created new functional entities and contributed to a functional shift of 21%, but minimally compensated for the functional space lost. Reconstructions showed that from the late Pliocene onwards, the global area of the neritic zone significantly diminished and exhibited amplified fluctuations. We hypothesize that the abrupt loss of productive coastal habitats was a key extinction driver. The importance of area loss is supported by model analyses showing that animals with high energy requirements (homeotherms) were more susceptible to extinction. The extinction event we uncovered demonstrates that the marine megafauna was more vulnerable to global environmental changes in the recent geological past than previously thought, and that in the absence of severe anthropogenic threats, its diversity would likely still be recovering today. During the Anthropocene, human activities have produced massive defaunation and local extirpations of these animals. How is the functional diversity of this already vulnerable fauna responding to current threats? What species are most vulnerable to extinction and are they different from the Pliocene? How would marine megafuanal extinctions affect the structure and function of future ecosystems? We aim to answer those questions on our current research.



Speaker

#### Documenting climate mediated changes in the Po river deltaic macrobenthic systems through latest Quaternary glacial-interglacial cycles

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Global changes present increasing threats to transitional ecosystems and their biodiversity. Latest Quaternary sedimentary successions are crucial for acquiring a historical perspective on modern ecosystems that have been shaped by long-term (glacial/interglacial) climatic oscillations.

This study aims to develop a regional historical perspective by using sediment cores from deltaic deposits of the Po river sampled within three key time-intervals: (1) Pleistocene interglacial (~125-120 ka), (2) late glacial (18-14 ka), and (3) present interglacial (< 6 ka). Quantitative analyses (> 600 samples and ~100,000 macrobenthic fossils) suggest that delta-associated benthic communities of ~125 ka re-assembled in the Holocene after the last glacial period. The striking similarity of those two interglacial time intervals is supported by the strong overlap of non-metric multidimensional scaling (NMDS) outputs and the high average density of fossils (0.53 and 1.00 spec/cm3, respectively). Moreover, the same dominant mollusc taxa recur in both time intervals. Specifically, ten out of the twelve most abundant Pleistocene species also belong to the top twelve Holocene species and the rank abundances of species from two time intervals are positively correlated (*rho*=0.60; *tau* =0.46 *p* 



Speaker

#### Live-dead fidelity of mollusk assemblages in the Suwannee Regional Reef System, an artificial reef in Florida, USA

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Artificial reefs are widely used for reef restoration, however, their impact on reef-associated softbottom benthic fauna is not well known. Comparisons between mollusk living assemblages (LAs) and sympatric (DAs)-surficial shell remains of past mollusk communities have been used to detect temporal changes in natural reef systems. However, to our knowledge, live-dead fidelity studies have not been carried out in artificial reefs. Here, we compared mollusk LAs and DAs in the Suwannee Regional Reef System (SRRS), Gulf of Mexico. The SRRS can be used to explore community changes in well-understood time frames since reef deployment dates are known. Mollusk LAs and DAs were sampled along transects by SCUBA at 1m, 10m, 25m, 50m and 75m away from the reefs. In both LAs and DAs, mollusk specimens were identified to the lowest possible taxonomic level and presence of drill holes was recorded in dead specimens to explore trends in drilling predation with increasing distance from reefs.

We hypothesized that the soft bottom benthic communities have been impacted by the SRRS over decadal time scales. We also hypothesized that composition of DAs will not vary with distance from reefs since they are time-averaged, recording community composition averaged over centennial time-scales. Composition of LAs were expected to vary along transects, resulting in the live-dead fidelity to increase with increasing distance from reefs.

Analyses suggest that LAs and DAs are significantly different in terms of most abundant species and overall faunal composition. Poor live-dead fidelity suggests that the recent shifts in faunal composition of local mollusk communities are not yet reflected in DAs. LAs are more similar to DAs further away from the reefs when comparing to sites that are proximal to the reefs, indicating that changes in faunal composition occur within a limited spatial halo around the reefs. DAs do not separate as proximal and distal in terms of species composition, recording no evidence of reef impact. Similarly, no distinct trends are observed in drilling frequency along transects. These findings suggest that the mollusk LAs have been impacted by the establishment of the SRRS. The DAs appear to primarily predate the reefs and reflect community structuring prior to reef deployment, thus providing a valuable baseline for the system.

Speaker

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#### The temporal dynamics of the Lessepsian invasion in the SE Mediterranean Sea reconstructed from sediment cores in a coralligenous substrate

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The opening of the Suez Canal in 1869 removed a long-standing biogeographic barrier and the largest marine biological invasion commenced. This man-made pathway has facilitated an almost unidirectional introduction of hundreds of species from the Red Sea into the Mediterranean, the so-called "Lessepsian invasion", which has profoundly altered the species composition and ecosystem functioning in the Levantine Sea.

A major shortcoming in our understanding of the invasion is the lack of data on benthic assemblages before the opening of the Canal as well as scant information on how the invasion progressed until the last decades. To reconstruct the pre-Canal baseline and the temporal change of the assemblages under the pressure of the invasion, we collected an 80-cm-long sediment core at 40 m water depth off Atlit, northern Israel, in a substrate with coralligenous assemblages. Such substrates isconsidered the most important Mediterranean marine habitat after *Posidonia* meadows in terms of biodiversity and productivity. Eight 1-cm layers were analysed throughout the core targeting shelled molluscs.

The uppermost layer shows a very high shell abundance (~380), in contrast to all other samples (< 100). Accordingly, raw species richness peaks in this first sample (~100); however, when rarefied to equal sample size, there is no significant variation of species richness down-core. Non-native species are present until the bottom of the core suggesting either that the lowermost layers do not predate the opening of the Canal or that there is a considerable degree of sediment mixing. Only three non-native species are consistently present down-core below 10 cm sediment depth (the gastropods *Cerithidium diplax, Rhinoclavis kochi* and the bivalve *Transkeia bogii*) while the uppermost layer contains five more non-native species. As in cores collected off southern Israel, these uppermost layers are characterised by sand, whereas mud dominates below 10 cm core depth.

Core age models are being produced to time-constrain the observed down-core changes in species composition and structure and quantify the degree of time-averaging.



Speaker

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#### Unprecedented increase in size of the bivalve *Corbula gibba* driven by the 20th century anthropogenic impacts in the northern Adriatic Sea

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Corbula gibba is an opportunistic, hypoxia-tolerant bivalve species widespread in the Mediterranean Sea. We hypothesize that population size structure of this species can represent an indicator of trophic conditions and ecosystem health in regions affected by anthropogenic eutrophication and frequent hypoxic events. We test whether present-day populations of this species dominated by the large-sized individuals (> 10 mm) have analogues in the Holocene record of the northern Adriatic Sea. To investigate spatial and temporal variability in the body size of C. gibba, we used Holocene death assemblages from the NW (Po prodelta) and NE Adriatic (Isonzo prodelta and Istria), directly dated with radiocarbon and amino acid racemization. Surveys of living populations indicate that during the late 20th century, C. gibba commonly reached sizes > 10 mm at all studied sites, irrespective of the differences in local productivity and sedimentation rates. Such large size classes are very rare, however, in the Holocene assemblages exposed to natural highstand conditions prior to the late 20th century. In contrast to stations at the Po and Isonzo prodeltas, where size distributions in surface death assemblages (from the upper 15-20 cm of the cores or bottom sediments) resemble those of the living populations, the proportion of largesized individuals in Istrian death assemblages remained small. In the latter location, characterized by lower sediment accumulation rates, the mixing of the late 20th century large-sized shells with much older, smallsized individuals generates the mismatch between non-averaged (living populations) and time-averaged (death assemblages) size distributions. Death assemblages off Istria are thus more inert to the late 20th century changes in the size structure of C. gibba populations compared to death assemblages at sites with higher sedimentation rates. The stratigraphic shift from right-skewed distributions to bimodal distributions with high abundance of shells > 10 mm, is a unique feature of the late 20th century and correlates with an increase in the frequency of hypoxia and delayed recovery of hypoxia-sensitive species – predators and competitors of *C. gibba* – in the wake of mass mortality events. Modelling the effects of time averaging on the shape of size-frequency distributions under varying proportions of normoxic and hypoxic regimes show that the 95th percentile size of *C. gibba* can be a reliable indicator of the frequency of past hypoxic events.

<sup>&</sup>lt;sup>°</sup> Speaker

#### Spatial and temporal ecological heterogeneity and anthropogenic impact in the northern Adriatic Sea during the Holocene transgression

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The shallow northern Adriatic Sea formed at the end of the last glaciation by the rising sea level. Since historical times, it has been strongly influenced by human activities (fishing, coastal development, pollution, eutrophication), making it one of the most degraded marine ecosystems worldwide. Our study reconstructs environmental changes and anthropogenic impacts since the onset of the Holocene transgression using down-core changes in faunal composition as indicators for ecological shifts. Sediment cores from seven sites in the northern Adriatic Sea were taken with a self-developed piston corer. They are all about 1.5m long and cover vastly different time spans, ranging from millennia in areas with low- to centuries in areas with intermediate- to decades in areas with high sedimentation rates. The quantitative analysis of molluscs, ostracods and foraminifera from these cores, coupled with extensive age-dating of bivalve shells, reveals major changes of benthic communities during the Holocene transgression. They are related to 1) the rapidly rising sea level (until ca. 6000 y BP), 2) natural environmental changes under more or less stable sea level until a few hundred years ago, and 3) major changes over the past centuries, with distinct amplification in the 20th century that we attribute to strong human impact. The micro- and macrofauna show similar responses to natural environmental changes during the Holocene transgression and confirm eutrophication, overfishing and oxygen depletionas the most important anthropogenic drivers of community shifts in the 20th century. Therefore, in the uppermost core intervals taxonomic and functional richness decline significantly, which is associated with a drop in epifaunal species and an increase in deposit-feeding and chemosymbiotic species. These changes are associated with rising concentrations of nitrogen and organic pollutants. Distinct epifauna assemblages, characterized by bioherms of filter-feeding organisms, developed only at certain periods and in certain regions of the study area with low sedimentation rates. A conspicuous oyster bottom is also visible in our sediment cores and on historical maps of the region, but due to the extensive use of destructive fishing gear it has meanwhile totally disappeared. Our results will help establish realistic baselines for restoration efforts for such richly structured epifauna.



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Speaker

#### Variation of benthic foraminiferal assemblages from an area with coralligenous substrate in a sediment core off Northern Israel

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The opening of the Suez Canal in 1869 connected the Mediterranean Sea with the Red Sea, breaking a long-standing biogeographical barrier. Since then, it has allowed the introduction of organisms (Lessepsian invaders) from the Red Sea into the Mediterranean Sea. These include benthic foraminifera, which are ubiquitous and abundant in the shallow waters of the Mediterranean Sea. Knowledge on native communities and non-native species in the Eastern Mediterranean Sea is very scant and dates back to a couple of decades only, thus encompassing only a fraction of the Lessepsian invasion process. Indeed, small sized organisms such as foraminifera have long been overlooked even more than other organisms contributing to the lack of historical background knowledge. Such lack of knowledge on the baseline foraminiferal communities and their change under the pressure of the Lessepsian invasion hinders our understanding of the invasion process, its progress and the impact of the non-native species on the ecosystem.

To overcome this problem, we analysed a sediment core collected off Atlit (Northern Israel) at a water depth of 40 meters in 2016. The sampling site is characterized by the presence of biogenic structures built by coralline algae. The entire core (~80 cm length) was cut in 1-cm-thick slices and the total assemblage of foraminifera (> 125  $\mu$ m) was determined every 5 cm. The sediment composition of the core is characterized by a distinct greater proportion of coarser sediments in the top 10 cm, consistent with a similar shift in sediment structure observed in cores collected at other sites in Israel.

The assemblage in the lower (older) part of the core shows a high diversity of porcellaneous and calcareous species, among which the calcareous species *Asterigerinata mamilla*, *Elphidium crispum* and *Planorbulina mediterranensis* dominate. In the top 10 cm of the core, the more recent assemblage shows an altered community structure, lower total abundances and the presence of non-native species in comparison to the lower core region. The two dominant non-native species are the larger benthic foraminifera *Heterostegina depressa* and *Amphistegina lobifera*, which thrive on hard substrate with sufficient light conditions. The introduction of Lessepsian species and the changes in substrate drove an overall shift of the foraminiferal assemblage.



Speaker

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### Assessing the impact of the Lessepsian invasion on soft substrate assemblages on the Israeli Mediterranean shelf – a molluscan live-dead agreement study

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The 'Lessepsian invasion' – the massive influx of tropical Indo-Pacific biota into the Mediterranean Sea via the Suez Canal – is the largest marine biological invasion and a major threat to native biodiversity. The lack of data on pre-invasion community composition, however, severely impairs our understanding on how the taxonomic and functional composition of shallow-water assemblages has been affected by the invasion, and the impact it had on native populations. Shelly death assemblages (DAs) encountered in surficial sediments represent a unique archive of past community states that enable overcoming this impediment. This is because they change more slowly (10-10,000 years) than the corresponding living assemblages (LAs; yearly scales of turnover). Strong and rapid directional changes - such as those due to human activities - are therefore not immediately captured by DAs, leading to a greater live-dead (LD) mismatch than expected due to natural processes alone. We analyzed and compared molluscan LAs and DAs collected along depth transects from 10 to 40 m in the SE-levantine Basin off southern and northern Israel. Samples were taken in spring and autumn from soft substrates ranging from fine sands to mud. Autumn LAs were dominated by Lessepsian taxa, both in terms of species richness (up to 60 % species) and abundance (up to 90 % of individuals) at almost all stations, while non-native individuals were less prevalent in spring. High LD-dissimilarity in taxonomic composition (Jaccard-Chao index) and low rank-order agreement of species relative abundances (Spearman's rho) suggest a strong and recent community shift. Species contributing most to LD- mismatch were either native species characterized by higher abundances in DAs or Lessepsian taxa more abundant in LAs. LD-differences in the proportions of trophic guilds were marked at several stations, including, e.g., a shift from a suspension feeder- to a micrograzer-dominated assemblage at 40 m depth off southern Israel; the reverse trend was observed at the 30-m-station of the same transect. Our comparison of LAs with DAs that still retain the signal of pre-impact assemblages highlights the magnitude of the Lessepsian invasion and its potential to alter the functional properties of shallow water ecosystems in the Levantine Basin.



Speaker

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# S11 - Data, dispersals and interchanges through time: a land mammal perspective

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# Horses and elephants through time, and the dispersal paradox

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Time and space are fundamental concepts at the core of paleontological thinking. The connection between both concepts remains partly conflictual. The arrow of time is the basis of stratigraphy, and dispersal is the basis of that part of biogeography called chorology. Horses and elephants are here chosen to illustrate the paleontological treatment of these concepts. During the 19th century since Albert Gaudry (1866) family trees of horses coexisted with phyletic gradualism. In 1893 Karl Zittel added to the tree the geographical dimension with active dispersal at the genus level. The shape of Zittel's tree remained the same during the 20th century culminating with George Gaylord Simpson's tree in an ecological context (1951). Dispersals of proboscideans were also the key explanation to elucidate the past distribution of elephants and relatives. Dispersals did occur, indeed. For example, numerous dispersals through the Bering land bridge since circa 15 Ma are among the most dramatic examples implicating gomphotheres, mammutids, amebelodontids, up to Pleistocene dispersal of mammoths. Yet, since dispersals explain any kind of distribution they can also logically be held as ad hoc hypotheses. As a consequence the status of such hypotheses is rather vague while, on the contrary, geographic arrows put on maps are very evocative. Arrows not only point to connection but also to direction, polarity. They are the best tool to demonstrate the efficiency of dispersals. It can be surmised that such arrows display more paleolocality geography than paleobiogeography. But at the end of the analysis, arrows – as solid tools – appear to depend firstly on phylogenetic trees.



Speaker

# Anatolia: a crossroads between Africa and Eurasia for elephants and mammoths?

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Elephantids are among the most popular and iconic of animals, and one of the best examples of mammalian evolution with their extensive speciation and traceable morphological changes. They are also valuable for correlation of Plio-Pleistocene deposits for having undergone rapid evolution over a wide geographical area. The record of fossil elephants of different evolutionary stages in Anatolia spans from Pliocene to Holocene times. Primitive mammoth specimens with low plate numbers and lamellar frequencies from Turkey were from Yukarisöğütöńú (western Anatolia) and may provide evidence of transition from M. rumanus to M. meridionalis. The fossil remains from Zengen (southern Anatolia), Ladik (northern Anatolia) and Denizli (western Anatolia) were identified as M. meridionalis as all these specimens have metrical and occlusal features typical for this species. Specimens from Dursunlu (middle Anatolia) and Suluova (northern Anatolia) were identified as M. trogontherii. The Dursunlu sample may be considered as a meridionalis /trogontherii transitional assemblage because of the metrical features of the mammoth specimens. In this case this could be evidence for the migration of M. trogontherii from Asia to Europe, and/or may represent an important meridionalis /trogontherii assemblage in Europe. Another interesting specimen is a mandible from the locality Kale Tepe-3 (middle Anatolia). With its plesiomorphic features and enamel pattern of m2s and m3s, this jaw documents one of the most primitive elephantids out of Africa and can be attributed to E. cf. planifrons, which makes it the most westerly known specimen of this lineage. Elephas maximus sub-fossil remains from Gavur Lake Swamp (southeastern Anatolia), dated to mid-fourth Millennium BP, represent the most westerly specimens of ancient Asian elephant. This locality is probably the most important Holocene elephant site in the region as the assemblage represents a large population. Because of its geographical location, Anatolia was central for the dispersal of elephantids between Africa, Asia, and Europe. Even if the fossils of different evolutionary stages from Anatolia are fragmented, scattered, and often lacking stratigraphic information, they have the potential to enlighten topics ranging from the evolution of early mammoths out of Africa to the past distribution of the recent Asian elephant.

S11 // Oral

Speaker

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#### New Eocene-Oligocene Asian fossils cast light on the early evolution of lagomorphs

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The ongoing study of the vertebrate taxa collected in the Late Eocene-Early Miocene composite sequences of Ulantaatal and Saint Jacques (Inner Mongolia, China) led to the discovery of large-sized early lagomorphs, whose dental morphological traits resemble those of family Leporidae. The high temporal density of sampling localities, abundance of remains, and long time span covered, allowed a detailed study of the evolution of such lagomorphs.

Some of the lagomorph species individuated in Ulantaatal and Saint Jacques pertain to the genus *Ordolagus* Burke 1941, others will be included in a new genus. The evolution of both genera could be followed since the latest Eocene. In the case of the new genus, it was possible to spot the transition between the rooted condition and the hypselodont one. The clade represented by the *Ordolagus* lineage + the new genus lineage probably originated from the Middle Eocene Asian genus *Gobiolagus* Burke 1941, and persisted at least through the Early Oligocene.

Very interestingly, convergent features were attained in dental elements of each lineage through time (large size, loss of dental roots, acquisition of additional elements on p3 occlusal surface). Even more interesting was to observe the difference in the achievement of such convergent features (modality of hypselodonty attainment, and different genesis of "leporine" lower molariform pattern).

Other leporine-like taxa appeared in late Early Oligocene. Evaluations are still ongoing to determine if some salient features (large size, hypselodonty, trigonid and talonid of lower molariforms connected lingually, lingual flexus in upper molariforms) developed in parallel with those of North-American leporids, as occurred in the above mentioned, older taxa, or if we are dealing with an actual late Early Oligocene dispersal of leporids from North America.

We envisage: (1) a careful evaluation of the phylogenetic relationships of Asian leporine taxa with respect to North American Leporidae, (2) a re-evaluation of the possible palaeobiogeographical scenarios (dispersal vs. evolution in loco), and (3) the individuation of the factors which triggered, at certain definite moments (latest Eocene and possibly late Early Oligocene), the appearance of convergent morphological characters in very distant lineages of lagomorphs.



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#### New insights into the early historical biogeography of New World hystricognaths (Caviomorpha, Rodentia) from the Paleogene of Peruvian Amazonia

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Caviomorph rodents represent one of the most successful groups of placental mammals from South America. Despite their modern and Neogene high diversity, the early evolutionary history of caviomorph rodents has long remained obscure. Until recently, the majority of Paleogene caviomorph assemblages has remained from middle (9/20) and high latitudes (7/20) of South America and only few are known from lower latitudes (4/20). Recent field expeditions in Peruvian Amazonia have led to the discovery of 18 new caviomorphs-bearing localities in the regions of Contamana and Tarapoto. They document three South American Land Mammal Age of the Paleogene: Barrancan (late Middle Eocene; Contamana), Tinguirirican (Early Oligocene; Tarapoto) and Deseadan (Late Oligocene; Contamana). These new fossils highlight the early paleobiogeography history of caviomorphs. The systematic study reveals the presence of 52 taxa including 17 new species. The late Middle Eocene localities yield the earliest representatives of the group. In these localities, the low taxonomical diversity, associated with a low morphological disparity including taxa that harbor very primitive dental features, reminiscent to those observed in coeval Old World hystricognaths, suggest that a short time range of caviomorph evolutionary history had undergone in South America prior the emergence of these rodents. A cladistic assessment with 513 cranio-dental characters and a comprehensive taxonomic sampling (107 taxa) including most families of the four superfamilies (i.e., Cavioidea, Erethizontoidea, Chinchilloidea, and Octodontoidea) was undertaken. For the first time, several stem Caviomorpha were recognized. Low latitudes of South America are thus viewed as the first diversity hotspot of early caviomorphs. A second radiation would have occurred during the Late Eocene- Early Oligocene and would correspond to the emergence of the four superfamilies. At this time, caviomorphs would disperse towards the middle and high latitudes. The geographic origin of modern superfamilies remains somewhat ambiguous, except for chinchilloids which would emerge in low-latitude regions. It is noteworthy that these two Paleogene diversification phases were contemporaneous with global climatic events and intense Andean uplift events. Finally, several late dispersals between regions at low, middle and high latitudes were highlighted during the Oligocene and Miocene.



<sup>&</sup>lt;sup>°</sup> Speaker

# The phylogeny of early Eocene perissodactyls and insights into their early dispersals

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Perissodactyls are nowadays known by horses, rhinos and tapirs. They suddenly appeared 56 Ma ago during the Paleocene-Eocene transition in the whole Northern hemisphere, but the hypothesis of an Asian origin is generally favored. The basal phylogeny of perissodactyls remains uncertain, but the revision of the European material brings new information about the phylogenetic affinities of the first European forms. Here we present a phylogenetic analysis of the early Eocene perissodactyls, including representatives of Equoidea, Ceratomorpha, Brontotherioidea and Chalicotherioidea. This analysis is based mostly on dental characters as cranial and postcranial information is lacking for the large majority of basal perissodactyls. The phenacodontid condylarths Tetraclaenodon, Phenacodus and Ectocion were set as outgroup. The parsimony analysis suggests that Radinskya and Cambaytherium are stem perissodactyl, and the European genus Hallensia appears closely related to cambaytheres. Their resemblances, such as a primitive bunodont morphology, would indicate a dispersal from India to Europe during the early Eocene. Pliolophus quesnoyensis and Pliolophus barnesi are sister taxa, and are found in a basal position within the perissodactyls, as Cymbalophus cuniculus. Equoidea appears paraphyletic. Brontotheres are nested within the paleotheres, but this could be due to their derived dental morphology. Pachynolophids form a monophyletic group including Propachynolophus and Pachynolophus. A tapiromorph clade is found, including tapirs, rhinos, chalicotheres, lophiodontids and isectolophids. Chalicotheres and lophiodontids are found sister-taxa. The Isectolophidae are found monophyletic, and include Chowliia sp. nov. from Le Quesnoy (France), the only known European isectolophid. Isectolophids are present in the entire Northern hemisphere as early as the earliest Eocene, thus indicating an early dispersal, probably from Asia, to Europe and North America. This analysis confirms the resemblances of some Indian and European perissodactyls or stem perissodactyls. It also indicates that a quick radiation and several dispersal events occurred between Holarctic continents during the early Eocene.



Speaker

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#### Examination of migration patterns during the Great American Biotic Interchange

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During most of the Cenozoic, South America was isolated from other continents and harbored an endemic mammalian fauna. Continental isolation ceased during the late Neogene, when the Isthmus of Panama established a land connection between the Americas and facilitated migration between the two continents, an event known as the Great American Biotic Interchange (GABI). Terrestrial mammals have a rich fossil record in both continents that serve to characterize diversity and migration patterns. The GABI was initially taxonomically balanced, with a similar number of North and South American lineages participating in the early stages of the interchange. However, Pliocene and Pleistocene records document an increase in the proportion of North American over South American derived mammals, which has been hypothesized to be the result of competitive displacement, ecological replacement, or differential predation. In addition, it has been acknowledged that environmental changes and geographic distributions affected the diversity and migration dynamics during the GABI. However, there is a bias in the mammal fossil record towards higher latitudes that challenges earlier research, as the patterns observed in the fossil record of extra-tropical regions cannot be extrapolated to the whole continent. Here, we present new paleontological studies that document the mammal fauna from northern South America during the GABI. The Pliocene and Pleistocene faunas are characterized by the predominance of taxa with a South American origin, despite their proximity to the Isthmus of Panama. In contrast, contemporaneous faunas from higher latitudes (i.e., in the southern cone) show a higher proportion of taxa with a North American origin, suggesting that biotic interactions and environmental differences influenced the timing and distribution of migrants.



Speaker

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#### Micromammals from the Pliocene and Quaternary deposits of North Anatolian Fault Zone: implications on age, paleoenvironment and dispersal in Anatolia

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Anatolia has constituted a gateway between Europe, Asia, and Africa-Arabia since the Paleogene, as documented by the paleobiogeography of small and large mammals. Furthermore, moderate climatic oscillations in the area during the Quaternary minimised the extensive loss of species diversity and provided a refuge for many immigrant mammalian groups.

Neogene tectonic evolution of Anatolia formed wide and significant mountain ranges and numerous basins where both acted as barrier/refuge environment. In contrast, North Anatolian Fault Zone (NAFZ) which constitutes the transform boundary between the Anatolian and Eurasian plates, controlled the evolution of narrow basins from the Late Miocene to the Pleistocene and provides a continuous sedimentary record. NAFZ is a key area for discovery of late Cenozoic mammals which would ensure a better understanding of regional geological history, permit a refined chronology and allow for correlating dispersal events.

Following these hypotheses, the exploration of Niksar, Suluova and Tosya basins from East to West was undertaken for collecting fossil micromammals. Rodent assemblage from the Umurlu locality in the Niksar Basin (e.g. *Arvicola mosbachensis, Microtus arvalis, M. arvalidens, Clethrionomys* cf. *glareolus, Apodemus flavicollis, Mesocricetus* cf. *brandti, Cricetulus migratorius, Nannospalax* cf. *xanthodon)* provides so far the youngest age of these adjacent basins, as early Toringian. The stratigraphic position of Yolpinar, Kizile grek and Kerimo glu localities in the Suluova Basin, ranging from late Villanyian to Toringian are refined based on *Mesocricetus, Arvicola, Microtus, Apodemus* species. In addition, the basin stratigraphy underlines a complex basin evolution from closed to open, and the presence of fish teeth indicates an early Biharian paleo-lake. Finally, localities such as Ortalica (1-2), Sapaca-Karasapaca and Kumkapi situated in the NE and SW parts of the Tosya Basin span the late Ruscinian–early Toringian, based on root condition of arvicolids (i.e. transition from *Pliomys, Mimomys* to rootless *Microtus*).

In conclusion, we aim to provide a biostratigraphic framework for the Pliocene–Pleistocene interval besides a pattern for diversity changes and possible dispersal events of key taxa throughout Europe, the Balkans and Anatolia. The contribution to poorly known small mammal fauna from the mentioned interval in Anatolia may offer considerable inputs in a paleobiogeographic perspective at the Eurasian scale.



Speaker

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# Yushe Basin, China: Late Neogene biogeographic affinity at temperate latitude

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The fluvial deposits of Yushe Basin contain multiple fossiliferous horizons that show the succession of terrestrial faunas in eastern Asia since the late Miocene. The 800 meter biostratigraphy has magnetostratigraphic temporal control. Chron C3An age fossils document the late Miocene (MN13 equivalent) of the area, and superposed assemblages represent early and late Pliocene faunas in the same basin. These are succeeded by an early Pleistocene assemblage constrained to Chron C2r. In the history of paleontological exploration of China, Yushe was important because it demonstrated superposition of Equus over Hipparion faunas. The terrestrial vertebrate faunas of Yushe are quite similar to their counterparts to the west at the same ~ 400 N latitude. Associations are dominated by hyaenids, suids, cervids, bovids, equids, and megaherbivores. Important appearances include canids, camelids, Ursus, Bison, and Equus. There are some characteristically East Asian genera like Sinomastodon and Proboscidipparion, but the Yushe fauna in the late Neogene is basically a Palaearctic fauna. Similarly for microfauna, biogeographic affinity of Late Neogene assemblages with faunas to the west is high at the genus and tribe level. Diverse leporid, squirrel, beaver, hamster, vole, and mouse assemblages resemble western faunas at the genus level, but species differences indicate that distinct lineages evolved in the two areas. Given no evidence of vicariance, divergence after dispersal seems likely. Other than the minor species differences in most higher taxa, characteristic East Asian elements (moles, pikas, zokors, and bamboo rats) distinguish Yushe Basin microfaunas from those at the same latitude of western Asia and Europe.

Speaker

#### Is the enigma of the origin of the bear dogs (Mammalia, Carnivora, Amphicyonidae) resolved? New evolutionary and paleobiogeographic scenarii

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Amphicyonidae, also known as 'bear dogs', represent an emblematic group of extinct mammalian terrestrial predators. They were abundant in Laurasia and Africa from the Eocene up until the end of the Miocene. The considerable morphological disparity and the wide geographic distribution of amphicyonids make their evolutionary history difficult to reconstruct. Even after 150 years of study, the phylogenetic affinities of bear dogs within Carnivora are still debated. In the past, Amphicyonidae have been considered as closely related to either Canidae or Ursidae, but most recent phylogenetic analyses found them as either the sister-group of the Arctoidea or at the base of the Caniformia. However, none of these studies has ever included both European and North American amphicyonids (with the exception of the oldest European genus *Cynodictis*).

The present work provides a revision of the morphology and systematics of several carnivores from the Paleogene of Europe. They are included into an updated taxon/character matrix that contains 252 osteological characters and 46 carnivoraformes species. Our results (maximum parsimony) suggest a novel hypothesis: Amphicyonidae is not monophyletic and is actually composed of: (1) European amphicyonids, which form the sister-group of all Caniformia and (2) North American amphicyonids, which are the sistergroup of Canidae. In the light of these results, we propose to rename these two clades: (1) Amphicyonidae and (2) Daphoenidae. European amphicyonids retain more plesiomorphic characters than daphoenids. This clashes with chronology, as their oldest occurrences date from the late Eocene, while daphoenids are documented earlier in the middle Eocene of North America. Nevertheless, our Bayesian palaeobiogeographic analysis advocates for an exclusively Eurasian history for Amphicyonidae and refutes a North American origin. Consequently, and contrary to what was previously thought based on the morphological similarities between early caniforms and the 'miacids' from the Eocene of North America, Caniformia have an Asian rather than North American origin. One crucial taxon is likely to strengthen our hypothesis: Miacis thailandicus from the middle/upper Eocene of Thailand. This taxon possesses several caniform synapomorphies and its inclusion within paleobiogeographic analyses will likely provide further support for an Asian origin of Caniformia.



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#### New data on the ruminant biostratigraphy from Mongolia and the Asia-Europe connection during the Oligocene

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In the frame of Mongolian-Austrian projects, a very precise biostratigraphic work has been realized, including radiogenic dating and correlation with European ages. No less than eight paleontological missions have been carried out between 1995 and 2012. Studying the ruminant collections from Mongolia, new biostratigraphical and evolutionary scenarios are available for these mammals.

The Ardyn Obo Formation (probable late Eocene, Mongolia) contains a very diversified ruminant fauna (including *Miomeryx altaicus, Lophiomeryx angarae, Lophiomeryx* sp.2 large, *Praetragulus gobiae, Gobiomeryx dubius*). *Praetragulus gobiae, Gobiomeryx dubius*, and a larger species of *Lophiomeryx* (*L.* cf. *chalaniati*) are also known in younger deposits from the Hsanda Gol Formation (Oligocene, Biozone A and B, Mongolia). The ruminants may not have been as affected by the "Mongolian Remodeling" that occurred at the Eocene-Oligocene transition as were other mammals. Similarly to Europe, the early Oligocene ruminant fauna is dominated by Tragulina, even if Pecora-like ruminants exist in both areas (Gelocidae in Europe and "*Eumeryx*" in Mongolia). *Lophiomeryx mouchelini* is simultaneously present in both regions.

The ruminant fauna from Europe and Mongolia experienced a remodeling at the end of the early Oligocene. Around 29 Mya, a speciation event occurred in Europe due to environmental changes after the *"Bachitherium* dispersal event". Nevertheless, the European ruminant fauna is still dominated by Tragulina. In Mongolia, ca. 28 Mya, the ruminant fauna is only composed of Pecora (including *Prodremotherium* and *Dremotherium* -like species). This deep remodeling seems to be linked to strong environmental changes toward more arid environments in Mongolia. First hypsodont ruminants and larger ruminants occurred. *Palaeohypsodontus* is known in Mongolia, Pakistan, China, and Turkey at ca. 26 Mya only.

During the latest Oligocene, synchronous faunal turnovers are observed in Europe and Mongolia. The "*Microbunodon* Event" in Europe shows the total renewal of the European ruminants at the family level with the appearance of *Dremotherium* -like species. The "Late Oligocene Extinction Event" in Mongolia characterizes a deep faunal remodeling. At ca. 25 Mya, MP28 *Prodremotherium elongatum* is known both in Mongolia and Europe, while *Dremotherium* -like ruminants may originate from Asia.



Speaker

# A near total replacement of ungulate fauna in the early Late Miocene of northern Pakistan

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The Harvard-Geological Survey of Pakistan Siwalik Research group continues to study fine- scale patterns of faunal change within and across mammalian groups and to explore abiotic and biotic causes of evolutionary change in the rich Neogene terrestrial record of the Potwar Plateau. One focus has been the faunal response to the development of C4 grasslands between 8 and 6 Ma when many forest-dependent taxa became locally extinct and the number of grazing taxa increased. Here we extend our work to investigate a major turnover that occurred within the ungulates during the early Late Miocene (perissodactyl megaherbivores excluded from analysis). While overall ungulate species diversity remained around 20 species, only two species present at 11.4 Ma persisted at 10.1 Ma. During this same interval, less taxonomic change occurred among both the small-mammal and megaherbivore taxa. Two other characteristics of the fauna change during the same time interval. Ungulate families Equidae and Palaeochoeridae arrived in the Potwar Plateau, and the size structure of the artiodactyl guild expanded.

Evidence for environmental change during the early Late Miocene is drawn from Siwalik faunal and sedimentological structural and geochemical indicators as well as regional and global climatic signals. Between 13.5 and 10.0 Ma, a small but measurable decrease in average stable carbon isotope values of enamel across artiodactyls suggests that average  $\delta^{13}$ C values of consumed C3 plants decreased during this time. This decrease may be related to changes in atmospheric CO<sub>2</sub> and/or in local and regional habitats. Two large consecutive eccentricity cycles centered around 10.75 and 10.65 Ma likely generated prolonged periods of extreme weather that affected local environments. Increased annual seasonality and greater variation on decadal to centennial time scales may have created conditions favorable to the probably more open-habitat tolerant equids that appeared at 10.8 Ma. Direct or indirect competition for resources may have been a factor that selected for larger body size or a greater range of size within artiodactyl families.

The Siwalik fossil record provides an important biogeographic dataset for Neogene fossil sequences and localities in Europe, Africa, and Asia. Current evidence suggests that few early Late Miocene ungulate taxa in the Siwaliks originated in eastern Asia; newly appearing species either immigrated from the west or evolved within the Indian subcontinent.



Speaker

### A subcomplete skeleton of "*Rhinoceros philippinensis*" from the early Middle Pleistocene of Luzon sheds light on mainland mammal dispersals to the Philippines

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Past migration patterns toward and within the Philippine archipelago remain a widely unsolved issue. Nowadays, a West-East main flow from Borneo via Palawan Island seems to be preferred by scholars while older studies were favoring a North-South way from China via Taiwan – this latter island being connected to the continent during some glacial periods whereas islands of the Philippine Archipelago never were. While the recent description of a tiger phalanx in uppermost Pleistocene sediments of Palawan is likely to feed the first hypothesis, the discovery of a canine fragment of Celebochoerus in the Cagayan Valley, North of Luzon Island, rejuvenated the second hypothesis, prolonging the North-South route to Sulawesi. Nevertheless, the fragmentary status of these fossils precludes any robust phylogenetic constraint to be proposed for testing such alternative hypotheses thus far. An almost complete skeleton of the controversial "Rhinoceros philippinensis von Koenigswald, 1956" was recovered in 2014 from early Middle Pleistocene sediments of the Cagayan Valley. In order to constrain the taxonomic assignment and phylogenetic affinities of this species and then to test potential migration patterns, a parsimony analysis was performed on 30 terminal taxa (including all recent rhinoceroses and valid representatives of Rhinoceros, either living or extinct) and encompassing 277 cranio-mandibular, dental, and postcranial characters. The topology of the strict consensus tree confirms the referral of "R. philippinensis" to a rhinocerotine closely related to Rhinoceros and it further allows for considering it as a valid species. Moreover, based on dental features, "R." philippinensis is retrieved as sister taxon to R. hayasakai, from the Early Pleistocene of Taiwan. Given the taxonomic sample considered and the regional tectono-eustatic context, the presence of this rhinocerotid in early Middle Pleistocene deposits of Luzon Island would be consistent with a dispersal from mainland Asia via Taiwan, most likely during the Early Pleistocene. During this time interval, global climate was cooler than present and constrained by 41 kyr orbital cycles. Sea levels were lower than today, varying up to 130 m, although the Philippine archipelago remained unconnected to mainland Asia. This study is the very first robust analysis of migra tion patterns to the Philippines and as such it provides insights for other terrestrial mammals, including humans.

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Speaker

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#### Early Pleistocene forerunners of the *Mammuthus*-*Coelodonta* faunal complex in Nihewan Basin, northern China

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The *Mammuthus -Coelodonta* faunal complex was the most widespread continental fauna on the earth, whose maximum extension covered almost all of the middle and northern part of Eurasia during the Late Pleistocene (MIS 5d-2), and some elements of the faunal complex even dispersed to North America. The prime time of the faunal complex was from late Middle Pleistocene to Late Pleistocene. The most important members of the faunal complex are woolly mammoth (*Mammuthus primigenius*), woolly rhino (*Coelodonta antiquitatis*) and steppe bison (*Bison priscus*). New fossil records show that the aforementioned species can be traced back to the Early Pleistocene Fauna from Nihewan Basin in northern China, where the joint occurrence of ancient Chinese bison (*Bison palaeosinensis*) with steppe mammoth (*Mammuthus trogontherii*) and nihewan woolly rhino (*Coelodonta nihowanensis*) marked the appearance of the early forms of the *Mammuthus -Coelodonta* faunal complex. In recent years, a quantity of such kinds of fossils has been unearthed at the Shanshenmiaozui Site in Nihewan Basin.



Speaker

#### A multidisciplinary study of upper Neogene continental deposits from Corque basin, central Altiplano, Bolivia: sedimentary evolution and faunal changes

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The Altiplano formed a broad Cenozoic inverted\_sedimentary basin (> 200 km wide) with up to 8 km of fluvio-lacustrine filling in various sub-basins. This work is focused on the Corque basin which recorded evolution of the central Altiplano and Neotropical terrestrial mammalian assemblages during the late Neogene. Indeed, this area is inferred to have experienced a rise from  $\sim$ 1,500 to 4,000 m, between  $\sim$ 10 and 6 Ma. Paleoclimates rapidly changed from warm climate at 10 Ma, with a mean annual temperature (MAT) ~20 °C, to the current highland climate (MAT ~8-9 °C). These series yielded both rich land mammal assemblages essential for late Neogene biochronology and interbedded volcanic tuffs ranging a ~10-2.8 Ma interval, marked by drastic faunal changes by the Miocene-Pliocene transition. A multidisciplinary study of late Neogene deposits from the Corque basin near the village of Pomata allows for describing the sedimentary evolution, refining chronostratigraphy through Ar/Ar datings of interbedded volcanic tuffs, and implementing the corresponding fossil record. The studied section encompasses the Totora, Pomata, and Mauri Formations, with 15 interbedded volcanic tuffs suitable for dating. The Totora Fm is mainly composed of continental fine-grained sediments yielding desiccation features indicating temporary emersions and some palynomorphs in finest sediments. Paleoenvironments correspond to ephemeral braided streams and lakes. In the channels, eastward paleocurrent directions indicate that sediments came from the Cordillera Occidental. The Pomata Fm begins few meters above an index volcanic tuff that crops out over the whole basin and consists of mud or sand-supported mass flow deposits yielding numerous terrestrial mammal fossils. The most conspicuous taxa are the mesotheriid notoungulate Plesiotypotherium achirense and new echimyid and caviid rodents. The upper surface of the Totora Fm, eroded, corresponds to an angular unconformity underlying the Mauri Fm. The latter starts with an index volcanic tuff (Toba 76; 5.34 +/- 0.003 Ma) and corresponds to four thinning upward fluvial sequences, each one starting with cross-bedded conglomerates/coarse-grained sandstones, passing upwards into fine-grained argillaceous sandstones. In these southward-flowing deposits, we recently found a new nothrotheriid ground sloth, Aymaratherium jeani. The erosion of previous units and the change in transport direction may be related to a major phase of relief growth.



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<sup>\*</sup> Speaker

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#### First partial cranium of the *Hyaenodon* type species, *H. leptorhynchus* (Mammalia, Hyaenodonta) – consideration on the niche partitioning of the European carnivorous mammals during the Paleogene

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*Hyaenodon leptorhynchus* is the type species of the taxonomically diverse and widely distributed hypercarnivorous genus *Hyaenodon* (Hyaenodonta, Eocene-Oligocene). Unfortunately, its cranium was unknown thus far.

We described the first partial cranium based on a specimen that has been discovered in fossiliferous deposits from the Séon Saint-André (Marseille, France; Chattian, MP26). This discovery is only the second report of this species in the early Chattian, filling a period of 2.5 My (from MP25 to MP26); indeed, only one occurrence (Rigal-Jouet, MP25) was reported until now for this period.

The specimen is preserved in a red marl matrix that does not allow the description of key morphological characters. Therefore, CT-scan was used to reconstruct the hidden parts of the specimen. The general morphology of the cranium reinforces the homogeneity previously observed in *Hyaenodon* despite its specific diversity. The fossil corresponds to a juvenile: it preserves its deciduous canines, and the P3 is almost fully erupted. For the first time the dental eruption pattern of the upper teeth is described for this species. Timing of dental eruption is similar to all known *Hyaenodon* species reported from North America and Europe at this ontogenetic stage.

Based on the body mass and general *Hyaenodon* body plan, we strongly suppose that *H. leptorhynchus* was a cursorial hypercarnivorous predator, hunting small prey such as small artiodactyls.

In order to understand the evolution of the ecology of *Hyaenodon* in Europe, we analyzed its taxonomic diversity during the Eocene and Oligocene and paid attention to the body mass of its representatives. We have compared these data with those of the Amphicyonidae (Carnivora, Caniformia) because these carnivorous mammals appeared almost at the same time as *Hyaenodon* in Europe. This comparison allows having a brief look and a first impression on the structure of the European carnivorous guilds and on competition dynamics in this particular type of niches during the Eocene and Oligocene. The diversity of *Hyaenodon* in size (from 4 to 50 kg) and morphology indicates that this genus was an important component of the European ecosystems. However, while the Amphicyonidae diversified and increased in size during this period, *Hyaenodon* remained stable in terms of size and species richness until its extinction (MP30).



<sup>\*</sup> Speaker

### Dental structures and microwear reveal mosaic diversity and disparity of euharamiyidans in the adaptive radiation of mammals during the Middle-Late Jurassic

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Haramiyida and Multituberculata may be grouped into Allotheria, an extinct group of mammals that are characterized by a unique dental morphology in which the molar has two longitudinal rows of cusps and the jaw movement in chewing consists of a palinal component. Multituberculates have a good fossil record so that their tooth occlusal pattern has been well known. In contrast, haramiyidans have been known mainly from isolated teeth, and their tooth identification and occlusal pattern remain equivocal. Recently, six genera of haramiyidans, represented by craniodental and skeletal material, were reported from the Jurassic Yanliao Biota of China. These discoveries have revealed a high species diversity and morphologic disparity in haramiyidans that lived in Jurassic forests. Associated dentitions of these species cast light on tooth identification and occlusal patterns that were previously inferred from isolated teeth. However, controversial views have emerged about tooth occlusal patterns among the Yanliao haramiyidans, which affect our understanding of the haramiyidan diversity, evolution, and phylogeny. Using scanning electron microscopy and computed tomography, we have obtained detailed morphologies and wear patterns from dentitions of individual animals that belong to Shenshou, Xianshou, and Arboroharamiya. The wear features show unequivocal occlusal relationship. We recognize at least three basic occlusal modes in haramiyidans, represented by Shenshou, Arboroharamiya, and Maiopatagium, respectively, and compare them with those of multituberculates and other mammals. If interpreted correctly, Maiopatagium pattern appears to be the most primitive one of the three, although interpretation of the evolutionary transformation from this pattern to others remains difficult. In contrast, the occlusal pattern of Shenshou is more primitive than that of Arboroharamiya (including Vilevolodon), and we consider the latter to be readily derivable from the former. These patterns reflect fundamental tooth morphological differentiations that represented adaptation to various diets in forestry ecosystems and show mosaic evolution of allotherians in a major adaptive radiation of mammals during the Jurassic. As tree dwellers, the extinction of haramiyidans was possibly attributable to the change from gymnospermdominant forests to angiosperm-flourished ecosystems during the Jurassic–Cretaceous transition.

Speaker

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### Important gaps in the fossil record of Paleogene hystricognathous rodents revealed by dental morphology-based phylogeny of taxa from Asia and Africa: paleobiogeographical implications

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Modern African cane-, dassie- and mole-rats, Afro-Asian porcupines, and South American chinchillas, guinea pigs, spiny-rats, etc., make up the natural group of the hystricognathous rodents (Hystricognathi Tullberg, 1899). The hystricognathy is described on their lower jaw, which shows the origin of the angular process distinctly lateral to the plane of the incisor alveolus (contra the same plane in all other rodents = sciurognathy). A suite of morpho-anatomical traits (notably dental) and genetic data also define hystricognathous rodents. Hystricognaths share a common ancestry with modern African gundis or Ctenodactylidae (sciurognaths), both forming the suborder Ctenohystrica. From a paleontological perspective, the origin of hystricognaths, as that of gundis, can be traced back to the Eocene of Asia, as they are both nested within the Asian "ctenodactyloid" radiation, also including other extinct sciurognaths such as the Eocene Chapattimyidae, Yuomyidae, Tamquammyidae, Gobiomyidae, and the extant Diatomyidae. Although phylogeny implies Asia as the ancestral homeland of Hystricognathi, curiously the oldest known fossil occurrences of hystricognaths are not from Asia, where they are so far known only from the latest Eocene, but from Africa and South America, where they appear suddenly in the fossil record of both landmasses by the late middle Eocene. This points out the incompleteness of the Asian fossil record for hystricognaths, but also that this group rapidly achieved a widespread distribution throughout the Old and New Worlds sometime during the middle Eocene. We have performed a cladistic assessment of the dental evidence documenting several early Asian "ctenodactyloids" and all Paleogene African and Asian hystricognaths known thus far (or recognized as such). Even if the dentary bone is not documented for several taxa, based on dental evidence we suggest that some late and middle Eocene Asian "ctenodactyloids" are stem hystricognaths and pre-hystricognaths, respectively, although they were not recognized as such originally (e.g. Dianomys, Ottomania, Anadianomys). This view partially plugs the gap in the Eocene Asian hystricognath record. However, this phylogenetic context implies many ghost lineages for some Asian and African taxa, thereby underscoring the still poor documentation of early hystricognaths. It also implies a complex early historical biogeography of the group, involving multiple dispersal events from Asia to Africa sometime during the middle Eocene.



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#### Lower Miocene pecorans (Mammalia, Artiodactyla) from Japan

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Pecoran fossils from the lower Miocene (Burdigalian) of Japan have not been clearly identified because they are fragmentary teeth or bones, without cranial appendages. In the early 20th century, some dental specimens from the lower Miocene were assigned to cervoids, 'Amphitragulus' and Dicrocerus. These taxa from Europe have been re-examined systematically to date, so that the lower Miocene pecorans from Japan should be updated by recent paleontological knowledge based on European species and new fossil records. The Burdigalian fauna from Japan comprises at least two taxa of pecorans with different size. A larger species was originally described as 'Amphitragulus' minoensis (Palaeomerycidae) from the Hiramaki Formation (ca. 18.4–17.0 Ma) of central Japan, and later, this species was combined with the genus Palaeomeryx. P. minoensis is similar to P. kaupi from MN4 (e.g. Artenay) in cheek tooth size and occlusal patterns. Although the holotype, right p4-m2, of P. minoensis is strongly worn, this species differs from P. kaupi, in having p4 with an unbranched anterior conid and molars with flatter lingual surface. Dicrocerus tokunagai (Cervidae) has been known for a smaller species distributed in the lower to middle Miocene of Japan, but new materials of a small pecoran show a different result in identification. All early cervids with two-pronged antlers (e.g. Procervulus and Dicrocerus) have the postprotocrista extending externally, often with a neocrista (or internal postprotocrista). However, the postprotocrista of an isolated upper molar from the Nakamura Formation (ca. 19 Ma) of central Japan does not have this synapomorphic character of crown cervids. Regarding lower molars from the Nakamura Formation, m3 has a welldeveloped entostylid connecting with the postentocristid, which is similar to that of Ligeromeryx (Lagomerycinae) from MN3 (e.g. Chitenay) rather than of all crown cervids after Procervulus. Previously described specimens of D. tokunagai, including the holotype, share all dental characteristics with the new materials from the Nakamura Formation, and they are replaced to a lagomerycin species. In this study, I conclude that the lower Miocene pecoran fossils from Japan include a lagomerycin species (ca. 19 Ma) and P. minoensis (ca. 18.4–17.0 Ma), which are correlated morphologically and stratigraphically with Ligeromeryx (MN3) and Palaeomeryx (MN4) from Europe, respectively.



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<sup>&</sup>lt;sup>'</sup> Speaker

#### Note on the zygodont mastodonts from the Pliocene-Pleistocene of Europe

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Parts of a zygodont mastodont skeleton, *Mammut borsoni* Hays, 1834, were discovered in the Otman Hill quarry from Colibashi village, Republic of Moldova. Both incisors are curved slightly downwards, like in the *Z ygolophodon turicensis* right half-skull (showing dentition exchange for the M2-M3 dex.) collected from Villefranche d'Astarac.

Only a few cases are known so far of zygodont mastodont skull fragments in the Old World, and most of them are fragmentary.

The *M. praetypicum* (Schlesinger, 1919) skull fragment described by Kubiak in 1972 does not allow for considering an upward curvature of its tusks. More so, this skull fragment that highlighted the main characters of the new species was lost.

The fossil locality of Millia, Greece, yielded impressive remains of *Mammut borsoni* but the upper tusks were not recovered fixed in alveoli. A drawing of the *M. borsoni* left maxillary fragment from Millia (Greece) shows the direction of the alveolus (together with the premaxillary and jugal) forming an angle of about  $54^{\circ}$  towards the occlusal surface of the M2 (present and in wear). The cranial fragments including the rostral bones from Otman Hill have a similar structure, the corresponding angles of this specimen being about  $65^{\circ}$  for the left fragment, and about  $62^{\circ}$  for the right fragment. These characters, important for the taxonomic definition of both fossil proboscidean specimens, allow us to deduce the direct relation between the Pliocene- Quaternary zygodonts and their Miocene relative *Z. turicensis* (Schinz, 1824).

The dentitions of *Mammut americanum* and of "*M*." *borsoni* are very similar, but the type species of the genus *Mammut* Blumenbach, 1799 is *M. americanum* (Kerr, 1799) in which the upper tusks are strongly curved outwards, and in some cases are also curving inwards more distally. Because of this, we consider the zygodonts from the Pliocene-Quaternary of Europe are not congeneric with *M. americanum*.

The difference in dental morphological features between *Z. turicensis* and "*M*." borsoni is very conservative. Considering that the Pliocene-Pleistocene European zygodonts are obviously closer to the sister species *Z. turicensis* in the morphology of both the upper and lower jaw teeth but also in the shape of the tusks, we consider logical their assignment to the genus *Zygolophodon* Vacek, 1877.



Speaker

#### Tooth remains of Late Pleistocene moschid and cervid (artiodactyls) from Yangjiawan and Fuyan Caves of southern China

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Moschid and cervid remains are significant elements of Ailuropoda -Stegodon fauna, and always account for a large proportion in specimen numbers. However, the systematic study of cervid fossils is inadequate for most of the Late Pleistocene Ailuropoda -Stegodon faunas, most of which only bear isolated tooth remains. The uniform tooth structures of cervid lead to the confused situation in taxonomic identifications of isolated teeth. The numerous cervid tooth fossils recently unearthed from Yangjiawan caves and Fuyan Cave give us a chance to address this issue. Based on morphologic, odontometric and CT scanning studies, six species have been recognized, including Moschus sp., Elaphodus cephalophus, Muntiacus muntjak, Mu. reevesi, Rusa unicolor and Cervus nippon. The cervid faunal compositions of these two sites are basically the same and most of the species can be distinguished from one another in tooth dimensions, except for M. muntjak and E. cephalophus; but the entoflexus of upper premolars, the metacone ribs of upper molars, the structure of p4, and the metastylid of lower molars can be used as distinguishable characters between M. muntjak and E. cephalophus. The cingulum and the entostyle of upper molars, and the metastylid of lower molars of *M. reevesi* are weaker than those of *M. muntjak. R.* unicolor possesses tapered entostyle and thick enamel, while the enamel of C. nippon is relatively thinner and the entostyle is columned. Moschus sp. usually has a Dorcatherium fold in lower molars, which is a diagnostic character.

S11 // Poster



#### S12 - Early animal life

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#### "Basal" Cambrian fossils fill a gap in the evolution of terrestrial euarthropods

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Since the discovery of the Burgess Shale, extraordinarily well-preserved soft-bodied fossils from Cambrian and early Paleozoic Lagerstätten worldwide have allowed deep insight into the early evolution of arthropods. Fundamental to this endeavor is the resolution of the base of the euarthropod tree, the composition of which determines the direction of broad evolutionary scenarios. Fuxianhuia and its relatives from the early Cambrian of China have long been considered to represent basalmost euarthropods, even in the absence of clear character polarization supporting the plesiomorphic condition of their morphologies. Recently, paleoneuroanatomy and a reinterpretation of large bivalved Cambrian arthropods have suggested instead that fuxianhuiids may be closer to mandibulates. Here, we reinvestigated the anterior anatomy of Fuxianhuia in light of new material from the Cambrian Chengjiang and Xiaoshiba biotas, from China. We found that Fuxianhuia possessed a pair of large, rounded plates with dentate masticatory margins lying behind several single sclerites. Posterior to the ocular sclerite is another sclerite bearing the antennules, and which therefore should be called the hypostome. The hypostome is closely followed by a larger, subtrapezoidal plate (previously interpreted as the hypostome) bearing the so-called "specialized post-antenn(ular) appendages." With such a configuration, the pair of large gnathal plates occupies the fourth somite, consistent with a mandibular affinity. Fuxianhuiids are therefore crown mandibulates, supporting paleoneuroanatomical observations and the view that isoxyids and cheiromorphs represent the basalmost part of the euarthropod tree. Our time-calibrated Bayesian analysis places fuxianhuiids as the sister group of myriapods, providing the first insight into the Cambrian origin of that terrestrial clade. This, in turn, sheds light on the shared identity of anterior head elements among mandibulates.



Speaker

#### Determining phylogenetic position of Ediacaran macrofossils *Dickinsonia* and *Andiva* using biomarkers

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The Ediacara biota appears in the palaeontological record just before the Cambrian explosion, and represents the oldest macroscopic complex organisms. The organisms themselves and the ecosystems they formed were "strange as life on another planet", so debate about the nature of these fossils is still ongoing, with interpretations ranging from marine animals or giant protists to lichen growing on land. Extremely low thermal maturity and lack of weathering of Ediacaran deposits in the White Sea Region (Russia) allowed organic matter and biomarkers (extractable organic molecules) of Ediacaran fossils to be preserved. Biomarkers contain information about biological molecules produced by organisms living in the past, and many of these molecules are specific to certain phylogenetic groups. We used biomarkers extracted from organically preserved Ediacaran fossils in the genera *Dickinsonia* and *Andiva* to determine their phylogenetic positions. These organisms largely or exclusively produced cholesteroids, a group of C27 sterols characteristic of animals (Metazoa). This striking molecular signal, in combination with palaeontological observations, establishes these two iconic members of the Ediacara biota as the oldest confirmed macroscopic animals preserved in the palaeontological record.



12 // Ora

Speaker

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# Scleritome animals from the early Cambrian of Australia: Disparity, affinities and evolution

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Lower Cambrian sedimentary packages from Australia are replete with an incredible array of organophosphatic, secondarily phosphatised or calcareous (often silicified) skeletal elements. A large proportion of these sclerites belong to lophotrochozoan animals and represent mineralised elements from larger, complex composite exoskeletons (scleritomes) prone to disarticulation post-mortem. Whilst discovery of exceptionally preserved specimens in Konservat-lagerstätten around the world has demonstrated the scleritome structure of some lophotrochozoan taxa (e.g. Halkieria, Orthrozanclus), reconstruction of complex exoskeletal architectures has proven difficult in some groups and more work is required to clarify zoological affinities. Material from the early Cambrian of Australia has been pivotal in revealing the phylogeny of some previously enigmatic groups, such as the tommotiids. We have documented partial scleritome material for the sessile filter-feeding eccentrothecimorphs Eccentrotheca, Paterimitra and Micrina, the tubiform ancestors of bivalved linguliform brachiopods that evolved via sclerite modification and reduction. Scleritome reconstruction for the camenellan tommotiids is less secure. However, in Dailyatia, rare sclerite composites, muscle scar position, and proportions of bilaterially vs asymmetrical left/right sclerite morphs indicate a complex scleritome. This likely consisted of a linear series of 2-3 rows of multiple, imbricating sclerites protecting a vagrant, benthic slug-like animal, and clearly distinguishing Dailyatia from the sessile, filter-feeding eccentrothecimorphs. Calcareous sclerites from halkieriids (Australohalkieria, Oikozetetes) and other multisclerite- bearing forms are generally only recovered as disarticulated remains in lower Cambrian shallow marine deposits from Australia, and scleritome evidence has remained elusive. However, here we report the discovery of a new enigmatic articulated scleritome animal from the lower Cambrian (Series 2 Stage 4) Emu Bay Shale Konservatlagerstätte of South Australia that appears to have a mixture of tommotiid and multiplacophoran traits, significantly adding to knowledge of early Cambrian scleritome disparity and evolution.



Speaker

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#### Arm-waving, tough and spiny: Hopeful "Collins" monsters from the Burgess Shale of British Columbia

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Panarthropods (Arthropoda, Tardigrada and Onychophora) have their roots in the lobopodians, a paraphyletic group of rare Palaeozoic worm-like animals with soft legs. Here we describe the original "Collins monster," from the Sanctacaris locality and a second form from the Tulip Beds locality, both from the middle Cambrian (Series 5) Burgess Shale of Mount Stephen in British Columbia. The two species possess a double row of ventral spinules arranged in a chevron-shaped pattern along the frontal lobopods and belong to luolishaniids, a clade of longlegged lobopodians currently retrieved as basal panarthropods. The "Collins monster" bears six pairs of elongate, clawed lobopods anteriorly, each with long and straight spinules as well as minute dorsal spines. The posterior section is made up of eight pairs of short and stout lobopods, each terminated by a single recurved claw likely pointing inward. The dorsum is armed with pairs of short and stout spines above the anterior lobopods one to three, and three sets of more elongate spines, two lateral and one medial, above each remaining lobopod pairs. The head is short, bears a possible pair of antennae, and is covered by an oblong dorsal sclerite. The second form is known from nearly 50 specimenspresumably mostly molts-and differs from the "Collins monster" in several aspects. The spinules on the anteriormost lobopods are much thicker and curved, and the spines along the outer lobopod margins and terminal claws are also much larger. The posteriormost five lobopods sport massive recurved terminal claws and display a series of seemingly imbricated external plate-like elements on their outer surfaces, each fringed with marginal spines pointing downward or sideways. The dorsal armature is characterized by having four rows of relatively stouter, conical spines with two successive pairs of short spines on the head itself. Remarkably, the spines tend to remain loosely connected to weakly sclerotized plates in dissociated material. These seemingly spine-bearing plates abut each other like pseudo-segments, fully covering the dorsal and lateral sides of the body, although there is no evidence of arthrodial membrane or joints. These cuticular structures would therefore showcase a convergent-or parallel evolution of thorough segmental hardening among luolishaniids, outside of the arthropod lineage.



Speaker

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# Revisiting the Chengjiang radiodonts after two decades of silence

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Radiodonta Collins, 1996 are lower-stem Euarthropoda bearing a series of characters that bridge the lobopodian-euarthropod transition. These characters, such as those of the head (compound eyes, head plates, mouth apparatus, etc.) and limbs (including frontal appendages, setal blades, and flaps), were primarily described based on articulated specimens from Cambrian Konservat-lagerstätten, and are all central foci in the study of arthropod origins. The early Cambrian Chengjiang biota (Series 2, Stage 3) in Eastern Yunnan, China, is the earliest of these Lagerstätten to bear abundant fully or partially articulated specimens of radiodonts. However, studies on this important material from Chengjiang were limited to two papers published in the mid-1990s. We began to re-investigate the Chengjiang radiodonts from 2014 onwards by identifying a new taxon, Lyrarapax unquispinus, illustrating for the first time that the mouth of radiodonts is not invariably a radial circlet of overlapping plates. Our subsequent and ongoing studies have revealed a surprising diversity of radiodonts in Chengjiang, with seven genera and nine species recorded by far, and have identified several fundamental new characters concerning the morphology of radiodonts, such as multiple pairs of gnathobase-like structures of an appendicular nature, mouth apparatuses composed of smooth and tuberculate plates that are not radially arranged, and other head components. This new information from Chengjiang not only allows us to clarify the evolutionary significance of radiodonts in understanding the origin of arthropods, but also provides a body of evidence to show that the diversification of radiodonts can be well categorised by morphological variations of their various feeding structures, such as the frontal appendages, the mouth apparatus and the gnathobase-like structures. This in turn was echoed by the diversification of their autecology, notably their feeding strategies.



Speaker

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### The Cambrian explosion in Iran: new insights from small shelly fossils of the Ediacaran-Cambrian transition in the Soltanieh and Alborz Mountains

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Little has been documented about the palaeontological record of the Ediacaran-Cambrian boundary in Iran. However, fossils from this time interval are of major interest to improve our understanding of the Cambrian Explosion of animal life. Microfossils from the earliest Cambrian sedimentary successions are of particular interest, as they belong to the oldest records of skeletal bilaterians. Exposures in Iran are critical for this purpose, promising diverse and well-preserved small shelly fossils (SSFs) from the Ediacaran-Cambrian Soltanieh Formation of the Alborz Mountains have been mentioned in brief reports. In this study, the diversity of the SSFs from the Soltanieh Formation in the Alborz Mountains is revised, and novel SSFs data from the Soltanieh and overlying Barut formations in the Soltanieh Mountains are presented. The Soltanieh Formation yielded species of the genera Protohertzina, Anabarites, Siphogonuchites, Lopochites, Lomasulcachites, Maikhanella, Purella, Aetholicopalla and other problematic microfossils. Species of Siphogonuchites, Pseudorthotheca, Oelandiella and other molluscs are reported for the first time from the Barut Formation. The data provide new knowledge to assess the palaeobiodiversity of the first skeletal metazoan benthic communities. Informative specimens are considered for the appraisal of the still-unresolved biological affinities of problematic SSFs. The comprehensive data on the stratigraphic range of the SSFs provide the opportunity to discuss the early Cambrian biostratigraphy of Iran and its global correlations. Faunal affinities with the Yangtze platform and the western Gondwana margin are debated.



Speaker

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# Dichotomous branched seaweed Eoholyneacea in the Tamengo Formation, Ediacaran, Brazil

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The Tamengo Formation represents the Precambrian/Cambrian boundary in the Corumbá Group, Brazil. Located in the state of Mato Grosso do Sul, it has been the target of paleontological studies exposing Ediacaran life forms, represented by metazoan fossils with biomineralized carapaces, such as Cloudina lucianoi, Corumbella werneri and Paraconularia sp., megascopic multicellular algae such as vendotaenids, and through trace fossils with the icnogenus Multina minima. Introducing the largest assembly of Neoproterozoic life forms recorded in South America, two new fossil records of the Tamengo Formation presented here are classified as macroalgae according to their morphological features. The first sample was found 5 cm below a Corumbella werneri level. It is 1.5 cm long and thickest at the base of the stalk with a regular dichotomous ramification narrowing as it rises upwards, with a possibly filamentous interior. At the top, the stalks overlap one another and in the tip of each one are preserved oval structures interpreted to have greater cellular activity responsible for growth because they have a greater accumulation of organic matter. The second specimen is 3.5 cm long, with regular dichotomous branches that can occur twice in the same stalk. It has striated stalks, a possible indication of being pseudo-parenchymal, with homogeneous thickness throughout the body. They show along the stems structures that resemble thorns and in the apical part, a structure interpreted as a membrane that connects the dichotomized stems. This fan-shape seaweed is similar to macroalgae carbonaceous compressions from the Ediacaran Doushantuo and Lantian formations such as Doushantuophyton. The two species fit into the Eoholyniacea family proposed by Hoffman (1994) for the macroalgae of Neoproterozoic due to the presence of branching, and they share similar features with the morphogroup characterized by delicate dichotomous branching proposed by LoDuca et. al.(2016) for specimens of early Paleozoic seaweeds. The occurrence of macroalgae in the Tamengo Formation highlights the Neoproterozoic/Phanerozoic transition in Brazil in a global context.

IPC 5

Speaker

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### Auroralumina attenboroughii: a new skeletonising cnidarian from Charnwood Forest, UK (Late Ediacaran ca. 561–556 Ma)

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"Deep water" Ediacaran communities in Charnwood Forest (UK) are dominated by frondose organisms, in particular, rangeomorphs and arboreomorphs. However, rare taxa, not referable to any currently defined Ediacaran morphogroup, are also present. We here describe *Auroralumina attenboroughii* n. gen. et n. sp., which we interpret as a crown group cnidarian. It is known from two specimens, each consisting of a pair of equi-sized goblets that branch (?bifurcate) from a point near their base and bear a dense crown of tentaculate structures. The goblets were constructed of a semi-rigid (probably organic-walled) material, have a tetra-radial symmetry, and were smooth except for a deep, narrow, longitudinal infold at each corner. The largest specimen stood at least 20 cm high. *A. attenboroughii* likely does not represent a solitary polyp, and the skeletal infolds may suggest the presence of septa-neither of which are considered the plesiomorphic condition for the Cnidaria. *A. attenboroughii* represents the oldest remains of the cnidarian crown group and, as such, can be used to calibrate the evolution of this clade. It possesses characters (e.g. a probably colonial state) that are considered derived in extant representatives, and so may expand the possible anatomical permutations of early-diverging Cnidara. The presence of clear crown group cnidarians suggests that early Late Ediacaran ecosystems were more complex than previously envisaged, with clear primary predators.



12 // Oral

Speaker

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### Anamorphic development and extended parental care in a 520 million-year-old stem-group euarthropod from China

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Extended parental care (XPC) is a complex reproductive strategy in which progenitors actively look after their offspring up to or beyond the first juvenile stage in order to maximize their fitness. Although the euarthropod fossil record has produced several examples of brood care, the appearance of XPC within this phylum remains poorly constrained given the scarcity of developmental data for Palaeozoic stem-group representatives that would link juvenile and adult forms in an ontogenetic sequence. Here, we describe the post-embryonic growth of Fuxianhuia protensa from the early Cambrian Chengjiang Lagerstätte, and show parental care in this stem- group euarthropod. We recognize fifteen distinct ontogenetic stages based on the number and shape of the trunk tergites, and their allocation between the morphologically distinct thorax and abdomen. Our data demonstrate anamorphic post-embryonic development in F. protensa, in which tergites were sequentially added from a posterior growth zone. The growth of *F. protensa* is typified by the alternation between posterior addition of segments, followed by the release of the anteriormost abdominal segment into the thoracic region. The transformation of the abdominal tergite into the anteriormost thoracic tergite is demarcated by the appearance of laterally tergopleural spines, as well as the appearance of walking legs. The new insights into the ontogeny of F. protensa allows for the interpretation of the life assemblage consisting of a sexually mature adult alongside four ontogenetically coeval juveniles, which constitutes the oldest occurrence of XPC in the panarthropod fossil record. Our findings provide the most phylogenetically basal evidence of anamorphosis in the evolutionary history of total-group Euarthropoda, and reveal a complex post-embryonic reproductive ecology for its early representatives.



Speaker

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### Fluctuation of shelf basin redox conditions in the early Ediacaran: Evidence from framboidal pyrite analyses of Lantian Formation black shales and fossils in South China

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Lantian macrofossils from the early Ediacaran Period (ca. 635 ~580 Ma) are preserved in situ on the bedding surfaces of the Lantian Formation black shales in southern Anhui Province, China. Previous studies suggest fluctuating redox conditions in the water just above the substrate in the Lantian basin in the early Ediacaran. This bottom water redox scenario lends support to an episodic flourishing, quick death and preservation of the macroscopic Lantian biota. To further distinguish the living and preservational environment of the Lantian biota, we carried out more detailed framboidal pyrite analyses. The studied material include fossilbearing layers and fossil bodies. The fossils in this study comprise Chuaria and fanshaped algae. The results show that the framboidal pyrite of fossil-bearing beddings has smaller diameter and narrower size range (with average diameter of 4.7-6.4  $\mu$ m, n=11) than the framboidal pyrite of the fossils (with average diameter of 6.5-12.0  $\mu$ m, n=32). Combined with the published lamina-by-lamina framboid statistical data, the results show that the pyritization of the Lantian biota in suboxic or anoxic (but not sulfidic) environment predates the matrix pyrite formation in a sulfidic environment, and that the Lantian biota have lived in an oxic environment. Furthermore, pyrite was lost in some fossil bodies as well as the fossil-bearing layers with only framboidal caves left, which suggests the return of an oxic environment. The evidences from the framboidal pyrite analyses indicate that the conditions in the early Ediacaran of Lantian basin fluctuated. At the same time, there are significant framboid diameter differences among different fossil types. Chuaria has the largest framboids, while fan-shaped algae have relatively smaller framboids. We concluded that the fossil pyritization process is as follows: when the water gradually transformed from oxic to anoxic and killed the oxygen-dependent organisms, the initial redox environment (not sulfidic) was unfavorable to the formation of pyrite in the host sediments and water column. But due to the high content of organic matter, these organisms were conducive to forming and maintaining more anoxic microenvironment, thus promoting framboidal pyrite formation, finally resulting in larger framboidal pyrite in the fossils than in the surrounding matrix. Chuaria is more conducive to form an anoxic

pyrite in the fossils than in the surrounding matrix. *Chuaria* is more conducive to form an anoxic microenvironment and larger framboidal pyrite because its globose body has smaller surface area to volume ratio than fan-shaped algae do.



Speaker

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### Palaeopascichnus from the Ediacaran of the Digermulen Peninsula, Arctic Norway and the age of the Varanger Ice Age

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Palaeopascichnids are possibly the longest-ranging macroscopic Ediacaran fossils (ca. 565-542 Ma). They are bedding plane-parallel modular fossils composed of series of closely spaced millimeter sized circular, sausage- or kidney- shaped units. Earlier regarded as trace fossils, they are now seen as body fossils: possible xenophyophoran protists or protists of uncertain affinities. The Cryogenian to lower Cambrian succession (Vestertana group) exposed on the Digermulen Peninsula starts with the glacial Smalfjorden, interglacial Nyborg and glacial Mortensnes fms, collectively known as the Varanger Ice Age. Together with the succeeding Stáhpogieddi Fm. they reflect changes from global icehouse to greenhouse conditions. The Stáhpogieddi Fm. starts with the Lillevannet Mbr. followed by the Indreelva Mbr., yielding Ediacara-type fossils. The highest member in the Stáhpogieddi Fm, the Manndrapselva Mbr, contains the Ediacaran- Cambrian boundary. Palaeopascichnus is found at three horizons within the Stáhpogieddi Fm. The youngest, within the Manndrapselva Mbr., is latest Ediacaran, based on associated trace fossils, as well as occurring below trace fossils from the Treptichnus pedum ichnozone. Palaeopascichnus is also present near the base of the Manndrapselva Mbr. The oldest occurrence is from a horizon transitional between the Lillevannet and Indreelva Mbrs. Age constraints on the Varangerian glacial deposits are poor and their relationship to Neoproterozoic glacial events is equivocal. Studies over the last several decades have placed the Smalfjorden Fm. within the globally developed Marinoan glaciation (ca. 645-635 Ma) based on the presence of cap dolostones. The Mortensnes Fm. has been aligned within the Ediacaran Gaskiers glaciation (ca. 580 Ma) on the basis of carbon isotope stratigraphy. However, alternative interpretations exist, including that of a Marinoan affinity for all of the Varanger ice age. Palaeopascichnus at the Lillevannet Mbr. to Indreelva Mbr. transition indicates that this part of the succession is younger than 565 Ma. Because the transition between the Mortensnes Fm. and the succeeding Stáhpogieddi Fm. is seemingly without major breaks in sedimentation, this is consistent with a Gaskiers, or younger age for the Mortensnes Fm. An older age (Marinoan) requires the discovery of major breaks in the sedimentary record.



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### Evolutionary significance of a middle Cambrian (Series 3) *in situ* occurrence of the pedunculate rhynchonelliform brachiopod *Nisusia sulcate*

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Exceptionally preserved, silicified and articulated complete shells of the rhynchonelliform kutorginate brachiopod Nisusia sulcata are redescribed from the middle Cambrian (Series 3) Marjum Limestone, Utah. Cylindroid sausage-like protrusions, emerging posteriorly between the valves, were originally interpreted as faecal in origin, but additional study under SEM shows that these features represent silicified pedicles, as they are attached in situ to other Nisusia. The Nisusia host most likely was alive at the time of attachment. Restudy of the pedicles of Nisusia provides new phylogenetic information on the anatomy of the earliest rhynchonelliforms. The silicified pedicles differ considerably from the pedicles of living crown group rhynchonelliforms in being strongly annulated, distally tapering, and were likely to have been rather more flexible. The Nisusia pedicles are more similar to the exceptionally preserved pedicles from other Cambrian rhynchonelliform brachiopods, including Kutorgina, Longtancunella and Alisina, but these emerge from the ventral apical foramen rather than from between the valves, as in Nisusia. Although generally similar, these two types of pedicles are unlikely to represent homologous structures since Nisusia is provided both with an apical foramen (possibly larval attachment) as well as a posterior adult pedicle. The similarities may be explained by similar type of accretionary growth from two different types of epithelia. The Nisusia - like pedicle appeared early within the kutorginates and rhynchonellates. The discovery of hollow spines in Nisusia sulcata further supports the generic assignation of the species.



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## The first evidence of disability in the "Garden of Ediacara"

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The romantic theory of the "Garden of Ediacara" proposed by M. McMenamin is based on the assumption that the proliferation of "peaceful" immobile organisms feeding by photo- symbiosis, chemosymbiosis, and osmotrophy made up the macrobiota of the Late Precambrian (Ediacaran). However, studies over the last two decades have shown the presence of mobile Metazoa, which cause damage to their prey in the benthic communities of marine shallow waters of the Late Precambrian of Russia and Australia. The bilateral animal Kimberella had sharp teeth by which it left scratches on the microbial mat and tore out large pieces of it. And it seems that the microbial substrate was not alone in experiencing aggression from this animal. There are imprints of attachment discs of macroorganisms belonging to the genus Cyclomedusa that show traces of having been disturbed by Kimberella. However, it is impossible to claim with certainty that the damage was caused to a living organism rather than to its carcass or even to a postmortal imprint. Evidence of damage to the bodies of living examples of the Metazoan Dickinsonia was found in one of the White Sea localities. The low but wide body of Dickinsonia consisted of numerous identical right- and left-handed transverse elements (isomers) that extended from the body axis in an alternating order. The growth of Dickinsonia was expressed in the appearance of new isomers at the posterior end, with each new element longer than the previous one. Several dozen specimens of Dickinsonia of various sizes and ages were found in the White Sea locality. The number of isomers varies from 20 to more than 170 pairs. Clear damage to the growth zone was found only in 11 large specimens. The area of damage usually is limited in extent and is located between the anterior and posterior regions of unaffected isomers. The healthy body elements surrounding the damaged areas bent to compensate for the missing tissue, indicating that the damage was sustained when the Dickinsonia was alive. The arrangement of variously deformed isomers suggests the accumulation of negative impact over time, and then its abrupt cessation, which led to a rapid recovery of the body's normal morphology. Young individuals that appeared in the basin later did not experience it at all. The nature of this effect is not defined, so it is not completely unambiguous that it was caused by another organism. Thus, despite the discovery of damaged individuals in the "Garden of Ediacara", the presence of predatory animals in the Late Precambrian has not been established yet.



<sup>&</sup>lt;sup>°</sup> Speaker

### Redefining the *Treptichnus pedum* zone at the Global Boundary Stratotype Section and Point (GSSP): a critical reassessment of the Ediacaran-Cambrian boundary

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The Cambrian explosion bisects the history of life, separating relatively simple pre-Cambrian life from the complex and diverse Cambrian fauna. Due to the paucity of the body-fossil record over this critical interval, trace fossils often offer the only available insight into these evolutionary milestones, representing a continuous record through the late Ediacaran-early Cambrian. The Chapel Island Formation (CIF) of Newfoundland provides an exceptional record of these innovations. Currently, the Global Boundary Stratotype Section and Point (GSSP) for the basal Cambrian boundary is located 2.4 m above the base of member 2 of the CIF, delineated by the lowest observed appearance of the Treptichnus pedum Ichnofossil Assemblage Zone (IAZ). Recently, researchers are facing difficulties when attempting to correlate sections worldwide, and a formal revision of the boundary has been proposed. We hypothesize that a revision of the ichnotaxonomy of the GSSP with an emphasis on trace fossil functional morphology may better illustrate evolutionary innovations at the Ediacaran-Cambrian boundary, and may provide further support for the position of the Ediacaran-Cambrian GSSP. Through a bed-by-bed study, the ichnotaxonomy of the T. pedum IAZ was revised, and a stratigraphic section was created. Twenty ichnospecies comprising thirteen ichnogenera were observed. The ichnospecies were grouped into five ichnoguilds, which were utilized to conduct an ecospace analysis of the section. The ichnofauna revealed a more gradual explosion of ichnofossil diversity at the boundary, and a more protracted transition between Ediacaran and Cambrian ecosystems than previously envisioned. The T. pedum IAZ in the CIF marks the appearance of novel methods of interacting with the substrate, as documented by sub-horizontal branching burrows (Treptichnids), equilibrium structures (?Bergaueria isp.), and complex vertical burrows (Gyrolithes scintillus ichnoguild). Additionally, it marks the evolution of novel body plans, as revealed by the presence of arthropod scratch marks (Dimorphichnus cf. obliquus). Notably, remnants of Ediacaran matground ecology are also present-chemichnial feeding styles are utilized by the Gyrolithes scintillus ichnoguild, and mat grazing remains a common feeding style. The revision of the CIF T. pedum ichnotaxa, as presented above, further illuminates the depth and rate at which this new lifestyle evolved, shedding light on the evolution of Cambrian mixground ecology.



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### Reevaluation of the morphology and affinities of the enigmatic vetulicolian animal, *Yuyuanozoon magnificissimi*, early Cambrian Chengjiang Lagerstätte, South China

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Vetulicolians are a group of enigmatic animals exclusively from Cambrian Lagerstätten, characterized by an anterior section with 5 pairs of lateral pouches and a posterior section that appears segmented. The precise affinity of vetulicolians is debated because there is a lack of consensus regarding the interpretation of their anatomical features. Yuyuanozoon magnificissimi is a vetulicolian species that was first described in 2003 based on a single specimen from the Chengjiang Lagerstätte (Cambrian Series 2, Stage 3, Eoredlichia-Wutingaspis trilobite Biozone), Yunnan Province, China. Although placed in the family Vetulicolidae, this species is notable in being exceptionally large-up to 20 cm long. Morphological observations on new specimens clarify the nature of the wide circular opening at the presumed anterior end of the animal, and the ovoid shape of lateral pouches within this anterior section. In particular, the shape of the anterior opening of Y. magnificissimi suggests significant differences from other vetulicolians. In reanalyzing the morphology of Y. magnificissimi, we have attempted to develop a unified terminology for the description of vetulicolians that avoids inferring animal relationships or functional morphology. We propose a bottom-up approach to interpreting these animals that examines their full range of morphological characteristics, without any preconception of affinity. From this new approach we hope that a more realistic picture of the interspecific variation of vetulicolians can be assessed, that will lead to a greater understanding of their wider animal affinities.



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#### Colonies, clones and modularity: a new view of Ediacaran fronds

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The Rangeomorpha and Arboreomorpha include some of the oldest large, macroscopic organisms in the fossil record, with specimens capable of attaining lengths approaching two metres. The seemingly rapid acquisition of large size in these groups has been widely assumed to stem from an underlying morphogenetic simplicity. However, the detailed morphology of many of these organisms remains poorly constrained, rendering assumptions about morphogenesis and phylogenetic placement premature. We here present morphological, morphogenetic and palaeoecological evidence to suggest that Ediacaran frondose taxa may variously have had modular, clonal and, perhaps, colonial body plans. Reassessment of *Arborea* from South Australia reveals a distinctive arrangement of internal anatomical structures that connect individual external branch units to the interior of the organism, consistent with a colonial construction. Filamentous structures amongst frond-bearing fossil assemblages worldwide reveal that rangeomorphs could be physically interconnected to other individuals of the same species by enduring stolonlike structures, over distances of tens of centimetres to metres. Furthermore, new morphogenetic data from several multifoliate rangeomorphs reveal potential evidence for biological modularity. Taken together, this information enables us to offer an alternative colonial hypothesis to explain the rapid transition to large body size in the middle Ediacaran.

Speaker

### Lower Cambrian phosphorite as a new taphonomic window to sponge early evolution: an example from the basal Niutitang Formation, Hunan, China

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Investigations of the early evolutionary history of sponges are impeded by the dearth of fossil records. Despite the existence of questionable Ediacaran sponge-like fossils, the earliest sponge spicules appeared from ca. 535 Ma. However, disarticulated spicules are of little taxonomic value, and almost all the articulated sponge fossils were reported only after the beginning of Cambrian Age 3, from Burgess Shaletype preservation. Here we report the finding of *in situ* and three-dimensionally preserved sponge fossils from phosphorites of the basal Niutitang Formation in South China, which are no younger than the Cambrian Age 2. These sponges are preserved as isolated, oval bodies in the nodular, carbonaceous cherty phosphorite. Petrographic observation shows that these phosphorites were mostly formed by authigenic precipitation. Spicules in these bodies are either completely embedded in cryptocrystalline phosphate, or immediately overgrown by early isopachous phosphate cements, leaving the remaining interspace filled by other components. Thin section observation and 3D reconstruction confirm that these spicules represent sponge skeletal frames preserved in situ. The diversity of the fossil sponge community in these phosphorites has not yet been fully explored. Two sorts of skeletal frames have been recognized so far: one is composed of hexactines in at least three size hierarchies; the other is dominated by diactines which are perpendicularly arranged in three dimensions. These fossils are here interpreted as stem group Hexactinellida. Apart from this, some of the disarticulated spicules scattered in the matrix are identical to typical modern demosponge spicules. This work indicates that the lower Cambrian phosphorites can be a new taphonomic window to study the early evolutionary history of sponges. Further taxonomic and geochemical analyses are required and ongoing to reveal more details.



Speaker

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# The importance of body size for Ediacaran communities of Avalonia

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One of the most striking evolutionary developments in the history of life on Earth was the appearance of large, complex organisms. This innovation is captured in the fossil record by the sudden appearance of immobile Ediacaran macrofossils ~580 million years ago. The anatomy of these Ediacaran organisms is fundamentally different from that found at other time periods, making it difficult to resolve their phylogenetic relationships or ecology. However, their preservation in large in situ bedding-plane populations means that their spatial positions reflect the biological and ecological processes that they were subject to in life. As a result, statistical analyses can reveal key insights into the ecological dynamics of these early communities. The 'E' surface at Mistaken Point, Newfoundland, Canada and Bed 'B' in Charnwood Forest, UK (both ~565 million years old), host two of the most abundant and diverse Ediacaran communities known. While there are similarities in community composition, the Charnwood Forest community has a conspicuously higher abundance of very large specimens coinciding with a more extensive population of smaller individuals. We used spatial point process analyses to identify inter-specific interaction networks of these communities. Species networks were compared to size networks to assess the extent to which these Ediacaran communities are size-structured, and the effect that the Charnwood Forest giants had on the rest of the community. These analyses illuminate the impact of body size on these first communities of macroscopic organisms.



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## Burgess Shale fossils shed light on the agnostid problem

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Ontogeny can provide crucial insights into evolutionary history, however, the rarity of completely preserved ontogenetic series in the fossil record often renders this information inaccessible to palaeobiologists. The importance of ontogeny has been particularly contentious in relation to the 'agnostid problem', the ongoing debate over the phylogenetic affinities of agnostids, a widespread and biostratigraphically-important group of Cambro-Ordovician arthropods. Agnostids were historically interpreted as paedomorphically-derived trilobites, based on their characteristic calcified tergum, with equal-sized cephalic and pygidial shields articulated by two free tergites. This hypothesis was called into question following the discovery of exceptionally preserved juvenile agnostids from the Orsten Lagerstätte, with putatively crustacean-like appendage morphology. However, these morphologies could also be interpreted as larval specializations, as appendages of any kind have hitherto been unknown in mature agnostids. Here we describe exceptionally preserved adult Peronopsis and Ptychagnostus from the middle Cambrian (Stage 5) Burgess Shale (Walcott Quarry and Marble Canyon), which facilitate the testing of alternative hypotheses of agnostid evolution. The digestive tract extends posteriorly from a saddle-shaped hypostome, terminating in an anus below the tip of the pygidial axis. A pair of ramifying gut diverticula extend laterally and frontally below the cephalic shield. The cephalon carries a pair of gracile spinous antennules, two pairs of specialized appendages with distally setose, oar-like exopods, and three pairs with endopods sporting distinctive, club-shaped exites. Each free tergite covers one appendage pair, similar to the posterior cephalic pairs. The pygidium bears at least three poorly preserved pairs of appendages of unknown morphology. By comparison with the Orsten specimens, many aspects of appendage structure are ontogenetically conservative, and therefore are not merely larval idiosyncrasies. The six cephalic appendage pairs evident in the new material contrast strikingly with the four known in trilobites and five typical of mandibulates. As such, agnostid morphology cannot be exclusively a result of paedomorphosis from a trilobite ancestor, yet it also seems at odds with a mandibulate affinity under prevailing views of character evolution. Informed by our findings, phylogenetic analysis (currently in progress) may further illuminate the agnostid problem.



Speaker

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### Diversity and structure of the middle Cambrian Marble Canyon paleocommunity, Burgess Shale, British Columbia

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Burgess Shale-type deposits are key to our understanding of the first complex animal communities. However, a clear view of the full complexity of these ecosystems is restricted to a handful of species-rich fossil localities, such as those found in the middle Cambrian Burgess Shale. Here we describe the palaeocommunity of the Marble Canyon fossil assemblage, part of the Burgess Shale, in Kootenay National Park (British Columbia). This study is based on approximately 20,000 specimens collected by the Royal Ontario Museum between 2012 and 2016 within a roughly five-metre-thick section at one site. Arthropods dominate in diversity (ca. 40% of species), ranging from the small bradoriid arthropod Liangshanella, to a number of large dinocaridids. The lophophorate Haplophrentis carinatus, the tubicolous hemichordate Oesia, and the benthic polychaete Kootenayscolex are also among the five most abundant species at Marble Canyon. The chordate Metaspriggina, which is rare in the Walcott Quarry, is also a distinctive element of this assemblage. Surprisingly, there is a near total absence of sponges and brachiopods. The benthic suspension feeding niche normally occupied by these taxa may instead be filled by Oesia and Haplophrentis, based on recent re-interpretations of their ecologies. Other taxa common to Cambrian localities that are depauperate at Marble Canyon include the priapulids, which distinguishes the Marble Canyon from the Chengjiang. Overall diversity remains relatively low in the upper part of the quarry and is mostly dominated by Oesia, Haplophrentis, and agnostids. The lower quarry yields substantially higher taxonomic diversity and niche disparity, including hemichordate and polychaete dense bedding planes and assemblages of large arthropods mainly represented by Sidneyia, Yawunik, and Tokummia. Like at the Walcott Quarry, patterns of faunal turnover seem to represent a mixture of temporally restricted taxa as well as species that are recurrent throughout the entire sampled interval. Future and ongoing work aims at integrating the Marble Canyon dataset with other major Burgess Shale localities to elucidate broader community patterns. One of the major goals of analyzing this expanded dataset will be to reveal the extent to which the Burgess Shale palaeocommunities (measured by niche occupation and relative abundances) varied in time and might have been affected by ecological or environmental idiosyncratic variations at particular sites.



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<sup>&</sup>lt;sup>\*</sup> Speaker

# The Early Cambrian origin of Pancrustacea revealed by micro-computed tomography

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Crustaceans and insects, collectively Pancrustacea, represent the most successful animal group thanks to their diversity and profound ecological impact. Early pancrustacean evolution remains problematic, however, as it is mainly informed by microfossils preserved as phosphatized juvenile stages or fragmentary carbonaceous compressions. We employed X-ray computed tomography to reveal the three-dimensionally pyritized limb anatomy of the Chengjiang euarthropod *Ercaicunia multinodosa* from the early Cambrian of China. *E. multinodosa* possesses various pancrustacean synapomorphies, including differentiated tritocerebral antennae, gnathal appendages and epipodite-bearing biramous trunk limbs. A phylogenetic analysis resolves *E. multinodosa* within stem-group Pancrustacea, alongside clypecaridids, waptiids and hymenocarines from Cambrian Burgess Shale-type deposits. *E. multinodosa* illuminates the early evolution of pancrustacean gnathal and trunk appendages, and represents the oldest unequivocal crown-group mandibulate known from complete macrofossils.



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Speaker

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#### Trade-offs in brood are and reproduction of Cambrian waptiid pancrustaceans

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Trade-offs play a crucial role\_in the life-history strategies of extant organisms and have shaped their past evolution. One significant trade-off is between the number of offspring and the amount of energy (including nutrition and parental care) allocated for individual offspring. Exceptionally well-preserved fossils from the Cambrian period allow us here to trace the earliest evidence of trade-offs in reproduction of pancrustaceans. We describe *Chuandianella ovata* from the early Cambrian Chengjiang biota of China (~520 Mya) which brooded numerous (at least 100 per clutch) but small ( $\emptyset$  ~0.5 mm) eggs under its carapace valves. *Waptia fieldensis*, a closely related species from the middle Cambrian Burgess Shale of Canada (~508 Mya), showed a similar mode of brood care but, in contrast to *C. ovata*, carried much fewer (up to 24 per clutch) but larger ( $\emptyset$  ~2.5 mm) eggs. The different clutch/egg sizes in these two closely-related waptiid crustaceans reveal possible trade-offs between quantity and quality of offspring through the early-middle Cambrian interval, probably in adaptive response to changes in marine ecosystems. We hypothesize that trade-offs in brood care have played an important role in the evolutionary success of pancrustaceans from the Cambrian through to the present day.



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#### Small shelly fossils from the Cambrian Series 2 Xinji and Houjiashan formations along the south and south-west margin of North China Platform

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The occurrence of abundant and diverse small shell-bearing metazoans known as Small Shelly Fossils (SSF) in the earliest Cambrian is one of the critical evidence for the Cambrian explosion. These SSF assemblages are represented by various animal groups and are dominant elements of the marine fauna during the Terreneuvian and until the extinction event of the upper part of the Cambrian Stage 2. However, many SSF taxa (molluscs, chancelloriids, hyoliths etc.) survived and diversified in Cambrian Epoch 2. Meanwhile, other shell bearing taxa, such as brachiopods, lobopodians and trilobites evolved and diversified at this time. In the last decades, many studies have been published on SSF from Cambrian Series 2 worldwide (Australia, Antarctica, South China, Tarim, Siberia, Greenland, Newfoundland and USA etc.). However, their evolution, diversity, and palaeogeographic as well as stratigraphic distribution are poorly understood. Abundant SSF assemblages have been reported form the South margin of the North China Platform in this time interval. However, many of them are problematic and need further study. Thus, we have undertaken to restudy the SSF assemblages from the Xinji and Houjiashan formations at several sections (Sanjianfang, Shuiyu, Luonan, Zhoujiaqu, Caijiawa and Xiaomeiyao) along the south and south-west margin of North China. We have distinguished nearly 40 genera and 50 species of SSF from North China including hyoliths, molluscs, brachiopods, bradoriids, tommotiids, chancelloriids, sponge spicules, echinoderm sclerites, lobopodians, halkieriids and other problematic sclerites. Many of these taxa had a very wide spatial distribution in the Cambrian oceans and may have potential for biostratigraphic correlation. The SSF assemblages from North China can be easily correlated with faunas from the Dailyatia odyssei Zone of South Australia. Thus, we consider the age of the Xinji and Houjiashan formations from North China as being late Stage 3 to early Stage 4 of Cambrian Series 2. The close similarity of SSF assemblages from North China and Australia indicates that North China may have been relatively close to Australia during this time interval.



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#### The diet of Cambrian worms: inferring feeding in Burgessochaeta setigera, a stem group annelid from the Burgess Shale

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Polychaete worms are key components of modern benthic marine ecosystems, dominate many communities in terms of biomass, and usually are microphagous, with suspension and deposit feeding being the most common feeding strategies. Macrophagy and carnivory are restricted among extant taxa to the aciculates, a clade (or grade) for which there is currently no fossil evidence until the Ordovician or very latest Cambrian. Ancestral state reconstruction using phylogenies of extant taxa suggest that macrophagy evolved once or possibly twice in annelid evolutionary history. However, reconstructing the evolution of ecological strategies in the absence of fossil evidence may provide a profoundly incomplete picture of the evolutionary history of diet in annelids. In that regard, Burgess Shale-type deposits are particularly significant. They provide unique windows into Cambrian marine communities, but, despite exceptional anatomical preservation, questions remain regarding the ecology of many constituent taxa, in particular, their feeding modes. Direct evidence of trophic relationships remain remarkably rare and so far, preserved gut contents have only been studied in detail in two Burgess Shale taxa, the arthropod Sidneyia inexpectans and the priapulid worm Ottoia prolifica. Here we describe gut contents of Burgessochaeta setigera, the most abundant polychaete from the Burgess Shale (Walcott Quarry). In contrast to other polychaetes from this site, Burgessochaeta specimens preserve gut contents (cololites) in three dimensions as calcium phosphate. Although the granular material in these guts is often difficult to identify, in several specimens, isolated trilobite glabella, free cheeks and thoracic segments are present. Preservation of trilobites in only a few specimens may indicate that Burgessochaeta fed opportunistically rather than targeting predation on heavily skeletonized prey. The body plan of Burgessochaeta is that of a generalized polychaete, lacking any obvious adaptations for carnivory or predation. There is no evidence of jaws, indicating that Burgessochaeta was capable of engulfing large food items using only the pharynx. The presence of macrophagy and carnivory in an ancient polychaete highlights that annelids explored diverse feeding strategies early in their history, but without the specialized structures for food gathering and processing typically associated with macrophagy in extant forms.



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#### Diversity and disparity of radiodonts from the USA

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Radiodonta, a group of large Cambrian euarthropod predators best known from the iconic Burgess Shale animal Anomalocaris canadensis, are often preserved as disarticulated body elements: frontal appendages, mouthparts made of plates, lateral flaps with transverse lines, setal blades, and carapace elements. These animals are best known from the Chengjiang biota and Burgess Shale, but radiodonts have been found worldwide in the Cambrian period. In this study radiodonts from the Great Basin (California, Idaho, Utah, Nevada, USA) and Kinzers Formation (Pennsylvania, USA) were restudied and placed into a modern taxonomic context. USA sites offer the opportunity to study the local and regional evolution of the group at high temporal resolution from the upper Dyeran (Cambrian Series 2 Stage 4), to the Drumian. Revision of the material revealed the oldest Amplectobelua and Hurdia from Laurentia, the youngest representatives of Stanleycaris, Caryosyntrips and Tamisiocaris worldwide, and a temporally staggered introduction of Anomalocaris and Hurdia to Laurentian basins. The frontal appendages of radiodonts were undoubtedly used in feeding, with different morphologies indicating different feeding styles. The disparity of frontal appendage morphologies was quantified using a character- based morphospace. This disparity was then analysed in the USA through time, showing a decrease from the oldest sites to the youngest. This correlates with the changeover between Anomalocaridids and Amplectobeluids, which dominate older sites, and Hurdiids, which dominate younger sites, but not with overall radiodont diversity. This local signal is also found worldwide, and demonstrates the decline of the best-known Cambrian apex-predators through the middle and late Cambrian.

Speaker

# The functioning of a trilobite visual system more than half a billion years ago

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For a long time, it seemed to be impossible that soft tissues could be preserved in the fossil record with the result that cellular structures, and very often the structure and function of such ancient sensory organs as eyes, remained undiscovered. It was generally thought that they would remain so for ever. However, exceptionally well-preserved fossil specimens from Lagerstätten and the progress of modern techniques such X-ray microtomography and the use of synchrotron radiation opened new perspectives. Arthropods with compound eyes are known from the beginning of the lower Cambrian, more than 500 million years ago. These eyes display visual surfaces with regular patterns of facets as exemplified by trilobites and other arthropods. Schmidtiellus reetae Bergström, 1973 is a redlichiid trilobite with phosphatic preservation from the lowermost Cambrian of Estonia, i.e. older than the Chengjiang and Burgess Shale faunas. It is equipped with the typical flat slit-shaped compound eyes of the early trilobites. In the holotype the surface of the right eye is abraded, allowing internal structures to be observed in details. This eye strongly resembles the compound apposition eyes of modern crustaceans and diurnal insects such as bees and dragonflies. However, it differs from them by the apparent lack of a lens and the fact that each visual unit with photoreceptors lies within a separate 'basket'. Mosaic-like vision was achieved by means of the rhabdom, a central light guiding structure which is part of the receptor cells, and possibly a crystalline cone, focusing light. Since chelicerates have no crystalline cone, this suggest that trilobites would have mandibulate affinities. Other enlightening results obtained via the on-going study of the enigmatic compound eyes of Devonian phacopid trilobites, indicate that under each of the big, sophisticated lens typical of the phacopid compound eyes lies a small aggregate of several visual units comparable with those of S. reetae. Thus, below each lens, these visual units formed a compound eye within a compound eye.



Speaker

#### On the origin of hyolith helens

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Hyoliths are enigmatic invertebrate fossils that were common in the early Palaeozoic and disappear after the end Permian mass extinction. The hyolith skeleton consisted of a calcareous cone-shaped conch, a lid-like operculum and at least in one group, the Order Hyolithida, a pair of elongate lateral spines or helens. The functional morphology and biological affinity of hyoliths have been debated for over a century, but the recent identification by Moysuik et al (2017) of a lophophore-like tentaculate filter-feeding organ in Cambrian specimens and the proposition that hyoliths may be closely related to, or even derived from, brachiopods have further inflamed the debate. Despite only being found in one of the two major groups of hyoliths, the Hyolithida, helens and their functional morphology have played a vital role for most interpretations and reconstructions of the hyolith animal. Helens have been suggested to provide stability on the sea floor, to support extensive external soft tissues, to provide the animal with limited benthic movement capability or even to facilitate swimming. The functional interpretation of Moysuik et al. (2017) is no exception as the filter feeding capability of hyolithids hinges on the assumption that the animal used the helens to lift the apertural part of the conch over the sea floor to avoid fouling the "lophophore". Our investigation of early Cambrian hyoliths from China has revealed that a certain sub-group of hyoliths, exemplified by the genus Paramicrocornus, lacked macroscopic helens, despite an otherwise hyolithid-like morphology. Instead of helens these hyoliths preserve clavicles of unusual morphology. Clavicles are paired internal ridges of hyolith opercula that previously have been interpreted to function in controlling the movement of the helens. The clavicles of *Paramicrocornus* and some other hyolithids from China consists of multiple rod-like elements arranged in a palisade-like structure. Individual rods exhibit regular growth during ontogeny while new rods were periodically added. We propose that hyolith helens may be homologous with the rods of the clavicles in *Paramicrocornus*. Isolated rods would develop into helens through a drastic increase in growth rate (allometric growth), perhaps evolving in tandem with changes in feeding behaviour from deposit to filter feeding. Through this process, the development of helens may have opened up new niches to the emerging hyolithids.



<sup>&</sup>lt;sup>'</sup> Speaker

# Hyoliths with pedicles: the origin of the brachiopod bodyplan

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The distinctive shells of hyoliths are familiar members of Sepkoski's Cambrian fauna, yet the precise phylogenetic position of this group remains uncertain: does their aragonitic shell microstructure point to a link with molluscs, or does their feeding apparatus indicate a lophophorate affinity? Here we describe a new orthothecid hyolith from the Chengjiang Lagerstätte (Cambrian Series 2 Stage 3) with a non-mineralized attachment structure akin to the brachiopod pedicle – the first report of a peduncular organ in hyoliths. Besides establishing a sessile, suspension feeding ecology for these orthothecids, the presence of an apical pedicle in combination with plesiomorphic characters (absence of larval setae; lophophore coiling direction) identifies hyoliths as stem group brachiopods. Phylogenetic analysis of Cambrian Brachiozoans indicates remarkable morphological plasticity in the tommotiid-hyolith grade that later gave rise to crown group brachiopods.

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## The importance of substrate for Ediacara paleoecology, paleoenvironment and taphonomy

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The Ediacara Biota, Earth's earliest ecosystem of complex, macroscopic, multicellular organisms, is preserved in terminal Ediacaran strata worldwide. In the Ediacara Member of South Australia, Ediacara fossil assemblages occur in intimate association with macroscopic, iterative organosedimentary structures, known as "textured organic surfaces" (TOS). TOS are a ubiquitous, diverse and commonly complex component of the fossiliferous Ediacara Member and likely included densely aggregated macroscopic multicellular organisms as well as microbial consortia. Systematic sedimentary and paleoecological analysis of 33 fossiliferous beds (nearly 300 square meters) has resulted in detailed characterization of the sedimentology, paleoecology and taphonomy of both Ediacara macrofossils and TOS. Particular macrofossil taxa and TOS appear to be facies-specific in their distribution. For instance, the iconic Ediacara body fossil Spriggina, as well as the TOS "weave" occur only along rippled, storm-deposited sandstone event beds. Conversely, Eoandromeda and the TOS "micropucker" each occur along planar-laminated and tool-marked fine-grained sandstone beds deposited below storm wavebase. The presence of a heterogeneous organic substrate appears to have strongly influenced the ecology of Ediacara benthic ecosystems in high-energy shallow marine settings, and to have fostered the emergence of complex, animal-style ecological strategies. TOS may have additionally played an important role in the fossilization of these communities. Moreover, the abundance, diversity and facies specificity of TOS suggest that these structures can be used to gauge whether paleoenvironmental and taphonomic conditions favorable for colonization by and preservation of Ediacara macroorganisms were present across a wide range of shallow marine paleoenvironments. TOS may therefore provide a means of constraining whether the absence of Ediacara-type taxa from either older or younger strata is evolutionarily meaningful, and for reconstructing the evolutionary ecology of the Precambrian-Phanerozoic transition.



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### Remarkably preserved chaetae of *Pelagiella* document the occurrence of torsion in development of an early Cambrian stem gastropod and support the lophotrochozoan affilation of the Mollusca

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Exceptionally well preserved impressions of paired bundles of bristles, protruding from the apertures of small, spiral shells found in the Kinzers Formation (Cambrian, Stage 4, "Olenellus Zone", 512 Ma) of Pennsylvania, are comparable to chaeta-bearing organs of annelids and larval brachiopods. The shells of Pelagiella, products of logarithmic spiral growth, are unequivocally molluscan. Elsewhere, species in this genus exhibit distinctive external shell sculptures, and their microstructural fabrics are typical of those of early molluscs. In some species, interior muscle scars characteristic of molluscs and not of wormtubes have been recognized on steinkerns. The chaetal organs reported here, not hitherto observed in any living or extinct mollusc, highlight the affinity of molluscs, annelids and brachiopods. They provide an affirmative test in the early metazoan fossil record of the inference from phylogenetic analysis of living taxa that chitinous chaetae constitute a deep homology of this lophotrochozoan clade. Pelagiella has been construed as a stem mollusc, as a monoplacophoran expressing partial torsion in its development, as a paragastropod, as an archaeobranchian, and as an archaeogastropod - in the last two cases implying full developmental torsion. Now, incorporation of the chaetal organs in a new reconstruction of the anatomy of Pelagiella verifies the anterior-posterior orientation of the animal. This prompts the interpretation of two fine, gracefully curving grooves preserved on a steinkern of *P. atlantoides* as sites of attachment for a long left ctenidium (gill) and a short one, limited to the anterior portion of the mantle cavity, on the right. This direct evidence of asymmetry in the organs of *Pelagiella* establishes it as the earliest gastropod confirmed to have undergone torsion. It was the emergence of this key adaptation, considerably earlier than hitherto documented, in a lineage arising from the paraphyletic helcionelloids -molluscs with simple, spiral, univalve shells that gave rise to the conchiferan classes - that initiated the subsequent evolutionary radiation of the Gastropoda in conjunction with the gradual development of increasingly complex ecosystems.



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#### A stem group echinoderm from the basal Cambrian of China

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Molecular phylogeny now provides a robust framework for illustrating how morphologically disparate groups of animals relate to each other, and in which order through history they emerged. Fossils however, are crucial pieces needed to complete this puzzle, capturing morphologies present in the stem group of living taxa that have long since been lost. Deuterstomes are a morphologically disparate clade, encompassing the chordates (that includes the vertebrates), the hemichordates (a grouping of small to large, vermiform enteropneusts and the minute tube-dwelling solitary to colonial pterobranchs) and the echinoderms (including starfish and urchins). The echinoderms together with their sister-group, the hemichordates, comprise the clade Ambulacraria, itself a sister group to the chordates. Although a monophyletic origin of the deuterostomes has been demonstrated by molecular phylogenetic techniques, the interrelationships between the three clades remain highly contentious, providing little guidance as to the nature of the ancestral deuterostome. Here we report, Yanjiahella biscarpa, a bilaterally symmetrical, solitary metazoan from the early Cambrian (Fortunian) of South China. Yanjiahella biscarpa possesses a characteristic echinoderm plated theca, a pair of long, distinct feeding tentacles but also has a ringed tubular stalk, reminiscent of the hemichordates. This combination of morphological characters suggests that Y. biscarpa occupies a position on the stem of the Echinodermata and not only represents the oldest echinoderm reported to date, but it also predates all known hemichordate occurrences and is among the earliest reported deuterostome. It confirms that echinoderms acquired mesodermal plating before pentaradial symmetry and that their early history is rooted in bilateral forms at the onset of the Cambrian Radiation. Yanjiahella biscarpa however, shares morphological similarities with both the enteropneusts and echinoderms and challenges previous analyses of the group, supporting an alternative hypothesis that the enteropneust body plan is primitive for the hemichordates. The presence of tubular structures across basal Ambulcrarian members further suggests that the last common Ambulacrarian ancestor was also tube dwelling, highlighting the role of tube construction in the early stages of deuterostome evolution.



<sup>&</sup>lt;sup>°</sup> Speaker

### Waptia fieldensis Walcott, a mandibulate arthropod from the middle Cambrian Burgess Shale biota

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Waptia fieldensis Walcott, 1912 is one of the iconic animals from the middle Cambrian Burgess Shale that had lacked a formal description since its discovery at the beginning of the 20th century. Our study based on over 1800 specimens reveals the external and internal anatomy of this shrimp-like arthropod with unprecedented details. The cephalothoracic region is covered by a flexible bivalved carapace, housing sensory organs such as long antennules, stalked compound eyes and possible olfactory neuropils nested in a pair of small lobate projections. A prominent median triangular sclerite covering additional sensory organs confirms the deep homology of this structure across euarthropods, and may shed further light on the ancestral labrum. The mandibles are large gnathal elements with marginal bump-like teeth, also bearing a three- segmented setose palp that recalls modern crustaceans. They were used in processing food in coordination with the adjacent elongated maxillules and three succeeding pairs of stenopodous appendages. These appendages were composed of subdivided basipods bearing long and robust endites and of crustacean-like, five-segmented endopods ending in long claws. A fourth cephalothoracic pair has similar endopods borne by annulated basipods. Thus, the following six pairs of lamellate and fully annulated appendages, likely playing a role in gaseous exchange and swimming, appear to be highly modified basipods rather than exopods. The abdominal region consists of six limbless cylindrical segments and ends up in a pair of subdivided caudal rami. Although Waptia is clearly a mandibulate arthropod, it differs from the body plan of extant crustaceans by the lack of antennae (A2) suggesting the presence of an intercalary segment as in extant hexapods and myriapods. While Waptia confirms the mandibulate affinity of hymenocarines, its inclusion in a phylogeny leads to the resolution of these bivalved taxa as part of an expanded Pancrustacea, providing a novel perspective on the evolutionary history of this hyperdiverse group. Waptia is interpreted as an active swimming predator of soft prey items occasionally clinging on epibenthic substrates.



<sup>&</sup>lt;sup>•</sup> Speaker

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#### Coronate-like medusae from the early Cambrian Kuanchuanpu Formation (ca. 535 Ma; China) and the early diversification of cnidarians

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The microfossils from the lower Cambrian Kuanchuanpu Formation (ca 535 Ma; Shaanxi Province, China) provides the unique opportunity to study animal life before the Cambrian radiation reached its peak. Their exquisite three-dimensional preservation in calcium phosphate enables high-resolution nondestructive techniques to be used, such as X-ray microtomography, for reconstructing their internal and external anatomy. This exceptional microfauna contains embryonic and larval stages of cnidarians and other animal groups such as worms and deuterostomes. We describe here Hanagyroia orientalis gen. et sp. nov., a new medusozoan with a pentaradial symmetry, characterized by five well-developed perradial oral lips around a remarkably large manubrium, a well-marked equatorial groove, and five short, interradial pairs of extensile tentacles at the bell margin. Internally, five broad and stout interradial septa join horizontally to form the claustra. The round medusa-like bell margin and equatorial groove of Hanagyroia are reminiscent of coronate scyphozoans. However, cladistic analysis resolves Hanagyroia as a stem-group cubozoan although it lacks some of the diagnostic features of extant representatives of the group such as the frenula, apertural lappets and velarium. Hanagyroia may represent an intermediate morphological type between scyphozoans and cubozoans. The gradual transition from embryonic to hatching stage with welldeveloped oral lips and strong tentacular buds, observed in our fossil specimens, suggest a possible sessile, direct development for Hanagyroia. This contrasts with the indirect development of extant cnidarians (including scyphozoans and cubozoans) that have a sexual medusoid stage producing a characteristic planula larva. Hanagyroia and other embryonic and juvenile cnidarians from the Kuanchuanpu biota bring to light major differences between modern cnidarians and their early ancestors in terms of symmetry patterns and developmental cycles.



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### Did the earliest sponges have biomineralized spicules?

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Molecular clock estimates and biomarker fossils suggest that sponge animals diverged in the Tonian or Cryogenian periods (1000-635 Ma). However, unambiguous sponge spicules are not found in the fossil record until after about 540 Ma in the earliest Cambrian Period. This discrepancy has been a major problem for paleontologists and evolutionary biologists. Emerging phylogenetic and paleontological data indicate that the earliest sponges may not have had biomineralized spicules. Thus, it is possible that the early sponges had a poor fossilization potential, offering a way to reconcile the conflicting molecular clock, biomarker, and spicular fossil data. In this talk, we present new paleontological data supporting the hypothesis that the earliest sponges may have had only weakly biomineralized spicules or even entirely organic spicules or skeletons. If correct, this hypothesis not only explains the lack of biomineralized sponge spicules in the Cryogenian-Ediacaran despite the divergence of sponge classes in the Cryogenian Period, but also offers a new search image for Ediacaran sponge body fossils.



Speaker

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### The first complete *Eophoronis* fossil from the Cambrian Chengjiang biota, South China, and its significance

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In contrast with most extant animal phyla that have representatives in the early Cambrian (e.g. Chengjiang fauna from China), the origin and early evolutionary evolution of Phoronida lacks convincing fossil evidence. Iotuba and Eophoronis from the Chengjiang fauna, were tentatively interpreted as primitive phoronids based on poorly preserved specimens. Alternatively, Eophoronis was compared with Louisella, a priapulid from the middle Cambrian Burgess Shale. Exceptionally well-preserved specimens allow here the first detailed description of *Eophoronis*. It has a ca 4 cm long cylindrical worm-like body. The surface of its trunk bears transverse ripples and dense setae (or cilia ?). The gut has a U-shape with a conspicuous expanded gastric area. Rows of tentacles form a horseshoe-shaped structure around the epistome in the anterior part of the body. Undetermined organic detritus attached to these tentacles suggest the presence of mucous secretion. The slit-shape mouth and the anus both open in the anterior region. A putative juvenile penetrates the body wall of the adult as seen in extant phoronids. One complete specimen is encrusted with tiny sand grains or organic debritus. This external and internal morphologies are typical of extant phoronids. Other features observed in the posterior part of Eophoronis are interpreted as possible ovaries (oocytes) and testis (sperm) attached separately along the intestine. This configuration is typical of hermaphroditic extant phoronids. In conclusion, Eophoronis is considered here as the earliest representative of Phoronida with anatomical features and encrusting habits comparable with modern forms.



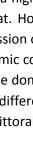
Speaker

#### Paleoecological analysis of Late Vendian benthic communities of the southeastern White Sea region

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Several localities of the White Sea Region (northern part of Russia) dated from the Late Vendian (Ediacaran) yield exceptionally well-preserved fossils of soft-bodied metazoans. Ten fossil assemblages of Flinders-style preservation (i.e. imprints on the bottom surfaces of sandstone beds) were chosen for study because of their high diversity and numerical abundance. The localities have the great advantage to have organisms and assemblages preserved in situ. A study of the population structure of these local assemblages was carried out on the basis of the distribution of specimens by size using a one-dimensional BIC analysis. About 1,800 specimens of fossils belonging to 25 genera and 29 species were used in calculations. We found that, within most assemblages, two distinct size classes occur in Parvancorina, Kimberella, Dickinsonia, and Aspidella. Less frequent forms are represented by a single cluster, probably due to the low number of specimens. The fact that specimens of different sizes co-occur spatially indicate separate age groups within populations. These age groups reflect the successive stages of a settlement of mobile and sedentary zoobenthos on the substrate surface. Combined results obtained from the quantitative and species composition of communities, calculated paleoecological parameters, the nature of microbial surfaces, and also the population structure analysis, allow to characterize settlement episodes, and the subdivision of communities into three groups. Each group reflects a particular stage (initial, middle, and late) in the existence of the biocenosis of Vendian macroorganisms within a given territory. The communities at the initial stage of development are characterized by a low diversity, a single age group in all fossils and the presence of an immature microbial mat. The communities at the middle and late stages of development are characterized by a high diversity, the presence of two age groups or more in case of the late stage, and a more mature mat. However, our results do not allow, unlike, for example, the Avalon complex, to characterize the succession of communities through time. This is due to the fact, that there are no major differences in the taxonomic composition of the studied communities. There are several endemic forms in some communities, but the dominating species remain the same in all of them. This indicates that all studied communities represent different stages in the development of similar biocenoses dominated by benthic organisms living in the sublittoral area.





Speaker

#### Recent studies on the Fortunian (lowermost Cambrian) cycloneuralians from South China

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Morphology-based phylogenetic analyses support the monophyly of Scalidophora (Kinorhyncha, Loricifera, and Priapulida) and Nematoida (Nematoda and Nematomorpha), the two groups being integrated into the monophyletic Cycloneuralia which is the sister group of Panarthropoda, in accordance the widely accepted Ecdysozoa hypothesis. Molecular studies have estimated that cycloneuralians originated in the Ediacaran Period and diversified in the early Cambrian. Fossils of cycloneuralians are abundant and diverse in the Cambrian Konservat-lagerstätten, but they occur mainly in Stage 3 and younger strata. In contrast, only a single cycloneuralian species had been reported from Stage 2, based exclusively on fossil embryos, and for a long time there has been no cycloneuralian reported from the Fortunian Stage. It was not until 2014 that the oldest known cycloneuralians were reported for the first time from the Fortunian Stage of South China, and to date, five genera and species as well as nine undetermined forms have been described, based exclusively on three-dimensionally phosphatized microfossils. Among them, Eokinorhynchus rarus was suggested to be a stem-lineage derivative of Kinorhyncha, and the first and only fossil species of Kinorhyncha. Qinscolex spinus, Shanscolex decorus and Dahescolex kuanchuanpuensis may represent stem-lineage derivatives of Scalidophora, whereas Eopriapulites sphinx was considered as a stem-lineage derivative of Cycloneuralia due to its plesiomorphic priapulid-like morphology. The Fortunian cycloneuralians exhibit cuticular sclerites of diverse morphology, even on one single specimen. For this reason, fragmentary trunk parts, disassociated sclerites, or single spines are difficult to assign to specific taxa. Their introvert scalids are internally hollow, suggesting that internally hollow scalids may be a plesiomorphic character of Cycloneuralia. Some cycloneuralian fragments reach several millimetres long and correspond to centimeter-sized original individuals that fell within the size range of macrobenthos. Thus, some of the Fortunian cycloneuralians belong to the macrobenthos. Finally, we suggest that the Cycloneuralia may have originated from the Fortunian macrobenthos, and that *Eopriapulites sphinx* may represent an ancestral cycloneuralian.



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#### The distribution and paleoecology of Cambrian Burgess Shale-type faunas in South China

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The Cambrian Burgess Shale-type (BST) fossil Lagerstätten have a global distribution from Laurasia to Gondwana. Exceptionally well-preserved soft-bodied fossils from these Lagerstätten provide unique information for elucidating the origin and early evolution of metazoans during the "Cambrian explosion". Over the past three decades, several famous BST fossil Lagerstätten have been uncovered in the Cambrian of South China, and attracted worldwide attention and public interests. Among them, the Chengjiang Lagerstätte from the Maotianshan Shale Member of the Yu'anshan Formation in eastern Yunnan is the earliest and one of the most significant Cambrian BST fossil Lagerstätten in the world. It has thrown new light on the origin and early evolution of major metazoan clades, such as arthropods and deuterostomes including the chordates. Another typical BST fossil Lagerstätte from eastern Yunnan is the Guanshan biota from the Wulongqing Formation and a new Chengjiang-type Lagerstätte from the Hongjingshao Formation, from which a number of soft-bodied fossils rivalling those from the Chengjiang biota have been found recently. The strata hosting Cambrian BST Lagerstätten occur throughout South China, show variation in taxonomic diversity, faunal composition and fossil preservation. Taxonomic composition of these faunas indicates that arthropods mostly dominated the shallow water facies, whereas sponges dominated the slope basin facies. Cambrian BST Lagerstätten in South China provide a good record of exceptionally preserved biotas ithrough time. Comparing these Lagerstätten within their chronological framework may give us important clues on the nature of evolutionary and ecological diversifications during the Cambrian explosion.



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# The anatomy of Arborea arborea: a late Ediacaran eumetazoan

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Organisms in possession of a frondose body plan are amongst the oldest and most enigmatic members of the soft-bodied Ediacaran macrobiota. Appraisal of specimens from the late Ediacaran Ediacara Member of South Australia reveals that the frondose taxon *Arborea arborea* possessed a fluid-filled holdfast disc and a stem whose dimensions vary independently of organism size within populations. Moldic preservation of internal anatomical features provides evidence for tissue differentiation and for bundles of tubular structures within the stalk of the organism. These structures connect in a fascicled arrangement to individual lateral branches before dividing further into individual units housed on those branches. The observed fascicled branching arrangement, which seemingly connects individual units to the main organism, is consistent with a biologically modular construction for *Arborea*, and suggestive of a colonial organisation. In conjunction with morphological characters previously recognised by other authors, including apical-basal and front-back differentiation, we propose that, to the exclusion of all non-metazoan possibilites, *Arborea* was a total group eumetazoan.



Speaker

## Distribution of *Sabellidites cambriensis* (Annelida?) in the Ediacaran–Cambrian succession on the Digermulen Peninsula, Arctic Norway

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Sabellidites cambriensis (Annelida?) is a characteristical element of the earliest Cambrian biota in Baltica, the Siberian platform, South China, and southeastern Newfoundland. It is a key fossil for the S. cambriensis Zone and the Rovnian Regional Stage (ca. the Fortunian Stage). Finds on the Siberian platform are important for correlation with eastern Baltica. In Avalonian Newfoundland, the Sabellidites cambriensis Zone brackets the Ediacaran-Cambrian boundary defined on the base of the Treptichnus pedum Ichnozone. Here S. cambriensis appears ca. 9 m below the GSSP level but T. pedum also extends 5 m below this level. In some, often thick, sections in eastern Baltica the first S. cambriensis occurs just below beds with T. pedum. The distribution of Sabellidites cambriensis has been studied in three sections on the Digermulen Peninsula, spanning the upper (third) cycle of the Manndrapselva Mbr. (MDE) of the Stáhpogieddi Fm. and the Lower Mbr. of the Breidvika Fm. Treptichnus pedum places the E-C boundary close to the base of the third cycle of the MDE. In the Bárdeluovttjohka section a few specimens are found in the upper ca. 20 m of the third cycle, ca. 8 m above the lowest record of T. pedum. Sabellidites then is highly abundant in the first 40 m of the Lower Breidvika Mbr. In the Avžejohka section, only the Lower Breidvika Mbr. could be sampled, with abundant specimens in the first ca. 35 m. In the Manndrapselva section, the third cycle yielded a few specimens. Sabellidites is then abundant in the first ca. 35 m of the Lower Breidvika Mbr. The sections show sparse occurrences of Sabellidites in the third cycle of the MDE, together with T. pedum and other fossils indicating the lowermost Cambrian. In the Lower Breidvika Mbr., the abundance is high in the initial ca. 40 m, after which no more specimens are seen. As S. cambriensis is found below both the GSSP and T. pedum in Newfoundland, it is per definition present in the Ediacaran. Defining confident intervals for the close stratigraphic occurrences of T. pedum and S. cambriensis in such thick sequences as seen in Newfoundland, on the Digermulen Peninsula, and on the eastern margin of Baltica would likely show no meaningful difference in the distribution. Therefore, for practical purposes, it is interpreted that they both first appear at the very base of the Cambrian.



<sup>&</sup>lt;sup>\*</sup> Speaker

#### Developmental patterns in leanchoiliid arthropods from the early Cambrian Chengjiang biota

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Despite being one of the dominant fossil groups, with thousands of specimens preserved across a broad spectrum of size, the leanchoiliid arthropods from the celebrated Chengjiang biota have not yet been studied from the perspective of development. However, examination of juveniles and larvae based on the abundant available material has revealed some surprising phenomena in the development of *Leanchoilia*, such as a metanauplius stage in *L. illecebrosa* and differences in the developmental rate of telson substructures in *L. obesa*, both indicating that leanchoiliid arthropods might have unique developmental patterns. Here we further investigate this issue by measuring a large sample of complete specimens of leanchoiliids from the Chengjiang biota. The results indicate that in both *Leanchoilia* and *Alalcomenaeus*, the length of the body (from the anterior of the head shield to the end of the telson) grew more quickly than the width, indicating a trend of the body narrowing during development. This trend is consistent with the niche differentiation between juveniles and adults reported in *L. illecebrosa*. Furthermore, in both genera, the trunk, head shield and telson have different growth rates, suggesting that differentiation in growth rates of different body parts might account for the diversification of Leanchoiliidae in the early Cambrian, as all these body parts, including their length and width and other features, have been used in distinguishing species and genera within the family.



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#### The deep evolution of Ecdysozoa

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Ecdysozoa is a super-clade comprising eight phyla of protostome animals, including arthropods and nematodes-the most diverse and most abundant of all animal phyla, respectively. Modern phylogenetic analyses support Ecdysozoa as a monophyletic group, but internal relationships remain unresolved, with conflict both within and between morphological and molecular hypotheses. Of particular concern is the monophyly of the vermiform subclade Cycloneuralia, which remains in common use despite generally lacking molecular support. Furthermore, previous studies utilizing molecular clocks suggest ecdysozoans diverged in the Precambrian, but ecdysozoan fossils are not identifiable until strata of Cambrian age. This lack of clarity in early ecdysozoan evolution cascades onto adjacent branches of the Tree of Life and presents a considerable constraint on interpreting the origins of animal biodiversity and the nature/existence of the Cambrian evolutionary "Explosion." By combining molecular and palaeobiological techniques to estimate phylogenetic divergence times with cladistic interpretations of exceptionally preserved Cambrian fossils, we seek to elucidate the evolution of Ecdysozoa during a critical phase in the establishment of the Phanerozoic animal-dominated biosphere. Our preliminary data from Bayesian analyses of phylogeny and divergence times across all 8 ecdysozoan phyla support a sister group relationship between nematoids and panarthropods (rendering Cycloneuralia paraphyletic), and an Ediacaran origin of Ecdysozoa.



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Speaker

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# The Ediacaran organism *Rangea* as a possible source of three different forms of macrofossils

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The iconic Ediacaran fossil Rangea schneiderhoehni was found in Namibia at the beginning of the 20th century. However, its body plan was properly described only in 2013 by Prof. P. Vickers-Rich and colleagues. The main body or crown of Rangea was egg-shaped and resembled a revolving door: it consisted of six radially located vanes attached to a longitudinal axial stalk. Six marginal stalks were laterally extended from the axial stalk, each bounding the vanes along the outer edge. The complex of these stalks represented a specific part of the Rangea body, which was filled with sand particles even during the lifetime of the organism. Judging by the characteristics of morphology and basal position of these parts within the body, they served a supporting function and contributed to the attachment of the sedentary organism to the substrate. The detailed study of Rangea is complicated by the taphonomic conditions. The known fossils were buried in a redeposited state with light-weight top parts bulging out and heavy, sandfilled bases having a very little chance of a joint burial. Only remains preserved in situ can give information on the habitat of this organism. In the Late Precambrian of the Russian White Sea area, typical fossil remains of Rangea in the form of imprints of joint vanes were found in burials within sandstone lenses. Sixfold star-shaped structures of Basisacculus stellatus composed of sandstone were also discovered here. They are close in morphology to basal parts of the Namibian Rangea but are isolated from the crowns. Along with the remains of typical Ediacaran organisms, several discoid imprints of Jampolium tripartitum resembling a positive form of Aspidella terranovica were found on the bottom of the sandstone layer in one burial. Jampolium is distinguished from other representatives of a large group of holdfasts by the presence of 3 or 6 deep radial furrows. The type of symmetry and close stratigraphic distribution allow us to connect the imprints of the crowns, the casts of the basal structures, and the imprints of the attachment discs together and assume that they belong to Rangea. The consequence of this conclusion is an implication that Rangea from the White Sea was a part of a typical community of benthic Ediacaran organisms that lived attached to the surface of a microbial mat.

Speaker

#### The oldest trilobites from Siberia

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The oldest trilobites of the Siberian platform occur in rocks dated from the Atdabanian (correlated with Cambrian Stage 3 in the International Chronostratigraphic Chart) based on findings of coeval faunas. The first trilobites appear in the upper half of the Atdabanian within the folded margin of the Siberian Platform (the Altay-Sayan folded area at Kuznetsky Alatau, Khakasia and Tuva region). The principal localities of the Siberian Platform are: the middle stream of the Lena River (the Pestrotsvet Formation), the "Isit" section and the "Zhurinsky Mys" section. Another where the These oldest trilobites are also found is other areas of the Siberian Platform such as the Fomich River Section (near Anabar Uplift) and the Kharaulakh Mountains (Tusera Formation). Typical taxa found in these localities are the following: Profallotaspis jakutensis, Profallotaspis privica, Repianella sibirica, Repinaella explicata, Bigotina malykanica (middle stream of the Lena River and Fomich River Section), Profallotaspis tyusserica (Northeast of the Siberian Platform). Resimopsis mariinica, Resimopsis basaica, Resimopsis ischirica, Kijanella magna, Mundocephalina plana, Bedjinella lubrica, Archaeaspis sp., Habrocephalus sp. are typical taxa of the Altay-Sayan folded area of the Siberian platform. The most ancient trilobites have weakly prominent facial sutures, although it was previously assumed that these sutures were completely absent. In the Atdabanian, the Siberian Platform is occupied by a relatively shallow water basin favourable to the development of trilobites. On the contrary, the Altai-Sayan folded area at the beginning of the Atdabanian, is characterized by a relatively deep paleobasin with volcanic-sedimentary sequences. During the upper half of the Atdabanian, areas with a shallower carbonate sedimentation became more suitable to trilobites. Thus, the later representatives of fallotaspids that do not have facial sutures are probably not the direct descendants of these ancient trilobites, as it was previously assumed. Perhaps, Profallotaspis and Repianella represent the same age complex and are not successively replaced one after the other. The later appearance of trilobites in the Altai-Sayan folded area may result from adverse conditions in this area at the beginning of the Atdabanian.

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#### Three Cambrian fossils assembled into an extinct body plan of cnidarian affinity

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The early Cambrian Problematica *†Xianguangia sinica*, *†Chengjiangopenna wangii*, and *†Galeaplumosus abilus* from the Chengjiang biota (Yunnan, China) have caused much controversy in the past and their phylogenetic placements remain unresolved. Here we show, based on exceptionally preserved material (85 new specimens plus type material), that specimens previously assigned to these three species are in fact parts of the same organism and propose that †C. wangii and †G. abilus are junior synonyms of †X. sinica. Our reconstruction of the complete animal reveals an extinct body plan that combines the characteristics of the three described species and is distinct from all known fossil and living taxa. This animal resembled a cnidarian polyp in overall morphology and having a gastric cavity partitioned by septum-like structures. However, it possessed an additional body cavity within its holdfast, an anchoring pit on the basal disc, and feather-like tentacles with densely-ciliated pinnules arranged in an alternating pattern, indicating that it was a suspension feeder rather than a predatory actiniarian. Phylogenetic analyses using Bayesian inference and maximum parsimony suggest that *†X. sinica* is a stem-group cnidarian. This relationship implies that the last common ancestor of *†X. sinica* and crown cnidarians was probably a benthic, polypoid animal with a partitioned gastric cavity and a single mouth/anus opening. This extinct body plan suggests that feeding strategies of stem cnidarians may have been drastically different from that of their crown relatives, which are almost exclusively predators, and reveals that the morphological disparity of total-group Cnidaria is greater than previously assumed.



Speaker

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#### New materials of Hiemalora from Dengying Formation in the Yangtze Gorges area, South China

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Hiemalora Fedonkin, 1982, first described from the White Sea, Russia, is characterized by central disc with radiated appendages. Hiemalora probably occurs from 565 Ma to 550 Ma, and has a wider geographic distribution, including the White Sea, central Siberia, South Australia, Ukraine (Fedonkin 1992), northern Norway, Canada, and possibly India. Hiemalora has been interpreted as a hydrozoan polyp or a body fossil with unknown affinities. However, more and more supporting evidence indicate that Hiemalora may represent a basal attachment disc and is just a part of Ediacara-type frondose forms. Although Hiemalora has been reported from numerous localities, rare specimens were preserved with the frond, except specimens of Hiemalora -like structures attached to the fronds of Primocandelarbum hiemaloranum found in the Mistaken Point Formation, Newfoundland. It is not certain whether they represent a single taxon. Hiemalora -type fossils are one of the most abundant ones in the Ediacaran Shibantan biota at Wuhe in Yichang, Hubei Province, South China. More than one hundred specimens have been collected from the gray-dark thin-bedded limestones of the lower to middle Shibantan Member. At the base of the Shibantan Member, a fossiliferous bed contains numerous Hiemalora specimens. One of them shows a Hiemalora attached to a frond-type structure. The frond, which is similar to Charniodiscus procerus, is composed of a prominent stem and a central stalk, with primary branches diverging from the central stalk, and ending at an undivided rim at the outer margin of the frond. The new discovery implies that Hiemalora is a holdfast attached to different kinds of fronds.



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#### Collective behaviour in trilobites from the Lower Ordovician of Morocco

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Ampyx is a blind raphiophorid trilobite characterized by a stout glabellar spine and a pair of symmetrical, very long librigenal spines projecting posteriorly. We describe here Ampyx priscus from the Lower Ordovician (Upper Tremadocian-Floian) Fezouata Shale of Morocco, near Zagora. This species occurs in monospecific linear clusters in which trilobites (mostly adult or subadults) are oriented anteroposteriorly with low angular inter-individual variation, lie in an upright position and often contact or override each other via their glabellar and librigenal projections. We analysed qualitatively and quantitatively more than 15 of these linear assemblages (with a maximum of 21 specimens per cluster) which all present the same characteristics and came to the conclusion that the alignment of trilobites results from the locomotion of a group and not from a passive transportation and accumulation by currents. Detailed observations of the surrounding sediment rule out the hypothesis made by previous authors of trilobites associated with sub-horizontal burrows in which they would have sheltered before being trapped and buried in groups. More likely, Ampyx priscus had a collective behaviour and was migrating in groups over the seafloor maintaining a single-row formation by physical contact (possible mechano-receptors) via its long projecting spines. This assumed collective behaviour recalls that of extant spiny lobsters which form long queues in response to environmental disturbances due to seasonal storms. Similarly, the aggregation of Ampyx priscus may have been triggered by such environmental factors considering that the Fezouata Shale was under distal storm influence. However, various alternative hypotheses need to be tested such as a collective reproductive behaviour enhancing access to potential mates, an anti-predator response, a cooperative feeding behaviour or less likely an increase of locomotion efficiency favoured by head-to-tail alignment.



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## A tale of three taphonomic modes: *Flabellophyton* from the Ediacaran Lantian and Dengying formations in South China

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Ediacaran macrofossils are typically preserved in three taphonomic modes. They can be preserved as casts/molds in siliciclastic rocks, casts/molds in carbonate rocks, or carbonaceous compressions in black shales. Only a few taxa are known to be preserved in more than one of these taphonomic modes. *Flabellophyton* is a genus that has been previously reported from lower Ediacaran black shale of the Lantian Formation (635–551 Ma) in South China and upper Ediacaran sandstone of the Ediacara Member (560–550 Ma) in South Australia. Here we report *Flabellophyton* from the upper Ediacaran limestone of the Shibantan Member of the Dengying Formation (551–541 Ma) in South China, making *Flabellophyton* the only genus that occurs in all three taphonomic modes. We also provide a systematic description of *Flabellophyton* based on material from the Lantian and Denying Formation in South China, recognizing three morphospecies-*F. lantianense* (Chen, Lu and Xiao) corr., *F. baculiforme* sp. nov. ms., and *F. obesum* sp. nov. ms. *Flabellophyton* is reconstructed as an erect epibenthic organism attached to marine sandy, carbonate, and muddy substrates. Its phylogenetic affinity remains uncertain, though a benthic algal interpretation seems plausible. The wide geographic, environmental, and stratigraphic distribution of *Flabellophyton* indicates its unusual environmental tolerance and dispersal range.



Speaker

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# Age variability of the Late Vendian microbial mats of the southeastern White Sea region

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Folded and wrinkled structures on the bedding surfaces of Precambrian sedimentary rocks have traditionally been interpreted as the remains of microbial mats. In the Vendian time, mats played an important role in the ecology of organisms, being both a substrate for settlement, a source of food, and a source of oxygen in photosynthetic shallow-water marine environments. Noticeable differences occur in the surface structure of microbial mats found in various fossils localities of the southeastern White Sea region. They cannot be explained only by topographical variations of the substrate, but are likely to be determined by the individual age of the microbial mats that developed along with their associated macroorganisms. The various textures of the microbial mat can be put into a sequence that is interpreted as evidence of the development and growth of the microbial mat. We recognized four types of mats: 1) an incipient mat is characterized by a shagreen surface with uneven distribution of tubercules. The plucking grooves and drag marks are seen on the hard ground underlying the mat, which appeared due to some abiogenic effects before the mat started to grow. Large areas with a smooth surface correspond to a lack of microbial mat that developed irregularly. 2) a thin, underdeveloped mat is characterized by a shagreen surface with an even distribution of tubercules covering an extensive area. The markings on the underlying hard substrate are indistinct 3) a mildly developed mat is characterized by a surface with evenly distributed fine tubercules. Because the mat was denser and thicker, no structure is visible on the underlying substrate. 4) a developed mature mat is represented by a coarsely tuberculate surface with an uneven distribution of tubercules. Unlike younger mats, mature ones grew slowly and could not recover quickly the physical damage caused by the activity of Kimberella and Proarticulata. The large corrugated structures of the mat that resemble the "old-elephant-skin texture" and the healed cracks are also observed in this particular type of mat. These structures were commonly interpreted as typical of a thick, mature, well-developed microbial mat in different publications. Spots of decomposed organics and filamentous algal thalli only occur on the surface of mature mats, indicating that the structure of the mat was changing with its age.



Speaker

# S13 - Evolution of Indo-Pakistan biotas from the break-up of Gondwanaland (Late Jurassic) to the initiation of the collision with Eurasia (Eocene): between endemism and dispersals

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# Organic carbon isotope records of the Paleocene -Eocene Thermal Maximum (PETM) event in India provide new insights into mammal origination and migration

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Lignite deposits in the west and northwest of India developed during the early Eocene in tectonic rift basins that formed by the rotation and early stage collision between India and Asia. The lithostratigraphic compositions in five lignite mines examined are very similar and separated into lower and upper lignite units by early Eocene marine transgressions that created lagoons. Organic matter contents in lignites and intercalated marine sediments are mainly terrestrial. Two organic carbon isotopes excursions reveal a lower excursion linked to the Paleocene Eocene Thermal Maximum (PETM) and an upper excursion linked to the Eocene Thermal Maximum-2 (ETM2). Uses of organic carbon isotope profile, supported by age control from both palynofossils and benthic foraminifera, helps to identify the relative age of the mammal bearing interval to the PETM event. The confirmed age supports the "into India" hypothesis for mammal migration and origination, and that Modern mammals may originate in Asia pre India-Asia collision and then spread out from Asia to Europe and North America and finally reach to India at the late early Eocene.



Speaker

# Dinosaur nesting sites of the Upper Cretaceous Lameta Formation of Lower Narmada Valley, India: an insight into dinosaur palaeobiology, nesting behavior and taphonomy – A preliminary report

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The Upper Cretaceous Lameta Formation of India has been a source of an extensive record of fossilized dinosaur eggshell fragments and nests. These sites are preserved in a sandy carbonate horizon of the Lameta Formation. A detailed field work conducted in the Lameta Formation of Madhya Pradesh (District Dhar) and Gujarat (District Kheda) recently has given us insights into dinosaur reproductive biology, nesting behavior and taphonomy. We have recorded more than sixty nesting sites from District Dhar and fifteen nests from District Kheda with buried, morphed and compressed eggs, eggshell fragments with both random and specific orientation and nests with mixed type. A closer inspection of these eggshells under scanning electron microscope shows them to belong to different oospecies grouped in the oogenera Fusioolithus and Megaloolithus. However not all eggshells show the characterizing orientation of growth lines due to the high amount of diagenesis that has altered the structure and replaced the calcitic units with silica. The presence of more than one oospecies may point towards a colonial nesting behavior that dinosaurs may have adopted to save the nests from predators. Some eggshells show resorption craters showing that embryo sucked the calcium from the egg for bone formation. Study of pore canals may help in determining if the eggs were buried or laid open and in comparing the reproductive patterns of dinosaurs with those of reptiles and birds. A few cases of multi-shelled eggs indicate pathology seen in modern day turtles owing to stressed adverse environmental conditions. Usually the nesting pattern shows the arrangement of eggs in a circular manner. The number of eggs range from one to twenty-two which may either indicate different nesting patterns adopted by different oospecies or taphonomical bias. Some nests show fragments oriented in a specific direction while other nests have eggs completely buried. The broken fragments indicate the hatching of the egg while the buried eggs indicate drowning of the nests by conditions such as floods that suffocated the embryo. The compressed eggs either indicate egg collapsing (fragments fall inside the egg after hatching) or structural deformities (compressional forces) that may have elongated it. Comparing the Indian oospecies with those of the Upper Cretaceous deposits of Gondwanaland and Laurasia points to a possible palaeobiogeographic link with the southern Europe and South America in the Late Cretaceous.



13 // Ora

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## New marine fish faunas from the middle Eocene (Lutetian) of Pakistan: implications for the origin of the Indo-Pacific fauna

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The early Paleogene was an important interval in teleost evolution, marked by the first appearance of many extant families. However, the teleost body fossil record of this time is strongly biased toward European and western Asian sites, with comparatively little information on faunas geographically closer to the modern Indo-Pacific. Beginning in the mid-1970s, a series of joint expeditions mounted by the Geological Survey of Pakistan and the University of Michigan collected articulated teleost remains from two geological units in Pakistan: the Habib Rahi (early Lutetian, 48-46 Ma) and Domanda (middle-late Lutetian, 46-40 Ma) formations. Both are marine deposits, with the Habib Rahi Formation corresponding to a more offshore facies. Fishes of the Habib Rahi Formation include nearly complete individuals. All specimens are compressed, but larger fossils show considerable relief. The fauna includes osteoglossomorphs, incertae sedis percomorphs, scombroids, and a palaeorhynchid that represents the most abundant taxon in the collection. Material from the Domanda Formation shows contrasting preservational modes as a function of lithology. The moonfish Mene, along with rarer remains of at least one other, larger fish are represented by compression specimens in a paper shale. Mottled shales yield abundant small clupeomorphs, isolated osteoglossid scales, and a possible carangid. Fishes from clays are less complete, but are preserved in three dimensions and include intact crania of a clupeomorph similar to *†Clupeopsis*, a catfish of uncertain familial affinity, and as yet unidentified percomorphs. These specimens are particularly amenable to study via microCT scanning.

Compared with modern and coeval faunas, the Habib Rahi and Domanda assemblages contain: (1) extant taxa widely distributed both today and in the Paleogene (e.g., scombrids); (2) groups that are today restricted to the Indo-Pacific but were widespread in the past (e.g., *Mene*); (3) extinct forms known previously only from older European or central Asian deposits; and (4) extinct taxa that were geographically widespread (e.g., marine osteoglossomorphs, palaeorhynchids). Taken together, this suggests considerable faunal overlap between Eocene marine faunas, a conclusion also supported by Eocene occurrences in Europe and the Americas of many groups now restricted to the Indo-Pacific.



Speaker

# Size variations amongst non-volant mammals from the early Eocene Cambay Shale deposits of western India: Implications for palaeobiogeography and palaeohabitat

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In the Indian subcontinent, the oldest Cenozoic record (early Eocene, ~54.5 Ma) of non- volant mammals comprise various groups including perissodactyls, artiodactyls, primates, proteutherians, lagomorphs, tillodonts, rodents and didelphimorphs. These taxa have been described from the subsurface Cambay Shale deposits of the Gujarat state of western India. Statistical analysis (at the ordinal level) of the size variations in the lower dentitions of the known assemblage of non-volant mammals from the Cambay Shale allows their size categorization into three broad groups: small, medium and large. Based on the data on a) phylogenetic relationships of large-sized perissodactyls (e.g., cambaytheres), b) age of the fauna, and c) the timing of collision between the Indian plate and Eurasia, the potential presence of a short-lived corridor for dispersal between India and Eurasia prior to-~54.5 Ma cannot be ruled out. Further, the overall data suggests the presence of cambaythere-like mammals in the late Paleocene of Indian and/or Eurasian continent(s), further emphasizing the need for rigorous search for Paleocene mammals (presently unknown) in the Indian subcontinent. In addition, based on a quantitative approach using Cenogram Analysis on non-predatory early Eocene terrestrial mammals, it is suggested that the mammalian community thrived largely in a closed canopied, forested and humid habitat. The Cenogram Analysis also confirms a strong correlation between dietary specializations in the specific body size ranges.



Speaker

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# The large mammalian fauna from the new vertebrate site of Pabbi Hills (Pleistocene), Pakistan

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An important new Pleistocene locality has been excavated in the Pabbi areas, northern Pakistan. The mammalian fauna of Panjan Sher Shahana shows that the locality dates to the Middle Pleistocene. Panjan Sher Shahana locality, with more than 11 species, is by far the richest mammalian Pleistocene locality of the Siwalik Group. According to the recovered faunal list, the Punjan Sher Shana fauna shows strong resemblance to faunas of the Siwalik localities of the Pleistocene period. The *Proamphibos* and *Elaphas* association, commonly found in the Siwaliks and the rare *Stegolophodon*, has been reported in the new locality. The Panjan Sher Shahana fauna is close in composition and ecology to other localities of the Pabbi Hills and shares taxa with the Pinjor Formation of the Siwaliks. The finds are consistent with a Pleistocene age of the locality.



Speaker

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## Charophyte gyrogonites from the Deccan intertrappean neds of India: palaeobiogeographic implications

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In the past, several charophyte species have been reported from the Upper Cretaceous Deccan intertrappean beds of India. Recent work on three different sections of Deccan intertrappean beds i.e., Jhilmili and Piplanarayanwar from Chhindwara District, central India and from Rajahmundry, Andhra Pradesh, eastern coast of India, has revealed the presence of six genera of charophytes. The Jhilmili section yielded Chara and Platychara, the Rajahmundry section has produced Pekichara, Maedleriella, Stephanochara, Psilochara, Chara, Platychara and the Piplanarayanwar section yielded, Pekichara, Chara and Platychara, Jhilmili and Rajahmundry intertrappean beds are regarded as Early Palaeocene in age on the basis of foraminifers and ostracods, whereas Piplanarayawar is considered as Late Cretaceous in age based on myliobatid fish Igdabatis and dinosaur eggshells. From the known fossil biota, brackish to shallowmarine depositional environment has been inferred for all the investigated intertrappean sections. The genus Chara has a cosmopolitan distribution during the Late Cretaceous and Early Tertiary, whereas Pekichara appears to have a cosmopolitan distribution with fossil reports coming from the Late Cretaceous and Palaeogene of USA, Peru, France, United Kingdom, Spain, Algeria, China, India, Mongolia, Iran. Platychara also occurs in the Late Cretaceous-Palaeocene deposits of Canada, Mexico, USA, Argentina, Bolivia, Jamaica, Peru, Belgium, France, Spain, China, India and Iran. Psilochara, on the other hand, is restricted to the Palaeogene of France and Romania. The genus Maedleriella has a wide geographic distribution having been reported from the Late Cretaceous - Palaeogene of USA, Peru, France, Spain, Algeria, China, Mongolia, and Germany. Stephanochara is predominantly known from the Late Cretaceous-Neogene of Laurasia (Europe, Mongolia, China, and Iran). The two genera: Maedleriella and Psilochara are being reported for the first time from the Early Palaeocene of the Indian sub-continent. Report of Psilochara from the Early Palaeocene of India which was previously documented from the Early Eocene of France and Romania extends its stratigraphic range to Early Palaeocene.Based on the current fossil occurrence of these taxa, it is inferred that during the Late Cretaceous- Early Palaeocene time, the Indian plate maintained close biogeographic links with the Laurasian landmasses contrary to the known palaeogeographic reconstructions.



## Isolation of the Indian subcontinent during its northward drift phase - Consequences for the evolution of life and biotic interchanges

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The Indian subcontinent remained isolated from other landmasses following its separation from Madagascar around 88 Ma ago until its suturing with the Asian mainland at about 50-55 Ma ago. Hence India was physically isolated from other landmasses for a total duration of 30-35 Ma. It is anticipated that the Indian plate could have developed an endemic fauna and flora during its Late Cretaceous-Early Eocene isolation phase. On the contrary, the fauna and flora from this geological interval furnished mixed signals some indicating endemic evolution, some demonstrating Gondwanan affinities and still others presenting Laurasian biogeographic links. The strongest evidence for endemism comes from the Upper Cretaceous Deccan intertrappean ostracod fauna with 98% species having a geographic distribution restricted to India. Likewise, adapisoriculid eutherian mammals and Vitaceae family of plants from the Deccan intertrappean beds, and cambaytheriid perissodactyls and Dipterocarpaceae plants from the Early Eocene of western India may have originated on the Indian subcontinent during its northward drift phase. But there are many Late Cretaceous – Early Eocene taxa which exhibit either Gondwanan or Laurasian biogeographic affinities. Leptodactylid, hylid and ranoid frogs, nigerophiid and madtsoid snakes, kurmademyine turtles, abelisaurid dinosaurs, baurusuchid and simosuchid crocodiles, and gondwanathere mammals point to biogeographic links with the Gondwanan continents. In the past, it has been suggested that the basal stocks of these clades had a wide Gondwanan distribution, possibly in the Cenomanian or even earlier, before the physical isolation of Indo-Madagascar from rest of the landmasses, and evolved in isolation in India and Madagascar during the Late Cretaceous. On the other hand, pelobatid and gobiatine frogs, anguid lizards, troodontid dinosaur, archaic ungulate mammal, charophytes and coryphoid palm Sabalites have closely related forms in Laurasian continents favouring a biogeographic connection between India and Laurasia during the Late Cretaceous. The Kohitan-ladakh-Oman Island Arc route seems to have played an important role in the biotic interchanges between India and Europe through intervening Africa.



Speaker

# Late Cretaceous origin of grasses supports evolution of hypsodonty in Gondwanatheria mammals: a case study from the Deccan intertrappean beds of Naskal and Kisalpuri, peninsular India

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Origin and expansion of angiosperms is one of the key issues of plant evolution during the Cretaceous Period. Amongst the angiosperms, grasses represent the most important and dominant constituents of the terrestrial ecosystem. The distribution pattern of C3 and C4 grasses during the geological ages are useful indicators to monitor paleoclimatic fluctuations and  $pCO_2$  levels. Silicified plant tissues (phytoliths) preserved in herbivorous titanosaurid sauropod dinosaur coprolites from the Upper Cretaceous (Maastrichtian) Lameta Formation, Central India, showed that at least five taxa of the Poaceae subclades were present on the Indian subcontinent during the latest Cretaceous. This taxonomic diversity suggests that the crown-group Poaceae had diversified and spread in Gondwana before India became geographically isolated. The Upper Cretaceous DeccanVolcanic-province of Peninsular India has been a rich source of vertebrate- fauna and flora. Gondwanatheria mammals, characterised by high-crowned teeth, represent a distinctive group of Late Cretaceous mammalsfrom the Gondwanan continents. Gondwanatherians were the first to evolve hypsodont dentition among all the known mammals of that time. It was considered that acquisition of high-crowned teeth in gondwanathere mammals is in relation to adaptation to a diet consisting of abrasive food material such as grasses. In view of the presence of grass phytoliths in the Lameta Formation of Central India, two gondwantherian mammal yielding intertrappean localities, Naskal and Kisalpuri were explored for grass remains. The study shows presence of well preserved and diversified grass phytoliths and pollen in the gondwanatherian mammal-bearing intertrappean beds of Naskal and Kisalpuri, respectively. Based on the close association of gondwanatherian teeth and grass phytoliths, we concur with the view that the early evolution of hypsodonty in gondwanathere mammals was in response to an adaptation to abrasive diet consisting of grasses. The present study thus supports co-evolution of grasses and gondwanatherian mammals during the late Cretaceous.



13 // Oral

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### New data on the early Eocene vertebrate assemblage from Tadkeshwar Lignite Mine, Western India

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The Ypresian Cambay Shale Formation at Tadkeshwar open-cast lignite mine in Gujarat, western India, has yielded since February 2014 numerous vertebrate specimens of terrestrial mammals, lizards, snakes, frogs, and birds as well as a few marine/brackish-water animals such as the shark Physogaleus, the ray Myliobatis, and teleost fishes. Here we report new fossils discovered from several layers intercalated at different heights between the two major lignite seams. Most of them belong to taxa already described from the nearby Vastan and Mangrol mines such as the adapoid primate Marcgodinotius indicus, the hyaenodontid Indohyaenodon raoi, the agamid lizard Tinosaurus indicus, the palaeophiid snake Palaeophis vastaniensis, the caenophidian snakes Procerophis and Thaumastophis, and the bird Vastanavis. The presence of these taxa in the three mines and at different levels suggests that the deposits between the two major lignite seams represent a relatively short time span and a single mammal age. The recently described gymnodont tetraodontiform fish Avitoplectus molaris is also remarkable as it is characterised by a lower jaw with fused dentaries and a series of molariform teeth that are unique among all known fossil and living Tetraodontiformes. Among the new specimens from Tadkeshwar are dentaries of a new adapoid primate and a new condylarth-like mammal. Most taxa of the Tadkeshwar vertebrates are of European affinities; some of them seem to be endemic to India, and a few are of Gondwanan affinities such as mesosuchian crocodiliforms and the giant madtsoiid snake Platyspondylophis attesting that the early Eocene was an important period in India during which Laurasian taxa coexisted with relict taxa from Gondwana before the India-Asia collision.

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### **S14 - Evolution of trees and forests**

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## The Plio-Pleistocene biogeographic history of *Parrotia persica* highlighted by a new plant-insect interaction

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Nowadays, plants and insects contribute to more than 70% of the biodiversity on Earth. Their interactions are crucial in the trophic structure of the continental ecosystems and have been subject to many studies in extant forests. However, these interactions occur since the Devonian and can be studied for example by means of the insect feeding traces found on fossil leaves. In 2007, Labandeira et al. (2007) compiled all the known plant-insect interactions in the fossil record, but new ones can always be found.

Our investigation in the fossil outcrop of Willershausen (3Ma, Germany) recently uncovered a new damage type, named DT297, exclusively found on the leaves of *Parrotia persica*. This plant disappeared from Europe during the Pleistocene and is now endemic of the Hyrcanian forest (Iran). This damage looks like a long bent concatenation of circular perforations less than 5mm in diameter. Another version of this damage, twice larger than the first version, was also found exclusively on *P. persica* leaves. This second version could be due to a different larval stage of the insect or to some taphonomic problems (such as the compression of some samples during the fossilization). Recently, the first version of DT297 was also observed on modern leaves of *P. persica* in Iran. This specific plant-insect interaction thus helps to understand the biogeographic history of *P. persica* during the last 3 Ma. The presence of DT297 at Willershausen and in Iran supports that the Hyrcanian forest is a good modern analogue to some late Cenozoic European forests.

At present, the genus *Parrotia* is also represented by another plant species, *P. subaequalis*, of which a small population exists in the east of China. Observations of those leaves suggest that DT297 could also be present in China. If it is confirmed, DT297 could help discuss the biogeographic history of the whole genus *Parrotia*.



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### The largest fossil forests in Africa: preliminary results from new and revisited localities from the Tete province (Mozambique)

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The largest fossil forests in Africa extend across vast areas in Mozambique. However, although fossil trees from Mozambique have been described since the 19th century, this rich paleontological heritage remains mostly unexplored. Moreover, an exhaustive survey of the numerous fossiliferous sites comprising fossil species extending from the mid-Permian (Moatize Formation) to the Middle to Late Triassic (Zumbo Formation) has never been performed.

A remarkable site in the Matinde Formation (Late Permian) extends for more than 75km with a nearly uninterrupted exposure of tree stumps, many resting in growth position. This site offers a unique glimpse into the forest ecosystems before the Permo-Triassic Extinction (~252 Ma). We recently carried out a preliminary survey and found that large trees (often around 2 m in diameter) coexisted in a densely populated environment. Moreover, the rare finding of several tree hollows in a 2 m-wide tree (PPM2017-31) suggests that they result from bacterial/fungal activity due to the tree old age. The prevalence and morphology of these structures is a paleoecological indicator of forest maturity and stress factors affecting individual trees.

During the 2017 PaleoMoz expedition (www.palniassa.net), we visited six fossil tree localities. Samples from each locality were subjected to X-ray diffraction analyses. In certain sites (Dôa and Carangache), fossil wood is entirely composed of silica. However, samples from other sites (Magoé and Zumbo) include variable proportions of ankerite, calcite, and ghoetite in addition to silica. These different chemical compositions can be used as a chemical signature for identifying specimens of unknown provenance housed in various collections in Mozambique, as well as for understanding the underlying fossilization processes.

The Mozambican fossil forests are uniquely positioned to provide insights into the Permo-Triassic

Mass Extinction event, due to their extension and outstanding number of specimens preserved, but also because various localities date from before or after the event. A full taxonomic revision of collected samples is ongoing and new expeditions are planned for the near future.

PC 5

Speaker

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# Using dispersed cuticles to evaluate canopy density variation in deep time: The loss of plant cover at the Cretaceous–Paleogene boundary (North Dakota, USA)

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The Cretaceous–Paleogene (K–Pg) mass extinction event is associated with profound changes in terrestrial plant ecosystems. These changes are especially well documented in North America, from the Hell Creek and Fort Union Formations in the Marmarth area of North Dakota. Those sediments record a drastic reduction in plant species diversity in leaf fossil assemblages, directly coinciding with mineralogical (boundary clay, shocked quartz) and geochemical (iridium anomaly) evidence of the Chicxulub asteroid impact. This reduction in diversity can also be tracked in the palynological record with the loss of many pollen taxa and the high abundance of fern spores (the fern spike event) immediately following the K–Pg boundary, all-together indicating drastic changes in the composition of plant cover.

In addition to pollen and spores, dispersed leaf cuticles are an abundant component of palynological preparations. A correlation independent of taxonomy has been illustrated between the size and shape of leaf epidermal cells and vegetal cover density, enabling the use of reconstructed Leaf Area Index (rLAI) from cuticles as a new proxy to track changes in plant cover architecture across the K–Pg boundary. We have conducted a preliminary test on the John's Nose section, north of Marmarth, which has been sampled at ~1 cm resolution for palynological analyses across the boundary clay. Results from the cuticle analysis show a significant decrease in rLAI directly coincident with the markers of the Chicxulub impact and the palynologically defined K–Pg boundary. These results provide the first direct evidence of deforestation as a result of the impact blast and/or associated wildfires.

The temporary loss of plant cover represents a key element in the discussion of extinction selectivity and recovery dynamics following the K–Pg mass extinction event. To investigate the link between K–Pg deforestation and its impact on animal evolution, we have performed paleoecological reconstructions and ecomorphological analyses on K–Pg boundary-crossing bird clades. Our results illustrate that the K–Pg mass extinction evinced strong selectivity for the survival of non-arboreal birds across the K–Pg boundary, which may be attributable to the temporary yet widespread loss of forest habitats.

In addition to its utility for reconstructing canopy density, the use of rLAI on dispersed cuticles serves as a new independent marker to identify the K–Pg boundary at localities where other direct evidence of the Chicxulub impact is not preserved.



<sup>&</sup>lt;sup>•</sup> Speaker

#### Softwood from the Boureau's collection: reexamination in the light of the ABIeS database

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The ABIeS database aims to become the equivalent for softwood anatomy of what Inside- wood database represents today for hardwoods. This project, begun two years ago, was intended for producing a knowledge database on the anatomy of extant and fossil coniferous woods.

In a first time, we initiated a work on softwood features. Although the main nomenclature of characters used in ABIeS is that proposed by the IAWA, a review of additional characters has preliminarily been carried out using key references on softwood anatomy. This led to the integration in ABIeS of additional original features. Emphasis has been placed on the qualitative features related to radial and cross-field pits, which are especially important for softwood identification but also on quantitative traits linked to fibers, rays and pits. All these characters were then tested in order 1) to assess their effectiveness and usability, 2) to evaluate their relationships and 3) to establish their efficiency to discriminate different taxa (at the species, genus or family level). A short list of features that seemed the most judicious but also the most commonly used by the wood anatomists' community was then set up. Finally, for this selection of features, a thesaurus was compiled in order to define, illustrate and explain the coding methodology.

In a second step of our project, we chose to illustrate extant genera diversity by including all material available in each family in the xylotheque of multiple institutions (MNHN in Paris, CIRAD in Montpellier and in the Royal Museum for Central Africa in Tervuren). For the largest genera, that are those with more than 10 species, we chose to code at least 20% of their species. The latter were selected from recent phylogenies in order to illustrate the diversity of the genera. Data on biological habit and ecological requirements of the different species were also provided.

The third step of this work was dedicated to the integration of some of the fossil woods of the Boureau's collection. This work allows us to re-examine many type specimens in the light of extant conifer anatomy, to evaluate their anatomical proximity but also to detect potential impact of ecological or bio-geographical parameters on the fossil wood anatomy.

This project, although initiated within the CR2P in Paris, has a collaborative purpose. We therefore warmly invite all the researchers interested in the study of wood anatomy of extant and fossil conifers to join us, to collaborate on the future achievement of such a worldwidely useful knowledge database.



<sup>&</sup>lt;sup>\*</sup> Speaker

#### A new Late Devonian heterosporous woody plant from South China

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Lycopsids are a very minor component of current terrestrial herbaceous floras. However, lycopsid fossil diversity shows a great diversity and disparity including heterosporous woody plants, e.g. the giant isoetaleans that populated the extensive Pennsylvanian wetlands. The earliest known isoetalean land plants come from late Devonian localities from China, but the time of origination of heterospory and secondary growth is still uncertain. Here, we describe *Lilingostrobus chaloneri* gen. et sp. nov., a new isoetalean lycopsid from the Upper Devonian (Famennian) Xikuangshan Formation of China (Hunan Province), which adds to the already impressive diversity of the Devonian Chinese lycophytes. *Lilingostrobus* shows a so far unknown combination of characters. This new plant is pseudoherbaceous, with a possible tufted habit, and consists of narrow axes with rare isotomies. The stem includes small quantities of secondary xylem. Each fertile axis bears one terminal strobilus comprising sporophylls ending in a very long upturned lamina. Microspores and putative megaspores have been found, but whether the plant has mono- or bisporangiate strobili is unknown. Importantly, our cladistic analysis identifies *Lilingostrobus* as a direct precursor of Isoetales, which provides new insights into the basal evolution of lycosids. Note: BCM and PG contributed equally to this work.



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# Systematic, evolutive, and functional implications of wood disparity in Mississippian lignophyte trees

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The Mississippian sees a major increase of the number of trees within the lignophytes, the clade that includes the now extinct progymnoperms and the seed plants. While arborescent lignophytes were only represented in the Devonian by the emblematic progymnosperm *Archaeopteris*, about 15 genera have to date been described in the Mississippian, mostly in volcanically influenced environments of the tropical belt. This informal and likely paraphyletic group of trees encompasses a great range of cortical and vascular anatomies and is a good candidate to compare systematic diversity and morpho-anatomical disparity in the plant fossil record. In this talk, we will more specifically explore some systematic, evolutive, and functional questions raised by the disparity of their wood anatomy.

We will first provide an overview of the significant wood disparity among these trees. They show a significant range of variation for important characters (tracheid diameter, radial pitting, ray size, etc), and some possess unique combinations of characters. In some cases their wood fits in the "classic" morphogenera *Agathoxylon* or *Dadoxylon*, others like *Dameria* or *Protopitys* are more comparable to Mesozoic morphogenera of uncertain affinities. The wood with small diameter tracheids and large rays up to 8 cells wide and over 100 cells high of large Mississippian trees such as *Pitus* or *Megalomyelon* has no equivalent among extant seed plants.

In a second step, we will look at these diverse wood anatomies in combination with other characters that have a stronger taxonomic value, especially primary vascular anatomy, and discuss how this raises important questions about plasticity, convergence, and biases in estimating plant diversity from isolated wood fragments. Different species within a genus of Mississippian lignophyte tree can have a different type of wood, especially in terms of ray size. On the other hand, several genera that differ widely in their primary vascular anatomy display a comparable wood anatomy. For example there are several genera that have a wood comparable to that of the different species of *Pitus* but that differ widely in terms of primary xylem strands number, size, maturation, as well the mechanism of leaf trace production, leaf trace anatomy and phyllotaxis, and/or bark anatomy.

Finally, we will discuss how this disparity compares to that of coeval non-arborescent lignophytes taxa and present future avenues of research investigating the functional properties of these woods.



S14 // Ora

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## The flora of the uppermost Middle Devonian Ronquières locality, Belgium: the hydraulic efficiency of three woody plants compared

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Secondary xylem first evolved some 400 million years ago during Early Devonian times. Earliest evidence comes from several euphyllophytes of small stature such as *Armoricaphyton* Strullu-Derrien et al. The small size of these earliest woody plants confirmed the hypothesis that the initial evolution of wood was most probably driven by hydraulic rather than mechanical constraints. The late Givetian plant assemblage at Ronquières locality represents one of the most diverse Middle Devonian flora, including representative of lycopsids, cladoxylopsids, progymnosperms and seed plant precursors. In this work, we studied three shrubby or arborescent woody taxa from the locality with respect to their hydraulic efficiency in an attempt to elucidate its role in the early evolution of forested vegetation. The three taxa are the following:

(i) a probable new cladoxylopsid genus consisting of a short length of a narrow axis including a small number of vascular strands of variable shape and size; each vascular strand includes a circular to elongate core of primary xylem surrounded by a narrow ring of secondary xylem.

(ii) the archaeopteridalean genus *Callixylon* represented by a small specimen consisting of a portion of secondary xylem with characteristic pitting, including several branch traces.

(ii) the stenokolean genus *Brabantophyton* (a taxon known from permineralizations only and considered related to early seed plants), consisting of a stem with a mesarch three-lobed protostele surrounded by a large amount of secondary xylem.

The hydraulic conductance of the three taxa has been calculated, and compared. The mechanical support resulting from the presence of secondary xylem has also been evaluated. Finally, the hydraulic efficiency of the three analysed Middle Devonian taxa is compared to that of the Early Devonian diminutive *Armoricaphyton*.



S14 // Oral

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### Skaar Ridge revisited: Insights into a Permian high latitude peat swamp forest ecosystem from Antarctica

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Deposits from the central Transantarctic Mountains of Antarctica provide considerable insights into the biodiversity and biology of high-latitude Permian ecosystems. On Skaar Ridge, permineralized peat deposits are thought to represent rafts of peat mires that were eroded into river channels and preserved by a three-phase permineralization. Due to this rare process, the permineralized peat preserves the anatomical structure of the plant, arthropod remains, and microbes in fine detail. The Skaar Ridge peat deposits are dominated by fragments of glossopterid trees, e.g., Vertebraria roots, Glossopteris leaves, wood (some with attached bark), and several examples of reproductive structures while understory components are scarce. Increased interest in plant-fungus interactions has revealed evidence of fungal wood decay, mycorrhizal associations, and glomoid spores and their development. The purpose of this contribution is to summarize some recent studies and illustrate how they push the boundary from classical systematic descriptions to paleoecosystem functioning. Leaf venation density is closely related to leaf hydraulic conductance and maximum photosynthetic capacity. An analysis of Glossopteris leaves demonstrates that the density of their venation would have given them a photosynthetic advantage over contemporary leaf types. It is less clear how Glossopteris leaf venation density is related to high paleolatitude light regimes. The production of epicormic shoots in glossopterids reveals the ability of these trees to produce opportunistic shoots in response to long or short-term stresses (perhaps recurrent flooding), while the production of a thick insulating bark allowed their cambium to resist significant temperature changes. The unique anatomy of the Vertebraria roots was well adapted to a peat swamp environment and may have produced their own facilitating growth substrate. An analysis based on compression-impression material indicates seasonal shedding of reproductive organs and scale leaves of glossopterids, suggesting a rapid response to conditions for dormancy. Finally, the record indicates that fungi were important elements of these Antarctic polar terrestrial paleoecosystems and likely affected (positively and negatively) the co-existing plants. Additional research combining descriptive studies and approaches in paleoecology will undoubtedly shed more light on the interrelatedness of constituents in these unique high-latitude Permian ecosystems.



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# Phototropism in wood trunks: Implications for the rotation of North China Plate?

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Living trees show phototropism, which means that they grow towards sunlight. It is the same situation with the in situ vertically preserved petrified wood. We measured the eccentricity of living trees and of fossil wood from the same latitude. The dominant direction of the eccentricity in living trees in North China Plate shows a southwest direction; the average value of data in the dominant sectors is SW  $219 \cdot \pm 5^{\circ}$ , which probably results from phototropism. The eccentricity data of the two in situ standing fossil trunks in Tiaojishan Formation, Liaoning, China is  $255^{\circ}$  on average: the eccentricity in petrified wood is thus  $31-41^{\circ}$  more southwest than that of the living ones. Comparing the average phototropism direction of Tuchengzi Formation (with almost the same latitude with Xiangshan) of SW 233.5° in the Late Jurassic of Yanqing Geopark, with the extant phototropism direction, shows a  $36.5^{\circ}$  difference in the phototropism orientations. The different eccentricity of the two formations might reflect the continuous clockwise movement of the North China Plate. The eccentricity of the wood in Tuchengzi Formation is  $19.5^{\circ}-9.5^{\circ}$  more to the southwest than that of the extant trees. Therefore, both  $31^{\circ}-41^{\circ}$  and  $19.5-9.5^{\circ}$  indicate that the North China Plate rotated clockwise from the Late Jurassic to nowadays, which is almost coincident with our palaeomagnetic results, which show a  $26.5^{\circ} \pm 5.5^{\circ}$  clockwise rotation of the North China Block since the Late Jurassic.



Speaker

#### A new approach to *Glossopteris* leaf taxonomy embracing morphometric analyses

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Glossopteris leaves are one of the most common and easily recognised Permian fossils across Gondwana, but they are morphologically conservative and taxonomic approaches to species differentiation have been varied, relying on visual estimations of relatively plastic characteristics such as shape, length etc. Species identification in the past has therefore proven to be subjective, inconsistent, and extremely challenging. To address these taxonomic challenges, we have produced the first morphometric study using Glossopteris leaves from two localities in the Karoo Basin of South Africa: a new site on the Ouberg Pass (Northern Cape Province) and Kwa-Yaya (KwaZulu-Natal Province). The Ouberg Pass lies in the southern Karoo Basin, in a region rich in fossils of terrestrial vertebrates of the Tapinocephalus Assemblage Zone. A detailed biostratigraphic framework, together with multiple ash dates in the immediate area, provided excellent context for this study of a well-preserved, middle Permian parautochthonous flora. The Kwa-Yaya locality, in the late Permian Emakwezini Formation of the Lebombo Basin in the eastern Karoo Basin, has yielded a superbly preserved and diverse, parautochthonous flora. For this study, 43 quantitative leaf features were measured and analysed to identify morphological characteristics that could produce well defined specimen clusters. The morphometric analysis included: leaf length, width, vein angles (proximal, medial, and marginal), mesh areas and width, and leaf area among other features. Fifteen qualitative features were also considered. Our results suggest that the use of the medial portion of the leaf produced the most discrete clusters; and that a combination of features (vein angles, mesh width, mesh area, and leaf area) provided the most reasonable grounds for morphologically defined taxonomic discrimination of species. This work has been used for the development of a standardized leaf characterization template that we hope will facilitate more reliable and consistent typification of glossopterid leaves in South Africa and other regions of Gondwana.



S14 // Oral

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#### Estimating the carbon content of an early forest

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The earliest forests composed of canopy trees exceeding 2 m in height date from the Middle Devonian. The best example is provided by the paleosol and associated fossils of Givetian age recorded at Riverside Quarry, Gilboa, New York. The canopy trees in these early forests belong to the Pseudosporochnales which, above ground, consist of a trunk topped by a small crown of short-lived branches. If the advent of trees and forests is believed to have deeply changed the composition of the atmosphere during the Devonian, this contribution has never been quantified. As a contribution to resolve this challenge, we present here an attempt to calculate the above-ground biomass and carbon content stored in a Middle Devonian forest structured like that reported at Riverside Quarry.

The first step consists of modeling of a 3-m high *Pseudosporochnus* tree using the AmapSim software and its computer simulator. The carbon content of the tree and of its components is calculated at any time during growth using the mean carbon density of two Carboniferous plants of comparable structure, *Psaronius* and *Medullosa*. The carbon content of a fully grown tree ranges between 837 and 1,300 g C. At 40% of development and beyond, most of the carbon is stored in the trunk. However, when considering the cumulative amount of carbon of the tree, most of the carbon synthethized during its life has gone to the construction of the short-lived branches.

Given some assumptions on the density and age of the trees, the carbon content of a *Pseudosporochnus* forest ranges between 4.3 and 15.5 t C/ha. These values are relatively low compared to those of extant forests, the closest analogs in terms of productivity being either thickets of young trees or environmentally constrained forests. The accuracy of the model is discussed and any conclusion about an adaptation of pseudosporochnalean forests to constrained environments must be taken with great care. Yet, it is interesting to note that previous authors reporting forests around Gilboa suggested that they inhabited either stressed or disturbed environments.



Speaker

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## New anatomically preserved conifer remains of subfamily Cunninghamioideae (Cupressaceae) from the Late Cretaceous (Maastrichtian) Quiriquina Formation of Cocholgue, south Chile

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The monotypic genus *Cunninghamia* of the conifer family Cupressaceae is now distributed in restricted areas of China, Laos, Vietnam and possibly Cambodia. Fossil records, however, show much higher species diversity and wider geographic distribution of the genus and its extinct sister groups including *"Cunnighamia* -like" species in the Northern Hemisphere throughout the Cretaceous. Recent molecular and morphological studies suggested that extant *Cunninghamia* together with the extinct sister groups comprise a subfamily Cunninghamioideae in the conifer phylogeny (Brink et al. 2009; Atkinson et al. 2014; Buczkowsky et al. 2016).

The Late Cretaceous (Maastrichtian) Quiriquina Formation yields calcareous nodules containing marine animals and plant debris of terrestrial origin. The plant debris are anatomically preserved, allowing structural description and taxonomic identification of some well-preserved specimens. Here we report new conifer shoots and a possible young seed cone that are attributable to the subfamily Cunninghamioideae of the Cupressaceae. The shoot consists of a main stem helically bearing linear sessile leaves adnate to the axis. The leaf exhibits a crossshape when it departs from the main axis and, distally, a flat lenticular shape in cross section. There is one collateral vascular bundle in the leaf, usually associated with three resin canals, a large central one abaxial to the bundle, and smaller ones on each lateral side of the leaf. Stomata occur on both sides of the leaf. The leaf anatomical structure is very similar to that of the extant Cunninghamia except its typical cross-shape at the base of the fossil. One shoot is terminated by a possible young seedcone that consists of multiple bract/scale complexes. The bract and the scale of the complex are mostly fused leaving a tiny tip of the latter on its adaxial side. The ovule is not preserved. The fossils can be described as a new genus of the Cunninghamioideae. The new fossils reveal the presence of an extinct group of basal Cupressaceae in the Southern Hemisphere until the end of the Cretaceous. The discovery expands the species richness and the geographic distribution of fossil Cupressaceae, documenting the evolutionary radiation of the subfamily Cunninghamioideae during the Cretaceous.

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#### A new gymnosperm stem from the Lopingian North China and its palaeoecological implications

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In the Permian equatorial and paratropical regions of Pangaea, intense aridity replaced the previously prevailing humid climate. The changing global climates and floras resulted in four distinct floristic zones: Cathaysian, Angaran, Euramerican, and Gondwanan. This first occurrence of a Cathaysian Flora was found in the North China block in the Cisuralian (Early Permian). With the increasing aridity in northern China, four floral turnovers were recognized in the Guadalupian (Middle Permian) and Lopingian (Late Permian). In the latest Permian, the Cathaysian elements were few, while the conifer-dominated vegetations covered the North China Block. Here, we report silicified tree trunks discovered in the Lopingian deposits of the Sunjiagou Formation in the Shanxi Province, southern North China. The characteristics of these silicified woods indicate that they belong to a new conifer taxon. The well-preserved fossil woods allow us to consider the palaeoclimate and landscape in the Lopingian North China block. The trunks we infer to be those of conifers evidently derived from substantial trees. Based on the palaeoecological analysis, we speculate that the trees derived from gallery forests along the rivers in the North China.

S14 // Oral

Speaker

### Pleuromeia from the Middle Triassic Linjia flora with typical Paleozoic elements recorded in Benxi, Northeast China

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The Middle Triassic Linjia flora of Benxi, East Liaoning, Northeast China, is a very interesting flora combining typical Paleozoic elements of Cathaysia, Euramerica, Angara and Gondwana (e.g. Lobatannularia, Oligocarpia, Psygmophyllum and Glossopteris), with the typical Mesozoic elements around the world. Although the Middle Triassic Linjia flora has been reported for about 40 years, and the Middle Triassic Linjia Formation is comparable with the Middle Triassic Ermaying Formation in Shaanxi, North China, its importance has not been taken into account because the index fossil of the Early to Middle Triassic, *Pleuromeia*, has not been found. Recently, the new species *Pleuromeia shaolinii* Zhang et Wang sp. nov., represented by 8 specimens, was discovered from the Middle Triassic Linjia Formation. Its stem is erect, attaining a diameter of 1.8 cm. Leaves are linear, at least 7 mm in length. The basal part of the stem is slightly thicker than the middle of the stem, attaining a diameter of 2 cm. A rhizophore with four lobes is developed below the basal part of the stem. The adventitious roots are attached to the rhizophore in an approximately helical order, with a diameter of 0.5-1 mm. An ovate heterosporous cone is borne at the apical part of the stem, attaining a length of 5.8 cm, and a width of 4 cm. The basal part of the cone is reduced to 2 cm in width. The upper to middle part of the cone possesses microsporophylls, while the lower part develops megasporophylls. Sporophylls are arranged in a spiral order on the cone axis. Both microsporophylls and megasporophylls are obovate, attaining a length of 15 mm and a width of 7.5 mm, bearing an obovate sporangium with a similar size, about 9 mm in length, and 5 mm in width. Leaf ligules are located at the upper part of sporophylls, whereas sporophyll scars are positioned at the lower part of sporophylls. Megaspores and microspores are trilete, up to  $300 - 400 \ \mu m$  and  $60 - 70 \ \mu m$  in diameter, respectively. The new species is similar to P. sternbergii in the morphology of the stem and rhizophore, but the latter differs from the former in its transversely rounded sprophylls.

The new finding of *Pleuromeia*, not only gives enough evidence to demonstrate that the age of the Linjia flora is correct, but it also shows the complexity of the Mass Extinction and Recovery from the Late Permian to the Middle Triassic, with a very special and important refuge present in the Middle Triassic in Northeast China for the Late Paleozoic elements from four phytogeo- provinces. It means that many Mesozoic elements probably originated from Northeast China because this area probably provided very special conditions to form a connecting link between the preceding elements of the Paleozoic and the following elements of the Mesozoic.



<sup>\*</sup> Speaker

#### **Phytoliths from conifers**

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Coniferous phytoliths in sediments are an effective tool for detecting the historical appear- ance of conifers. However, at the timberline in mountainous areas, such coniferous phytoliths are easily confused with grass phytoliths. This study analyses modern phytoliths from 17 conifers. Six common types and six rare types were identified. The conifers studied produce abundant blocky polyhedral and cubic (in the average 30–40  $\mu$ m size range), blocky scrobiculate (average 30–40  $\mu$ m), tabular elongate unsculpted (length 50–100  $\mu$ m, width 10–20  $\mu$ m), tabular elongate cavate (length 50–150  $\mu$ m, width ~10  $\mu$ m), tabular elongate dendritic (50–100  $\mu$ m × 10–20  $\mu$ m), and irregular oblong (20–40  $\mu$ m) phytoliths. This paper aims to show morphological characteris- tics of coniferous phytoliths in China, and to show how the common coniferous phytoliths differ from similar grass phytolith types, such as blocky polyhedral coniferous phytoliths from silicified parallel epipedal bulliform cells produced by grass. Blocky polyhedral and cubic phytoliths are the commonest coniferous phytoliths found in the sediments, but need to be carefully distinguished from grass parallelepipedal bulliform cells. This study indicates that clearly protruding ridges and irregular inward edges are essential features of cubic and polyhedral morphotypes produced by conifers. Results of this paper might provide important material for the study of palaeovegetation and palaeoecology of mountainous areas, especially at the timberline.

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## New cones of aff. *Welwitschiostrobus* from the Crato Flora, Late Aptian of Northeastern Brazil

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The Araripe Basin is renowned worldwide due to its Late Aptian (Lower Cretaceous) fossiliferous richness. Fossils of several plant groups have been discovered during the last century (such as lycopodiophytes, monilophytes, coniferophytes, cycadophytes, gnetophytes and basal magnoliophytes), as well as those of animal groups (such as arthropods, fishes, amphibians, turtles, crocodiles, dinosaurs, pterosaurs). Among the plants, gymnosperms are distinguished by their marked presence in the flora, making up approximately 60% of the diversity. The Gnetophytes, in their turn, have a great presence, mainly in the layers belonging to the Crato Member (Santana Formation). They are represented by the families Welwitschiaceae and Ephedraceae. Nowadays, the family Welwitschiaceae is represented by a single surviving specie, Welwitschia mirabilis. These plants are characterized by their undeveloped woody stem, two cotyledons which are lost during the plant development, and two permanent large and long strap-shaped leaves that show continuous growth lasting for all the plant's life due to the presence of leaf basal meristems. Nonetheless, the Crato Member flora presents a set of fossil plants which are interpreted as possible Welwitschiaceae, such as Cratonia cotyledon, Priscowelwitschia austroamericana, Welwitschiophyllum brasiliense, and Welwitschiostrobus murili. Recently, new samples were collected that represent tree stems with sixteen well-preserved cones, all connected in a system of striated articulated axes in the first analysis, and resembling the cones of Welwitschiostrobus. The major stem dichotomizes until 6th order, the medium stem until 3rd order and, the smaller until 2nd order, all bearing similar reproductive cones. All branches havea similar size, on average 890±110 mm. The cones have a terminal or axillary position, and are, on average,  $510\pm110$  mm long and  $14\pm3$  mm wide in the basal region, a larger value than those described previously. Some cones also present basal bracts. The scales are distributed pseudoverticillately along the cone, and they tend to be more rectilinear with an acute apex in the apical region and falciform, yet with an acute apex, in the basal region of the cone.



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### Diversity of trunks of genus *Cycadeoidea* Buckland ex Lindley et Hutton (Bennettitales) in the lower Cretaceous deposits of north Spain

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Remains of silicified bennettitalean trunks assigned to genus *Cycadeoidea* are relatively abundant in lower Cretaceous rocks from the area of Salas de los Infantes (Burgos Province, north Spain). The fossils occur in sandstone deposits of continental fluvial origin corresponding to the Pinilla de los Moros Formation (Upper Hauterivian-Barremian) and Castrillo de la Reina and Abejar Formations (Barremian-Aptian).

These records range from centimetric-sized fragments of ramentum to nearly complete trunks up to 75 cm long and 40 cm wide, which preserve numerous rhomboidal scars of leaf bases and complete cones embedded in the trunks.

At the moment, four different types of trunks have been identified, which differ both in their morphology, size, and cone shape. Polished sections of some of the trunks show preservation of their internal structure, and thin sections present different parts of cones including seeds inside. Cones differ both in their sizes and in the arrangement of morphological components. These morphologies may represent either taxonomic or developmental differences. Some of these trunks are morphologically similar to certain species coming from coeval sites in southern Eurasia and northwestern North America. Further detailed morphological studies are needed for taxonomically identifying these trunks.

These fossils particularly constitute an important paleontological heritage that can be contemplated currently in the Museum of Dinosaurs of Salas de los Infantes and also in another fossil site for public exhibition shortly.



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#### Archaeopteris, the earliest tree in South Africa, makes its appearance in the Upper Devonian (Famennian) Witpoort Formation

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The Late Devonian witnessed emergence of the first large woody trees, in the form of the cosmopolitan genus Archaeopteris. These formed the dominant species in the pioneering low- land forests that would ultimately lead to a complete reset of global environmental systems. The original description of Archaeopteris notosaria in 1995 was from the upper part of the Famennian aged Witpoort Formation (Witteberg Group, Cape Supergroup). It was particularly significant as all previously described Archaeopteris had come from tropical to warm temperate palaeoenvironments, principally in Laurussia and the northern continental blocks. By contrast, the Waterloo Farm lagerstätte, from which Archaeopteris notosaria was described, is situated in southern Gondwana, at high palaeolatitude (currently reconstructed as being within the Devonian Antarctic Circle). This was the first evidence that cosmopolitan lowland forests had achieved a truly global distribution by the end of the Devonian. The original description relied on portions of leafy branches, and a single poorly preserved fertile fragment. New material has been provided by excavation of a stratigraphically lower site discovered during roadworks in the mid portion of the Witpoort Formation. Not only does this provide a slightly earlier record for the arrival of Archaeopteris in Southern Africa but is also significant in that the new material provides additional anatomical information. It includes impressions of two whole branches, one vegetative and one fertile, as well as a fragment in which the structure of the fertile zone is clearly apparent, revealing the type material to have been incomplete.



Speaker

### (Pro)Gymnosperms from the Early Carboniferous of the Montagne Noire: morphoanatomical disparity of wood and functional implications

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For a long time, studies on evolution have conflated two distinct concepts: diversity and disparity. Indeed, while diversity is about the number of species in a group (species richness), disparity refers to the morphological variation. Studying the evolution of Lignophytes increases our knowledge of the evolutionary history of the group that includes the majority of extant plants (gymnosperms and angiosperms). While the Late Devonian marked the divergence of Lignophytes from others Tracheophytes (by diversification of their fertile organs), the Early Carboniferous represents the radiation of their vegetative structures. It opened up a new era where these plants showed a higher morphological diversity and a hypothetic high vegetative disparity for the first time. Lignophytes are woody plants and their secondary xylem is developed to assume both functions: conduction of water and support of plant body. Hence, studying the disparity of their wood anatomy could bring to light different bodyplans and *in fine* different strategies. For example, if a wood presents large tracheids and a lot of parenchyma, conduction is favored upon support and this kind of wood could belong to a liana.

Studied specimens were found in the Lydiennes horizon of the Montagne Noire (South of France), either in phosphatic nodules or loose in the matrix. This formation is considered middle Tournaisian in age, based on conodonts. Specimens belong to nine genera: *Protopitys, Stauroxylon, Calamopitys* (3 species), *Faironia, Stenomyelon, Triichnia, Lyginopitys, Tristichia,* and *Eristophyton*.

First of all, the project consisted in the creation of a database with quantitative (e.g. tracheids diameter, pit diameter) and qualitative (e.g. pit shape, presence of axial parenchyma) wood features. Preliminary results show a large diversity (e.g. tracheids diameter ranging 19-132  $\mu$ m, rays 1-more than 70 cells high), which supports that some of these species may be trees while others were more like lianas.

The second step will be to conduct morphospace analyses to explore morphoanatomical and functional disparities so as to be able to reject or not the hypothesis of a high wood disparity in these Montagne Noire species. With this further study, the aim is also to be able to answer questions such as how wood disparity in the Montagne Noire compares to wood disparity of the Lower Carboniferous Lignophytes in general? Is there a disparity peak at this period? How does this wood disparity vary during following periods?



<sup>'</sup> Speaker

S14 // Poster

#### A Jurassic forest reconstruction and palaeoecology in the Sichuan Basin of southern China

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The Jurassic system is well developed in the Sichuan Basin of southern China. It represents a fluviallacustrine deposit with hot and arid climate conditions. In particular, the Upper Jurassic formations are represented by two lithological units, including the Suining Formation and the Penglaizhen Formation. Previous studies show a variety of invertebrate and vertebrate fossils found in the Upper Jurassic deposits, including bivalves, ostracodes, conchostracas, dinosaurs, and turtles. However, fossil plant remains are very rare in the Upper Jurassic deposits of this basin due to the severe climate conditions. In recent decades, over 500 fossil wood specimens have been discovered in the Upper Jurassic Penglaizhen Formation in Shehong County of Suining City, Sichuan Province. On this basis, a petrified forest national geopark was established in this region. These fossil woods are systematically ascribed to several conifer taxa, including Agathoxylon, Brachyoxylon, and Xenoxylon, belonging to the Araucariaceae, the Cheirolepidicaceae, and incertace cedis conifers as well. Based on field mapping of these fossil wood logs and trunks, we use software to make a forest reconstruction, showing the vegetation aspects of the Late Jurassic episode. Furthermore, we use growth ring proxy analysis to infer and explore the palaeoclimate and palaeoecology of this fossil forest. We show that this fossil forest devastation was triggered by the severe seasonal flooding events in the Sichuan basin, and that the prevailing warm and hot climate conditions was sandwiched by short climate cooling event.

Speaker

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# S15 - Experimental approaches in palaeontology: new data from old fossils

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### Experimental analysis of how character loss biases interpretations of exceptionally preserved, soft bodied organisms

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In the exceptional deposits that preserve fossilized remains of soft tissues, it is tempting to think of the fossils themselves as essentially complete, and assume that we can reconstruct what they were like as animals by reading anatomy directly from the fossils. This would be a mistake: all fossil remains lie somewhere on a spectrum of decay, at one end of which is complete loss of all information (no fossil preserved). Exceptionally preserved remains lie towards the other end of the spectrum, but no fossils avoid decay completely, and the degree to which anatomical information is lost during decay and preservation can be hard to determine. For decades, taphonomic experiments have been used to investigate postmortem processes and their role in exceptional preservation, but a wide range of known and unknown variables influences how soft tissue remains become fossilized - variables that at first sight might seem to limit the applicability of experiments to analysis of fossils. Focussing on character-based experimental decay I have worked with a small group of colleagues (particularly Sarah Gabbott, Duncan Murdock and Robert Sansom) to develop methods that allow clear analysis and quantitative testing of the repeatability and comparability of taphonomic experiments. Our approach allows factors that retard onset of decay to be differentiated from those that reduce the rate of character loss, and demonstrates that sequences of character loss are generally unaffected by the conditions in which carcasses decay. Empirically derived sequences can thus be applied to exceptionally preserved fossils to disentangle the relative importance of, and interactions between decay, maturation, and mineralization, and to inform our interpretations of fossil morphologies. Far from being of limited value, data from well-designed taphonomic experiments provide fundamental new insights into the processes and biases that have produced exceptionally preserved fossils, and the degree to which these processes distort our understanding of anatomy, function and ecology.

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# Absolute and meso-wear in goats fed diets of different abrasiveness for half a year

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In herbivores' natural diets, the main abrasive factors contributing to tooth wear are phytoliths and grit. However, the different aspects in which they impact tooth wear and the timeframe a wear signature takes to develop, still remain unexplored.

The effect of intrinsic (phytoliths) and extrinsic (grit) abrasives was investigated on 28 adult female goats. The animals were kept in four groups, in a controlled feeding experiment over a six-month trial period. The four pelleted diets differed in their degree of abrasiveness (without phytoliths: lucerne L; phytoliths: grass G; increased phytoliths: grass/rice hulls GR; external abrasives: grass/rice hulls/sand GRS), and were supplemented with a necessary minimum of lucerne hay (lucerne group) or grass hay (the other groups). Tooth morphology was captured by medical CT scans at the beginning and end of the experiment. These scans, as well as the crania obtained postmortem, were scored using the mesowear method (cusp shape, occlusal relief). Comparisons between diet groups showed no significant effect after 0.5 years. However, when assessing the difference in mesowear signal between measures made at the start and end points of the experiment, significant effects emerged. In accordance with the theory of mesowear, the GR and GRS groups indicated significantly higher wear than the other diet groups. A feeding period longer than 0.5 years is deemed necessary for a mesowear signal to clearly develop in adult animals.

The accumulated 3D data was also used to gauge absolute wear of tooth crown material by quantifying volume loss. Significant differences in volume loss between the diets, consistent with abrasiveness, were made evident by 3D volume analysis of the upper left M2, with increased loss observed in the GR and GRS groups. Through these measurements, a simultaneous volume gain was noted, caused by root growth - despite the fact that all animals possessed permanent adult dentition. Overall, tooth volume loss was significant by the end of the experiment and a correlation was found between crown volume loss and root volume gain. This could imply the existence of a hitherto unknown feedback mechanism that attenuates wear caused by abrasive diets, even in animals with closed roots.



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# Diagenetic alteration of dental surface textures by sediment transport: a tumbling experiment

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3D dental surface texture (3DST) is a powerful proxy for assessing tooth function and determining the mechanical properties of ingesta. Abrasion and/or attrition cause material loss and result in specific wear features on the enamel surface. Wear features at the  $\mu$ m-scale are related to feeding patterns and can be used to distinguish between soft or hard-object feeding in herbivores and faunivores.

However, taphonomic processes during burial, transport and fossilisation may alter original enamel surfaces and obscure ingesta-related 3DST. In this study, we performed tumbling experiments on teeth from three species of extant vertebrates with well-known feeding behaviours to evaluate the physical effects of fluvial transport on 3DST and to assess whether diet-related features are overprinted. Isolated teeth were tumbled in sediment-water (1:1.6) suspensions using different grain size fractions (63-125 $\mu$ m, 125-250 $\mu$ m, 250-500 $\mu$ m, 2-8mm) of siliciclastic Rhine river sediment. Teeth of the herbivorous rodent (*Otomys* sp.) and two large ungulates, a grazer (*Equus* sp.) and a browser (*Capreolus capreolus*), were treated for time intervals ranging from 30 mins to 366 hrs. 3DST was measured on exactly the same occlusal enamel areas both prior to and after tumbling, using ISO-norm texture parameters.

The main goal was to assess if ingesta-related differences in 3DST of grazers and browser were preserved after the tumbling. Prior to tumbling, 12 texture parameters were significantly different between the two ungulates. After 16 hrs of tumbling, these 12 parameters remained significant and four additional parameters became significant. Subsequent tumbling for 336 hrs changed the significance-levels of some parameters: nine were still significant, including two new ones, while six lost their significance. Rodent teeth did not show any significant changes in 3DST. During tumbling, volume and flatness parameters remained relatively stable. Most significant alterations of the 3DST were found for the medium grain size fraction.

The 3DST of the tumbled teeth will be compared to those of fossil teeth from different fluviolacustrine depositional settings to assess if the experimental 3DST alteration resembles that caused by natural sediment transport.

Overall, our experiment provides promising insights into the stability of ingesta-related 3DST of mammal teeth during fluvial transport and helps to identify suitable 3DST parameters for dietary reconstruction in fossil vertebrates.



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<sup>\*</sup> Speaker

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# The ruminant sorting mechanism: an innovative digestive strategy that washes off external abrasives before chewing

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In ruminants, the major contribution to particle size reduction of ingesta does not occur during ingestion but during rumination mastication. Historically, the less robust mandibles of ruminants (as compared to perissodactyls) and lower hypsodonty have been accounted for by a concept that material regurgitated from the rumen is softened, 'soaked', and therefore requires less masticatory force (and hence less robust mandibles) than freshly ingested material. Ingestive chewing in horses is very regular in the rhythmicity of its motions and resembles rumination chewing but not ingestive chewing in cattle and camels, raising the question why the latter do not apply this efficient chewing pattern already during ingestion. A convenient answer is that ruminating herbivores avoid wear-intensive chewing during ingestion and postpone it until after the ingesta has been exposed to forestomach fluids, which potentially wash off external abrasives (but cannot remove internal abrasives).

In a pilot study, we investigated the location of sand accumulation in the forestomach of goats fed a diet containing sand for several months before taking a full-body CT scan in the natural resting position, and before sampling different locations of the forestomach after slaughter. The results indicate that the dorsal rumen contents - from where material for rumination is recruited - was comparatively depleted of sand.

The resulting hypothesis is that a diet of a certain phytolith content should affect ruminants and non-ruminant herbivores alike; in contrast, a diet of a certain external abrasives content should affect ruminants less than nonruminant herbivores. Preliminary results from comparative feeding experiments with goats and rabbits support this hypothesis.

It should be further assessed whether environment reconstructions based on hypsodonty indices or tooth wear proxies become more accurate if this difference between ruminants and nonruminant herbivores is taken into consideration.



Speaker

#### The present is the key to the past: assessing how extant marsupials track their environment to clarify mammalian responses to climate change

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Dental microwear texture analysis (DMTA) and stable isotope analysis have long been used to clarify the paleobiology and paleoecology of extinct animals. However, not all animals record their local environment similarly-with some tracking relative aridity and others tracking meteoric water via oxygen isotopes. Additionally, there has been significant debate regarding if DMTA records an animal's diet or local environment (e.g. grit on the landscape). As understanding dietary proxy data is critical to assessing faunal responses to climate change, the ecology of our ancestors, and a broad diversity of questions, it is necessary to assess if and how extant taxa track their local environment. Here, we use extant wild-caught marsupials to "experimentally" test how these animals record their local temperature, precipitation, and/or relative aridity. We developed a DMTA and stable isotope baseline of extant possums, koalas, and macropods consuming a broad range of diets and/or occupying a broad geographic range, including: Dorcopsulus vanheurni, Macropus fuliginosus, Macropus giganteus, Osphranter robustus, Osphranter rufus, Phascolarctos cinereus, Notamacropus rufogriseus, Petrogale lateralis, Setonix brachyurus, Trichosurus caninus, Trichosurus vulpecula, and Wallabia bicolor. By examining a range of taxa from overlapping environments and across a range of habitats, we clarified that dental microwear is reflective of diet and less affected by environmental variables including evaporative conditions. Results demonstrate the ability of DMTA variables to differentiate between tough and hard food consumers, i.e. extant grazers and woody browsers, respectively. Additionally, koalas record a tough folivorous diet even when consuming leaves lacking phytoliths. When comparing M. giganteus and M. fuliginosus individuals that were killed during "normal" conditions to those killed during extreme droughts, DMTA reveals dramatic dietary shifts in both taxa to include more woody material during periods of extreme aridity. Further, the majority of these marsupials track relative aridity via oxygen isotopes, providing confidence that fossil taxa within the same family can similarly track local climates through time. Collectively, these data reveal how mammals record a range of climates including extreme droughts, and help document the utility of DMTA for recording diet while stable oxygen isotopes in kangaroos, possums, and koalas all record evaporative conditions. The present is the key to the past: assessing how extant marsupials track their environment to clarify mammalian responses to climate change.



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# The positional repertoires of hominins: New insights from extant primates

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With regard to the diversity of positional (posturo-locomotor) capacities of extant non- human primates, it is very likely that our ancestors and extinct non-human primates were also able of various posturo-locomotor modes. Furthermore, the most obvious variations between extant primates are mainly in size and shape (i.e. morphotypes) that are shown to be strongly related to locomotor performances. In this context, understanding the diversity of the positional repertoires in extant species in relation to size, morphotype and environment may help to model evolutionary transitions in extinct species' positional repertoires. For this aim, we conduct experiments 1) in the frame of the Motion Analysis of Primates platform at the CNRS Primatology Station (Rousset, France) where we have a long experience of integrative studies (biomechanics, morphology and positional repertoire) of longitudinal samples of the olive baboon, Papio anubis, and 2) in Zoological parks on the morphometrics of different gibbon species, Nomascus gabriellae and N. siki, in the zoos of Besançon and Mulhouse and on bonobos, Pan paniscus, in the zoo of Planckendael. By collecting radiographs, making external measurements (segment lengths and diameters) and quantifying posturo-locomotor behaviours, we increase our understanding of the relationships between bones, body mass distribution and positional behaviours. By using a developmental perspective, our results suggest strong relationships between limb mass proximal migration and the variations in the proportion of climbing behaviours. We also found a marker, in the skeletal proportions of the foot, for the proportion of grasping behaviours in baboons. Based on these results and on the functional relationships between body mass distribution and posturo-locomotor repertoires found in the literature, we propose a meta-analysis of the changes in morphotypes in Catarrhini species. This multivariate analysis allows us to predict the emergence of new positional repertoires, including its diversity, in relation to morphotypes and bone size during the evolution of primates, including hominins.



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#### Inhibitory cascade and serial segmentation in teeth, limbs and body segments: from trilobites to hominids

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Many animal bodies display serial structures made up of repeating segments of similar size and shape, including teeth, limb/finger bones/segments and body segments. Gradations in size and shape are often apparent in these series, forming a 'morphogenetic gradient'. One model for the developmental control of the size of adjacent segments is the inhibitory cascade. This model was first established in mouse molars, showing that teeth form a linear pattern in size along the tooth row, but the slope of this linear pattern varies among species. The inhibitory cascade has considerable power in explaining tooth size development and evolution in humans and fossil hominins, allowing us to predict the sizes of undiscovered teeth based on this developmental pattern. The inhibitory cascade has also been inferred to influence the size of other segmented structures in the vertebrate body, including phalanges, limbs and somites/vertebrae. Given the apparent widespread presence in vertebrates, we hypothesised that the inhibitory cascade mechanism influences non-vertebrate appendage and body structures. A key example is the basal arthropod group trilobites, which have serial segments in the thorax. From measurements of segment sizes in trilobites, we show that the inhibitory cascade strongly controls relative segment size in the pygidium in 51 out of 53 species, and also explains thorax segment size in adults of 69 out of 99 species of trilobites. Our results suggest that the developmental mechanism of the inhibitory cascade was present early in arthropod evolution, and is likely influential throughout the animal kingdom.



Speaker

### Cracking the link between brain and skull in Archosauria: evolutionary and developmental perspectives

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The brain has a primacy in both neural control and early cranial development. Extant birds underwent through a dramatic enlargement of the brain in comparison to other reptiles. This process caused important changes to the bird skull, in particular the skull roof. However, a link between the brain regions and the skull roof elements was never formally addressed. Moreover, disagreement regarding the homology of the skull roof elements in birds with other reptiles arose in literature, due to the lack of a comprehensive approach tangling their evolution and development.

3D morphometric analysis recovers stem diapsids, stem archosaurs and early dinosaurs tightly clustered. Birds and *Archaeopteryx* are divergent. Correlation tests between the boundary of brain regions and the suture between frontal and parietal were statistically significant, suggesting a deep evolutionary link between brain regions and skull roof elements.

We implemented our evolutionary scenario with developmental data. Developmental series of *Alligator* and *Gallus* were assembled. CT scan, immunofluorescence and confocal imaging were combined to track mesenchymal condensation and ossification patterns of the skull roof along the development of the brain and its regionalization pattern. Mesenchymal cells condense early in organogenesis between the forebrain and midbrain and hindbrain. However, it is only after establishment of the facial region and its chondrogenesis that the mesenchymal condensations of the primordial skull roof start to express Collagen I. We found no support for Sox9 and Collagen II expression in these mesenchymal condensations. Birds show a delayed patterning of the skull in comparison to reptiles. We suggest this is due to the positive allometry of the bird brain, contrary to the negative trajectory observed in reptiles. Early ossification centers for frontal and parietal appear with a one-to-one relationship with forebrain and midbrain and midbrain between brain regions and skull roof elements slightly decouple later in ontogeny.

In conclusion, the skull tracks the development and evolution of the brain. Non-coelurosaurian taxa show a conservative skull roof and brain morphology, whereas a strong paedomorphic signal and hyperenchephalization are found in Eumaniraptora. Skull roof elements are extremely conservative and there is little evidence for a wholesale restructuring of skull roof composition in birds as suggested by recent studies.

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### Can studies on the interplay between the musculoskeletal system and performance shed light on the paleoecology of extinct species?

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The reconstruction of the palaeobiology (ecology, behaviour and lifestyle) of an extinct species is a difficult exercise. Unfortunately, a fossil is rarely well-preserved; and thus teeth, bones, or parts of bones are the main material with which palaeontologists work due to the fact that soft tissues rarely fossilized. As such palaeontologists need to understand the adaptive nature of the morphology of the skeleton in extant species and its relation to locomotion, or behaviour while accounting for effects of shared ancestry. Palaeobiological reconstructions assume that the morphology of a species reflects its ecological adaptation(s). Bones allow movement and, whilst supporting loads, also need to respond and resist to muscular forces. As bones are shaped by force and motion, their morphology is likely to be intimately related to the movements executed. Thus, to understand the adaptive nature of the morphology of the skeleton it is essential to study the relationships between bones and muscles in living species and their relation to ecology and behaviour while taking into account potential effects of shared ancestry. In this presentation, we show how the study of the musculo-skeletal system of the cranium in relation to bite force performance allows for integrative inferences of performance and diet in extinct species of strepsirrhine primates. To do so, we use a data set of 21 living species of strepsirrhines for which data were collected on the shape of the bones of the masticatory system (cranium and mandible), the architecture of the masticatory muscles, as well as in vivo data on isometric bite force. Our results show that the masticatory muscles have a significant impact on cranial shape in comparison to mandibular shape. In contrast, bite force strongly impacts mandibular shape but not cranial shape. Thus, we focus on the cranial shape to reconstruct the myology of extinct species, whereas we use mandibular shape to reconstruct the bite force. These quantitative inferences on extinct species allow us to shed light on the evolution of diet in extinct species.



Speaker

#### Macrowear and tooth enamel mechanical properties

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Dental macrowear occurs when the amount of enamel removed is evident to the naked eye. The degree of macrowear can be scored and used to identify population differences related to diet. Though excessive macrowear can compromise the utility of a tooth, many mammalian species rely on a degree of enamel wear to maintain tooth functionality. Thus, the factors affecting macrowear hold important information about dietary adaptation. The loads required to cause wear are described mathematically as a function of the mechanical properties of enamel. Here, we review research exploring the link between macrowear and mechanical properties, and implicate the angle between enamel prisms and the occlusal surface as an important factor in wear-resistance. This angle changes as macrowear accrues, which affects the mechanical properties and has implications for further wear-resistance. To explore changes in wear-resistance with macrowear, we test the hypothesis that mechanical properties at the occlusal surface will change as crown height is reduced. We use nanoindentation to map the mechanical properties and microstructure of enamel in a baboon molar as its cusp height is reduced. Our results show how mechanical properties differ with degree of wear, and add to our understanding of their role in resisting macrowear.

Speaker

### Wrinkling of the occlusal enamel surface in Anthropoidea: insights from virtual modelling and dental topographical analysis

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During the course of evolution, various primate clades (Pitheciidae, Pongidae, Hominidae and the extinct Omomyidae) have acquired complex occlusal surfaces displaying dental wrinkles, located in the molar central basins and on cuspal inner slopes, in addition to the main cusps and crests. Early dental morphologists defined wrinkles as generated by localized thickening of the enamel (sometime referred as crenations), with than a lack of concordance between the enamel-dentine junction (EDJ) surface and occlusal enamel surface (OES) for the expression of these localized features. Hence crenations differ from features which are reflected by the surface of the dentine like folds and true cusps.

Among fossil and extant primates, taxa convergently show various degree of 'wrinkling' of their occlusal enamel surfaces suggesting potential functional values for this feature. Wrinkled basins are hypothesized to be involved in trapping/stabilizing the food item, in increasing dental longevity in relation, for instance, with wear resistance and/or stress dispersal during crushing, or in draining fluids away during food comminution by producing a network of narrow valleys. This make crenations especially interesting in terms of dental evolution. It also highlights the need to investigate the relationship between wrinkling and enamel thickness variation in primates.

Here we aim to quantitatively characterize wrinkle development in anthropoid's occlusal basin using dental topography approaches. Besides, the relative implication of enamel thickness variations in influencing the wrinkling expression (as crenations) is investigated.

We performed a quantitative study of OES in anthropoid upper molars, which were investigated using microCT and 3D surface analysis. Dental topographical variables (eg orientation, curvature, ambient occlusion) were computed for each mesh's occlusal surface and wrinkles were detected using combinations of these variables. Furthermore, the 3D enamel thickness (3DET) was computed for each molar as the minimum normal Euclidean distance from each OES polygon to the first EDJ polygon intersected.

Our method allows a better understanding of the wrinkling expression and its quantification on molar occlusal surfaces. Our approach will allow to test the functional hypotheses related to wrinkling in extant primates, and to interpret their convergent emergences in distinct primate lineages, including early Hominines like *A. afarensis* and *P. boisei*.



<sup>.</sup> Speaker

#### Functional locomotor morphology of Lophiodontidae (Perissodactyla: Tapiromorpha) with comparisons to potential modern analogues

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The Lophiodontidae are an endemic Eocene family of odd-toed ungulates (Perissodactyla: Tapiromorpha). A number of studies have been conducted into the biology and ecology of lophiodontids, drawing comparisons to tapirs based upon dental morphology and jaw mechanics. Here, we explore another aspect of lophiodontid biology – locomotion – to ascertain whether modern tapirs represent a viable analogue for lophiodontid locomotor morphology and behaviour. We laser scanned 65 forelimb bones from three species of lophiodontids, with additional specimens examined from published articles. A 3D geometric morphometric analysis was used to compare lophiodontid bone shape to modern tapir and contemporaneous perissodactyl forelimb bones. Measurements pertaining to biological or mechanical outcomes were also taken from scans (e.g. body mass measures, lever-arm ratios, long-bone ratios). Principal components analyses and neighbour-joining trees were used to visually compare morphological variation, with significant differences assessed using perMANOVAs, ANOVAs and Tukey WSD post-hoc tests. Mass estimates from humeral measurements suggest lophiodontids in this study approximate modern New-World tapirs in average body mass (155-240kg). Results from shape analysis of the humerus suggest that interspecific variation within the genus Tapirus is greater than differences between lophiodontids and tapirs; however, manus bones demonstrate significant differences. Lophiodontid unciform and metacarpals exhibit flattened distal joint surfaces; this disperses compressive forces across the joint facet, indicative of greater loading. In contrast to shape analyses, lever-arm ratios for upper arm muscles show similarities between lophiodontids and modern New-World tapirs. Long-bone ratios (proxy for locomotor style) demonstrate similar forelimb proportions in modern tapirs and Paralophiodon when compared to contemporary Eocene perissodactyls. Our morphological analyses suggest lophiodontids were not capable of moving as swiftly as modern tapirs; greater loading over the manus was most probably as a result of increased mass in the shoulder and cranial regions in lophiodontids. With the data available, we believe that modern New-World tapirs adapted for greater loading over the manus (e.g. Tapirus bairdii) represent the most viable locomotor analogue for lophiodontids.



<sup>&</sup>lt;sup>°</sup> Speaker

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# Wear at different levels of resolution in rabbits fed diets of different abrasiveness

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To assess the effects of internal and external abrasives on tooth wear, we performed a controlled feeding experiment in rabbits fed diets of varying phytolith content and with addition of sand as an external abrasive. 16 rabbits were kept individually, each fed four pelleted diets of varying abrasiveness (no phytoliths: lucerne L; phytoliths: grass G; more phytoliths: grass and rice hulls GR; external abrasives: grass, rice hulls and sand GRS) for 2 week-periods at random order. Wear was quantified as absolute p3 length using burr marks, relative cheek tooth length (in proportion to length on lucerne) measured from CT scans, and at the end of the experiment on macerated skulls as mesowear and 3D surface texture analysis.

The 2-week-periods proved sufficient to show a significant difference of tooth wear. The wear effect was more prominent on maxillary than mandibular teeth. The relative length of the upper cheek teeth showed an additional effect of the tooth position on wear pattern. In GRS the upper third premolar had the largest decline in relative tooth length compared to others in the same tooth row. The hypselodont teeth compensated for wear by increasing growth in response to it.

The different wear patterns of the upper and lower cheek teeth were also discernible in the mesowear scores. The upper cheek teeth had more rounded cusps and a flatter occlusal relief. The impact of diet abrasiveness on the mesowear signal was only clearly visible for the most abrasive diet due to the limited sample size. However, for the second upper molar and the first lower premolar a trend of the mesowear score inverse proportional to the diet abrasiveness could be shown.

Complementing the previous findings, the 3D surface texture analysis identified increasing roughness and larger volume in surface texture features with increasing abrasiveness of the diet (L less than G less than GR less than GRS). Surface textures of antagonistic upper and lower teeth were significantly different in the L, G, and GR diets, with rougher and more voluminous textures for the upper teeth, contradicting the concept that gravity makes lower molars more susceptible to impact from abrasives, but supporting the concept of upper and lower molars as an inverted pestle-and-mortar system.



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### Tooth wear, diet and ecology : From French countryside sheep to extinct antelopes from the Omo valley, Ethiopia

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The Shungura Formation, Lower Omo Valley, Ethiopia have yielded major Plio-Pleistocene paleontological and archeological contents. This formation is subdivided into 12 geological members dated by radiochronological and magnetostratigraphy methods. Next to biogeochemistry, dental microwear textural analysis constitutes an alternative approach to explore feeding ecology and thus evolutionary hypotheses thanks to this accurate chronostratigraphic framework. However, recent studies have challenged our understanding in tooth wear and have hypothesized that dental microwear textures might not reflect differences in diet but in dust or grit contents. Such assumptions may have severe consequences as our present objective is to investigate ecological segregation between taxa of bovids and to track changes in food resources in a context of environmental changes (increase of aridity).

To assess the contributions of biotic and abiotic factors in tooth wear, we conducted a controlled food testing on 180 sheep fed on different dust-free and dust laden fodders. These fodders were composed of either herbaceous dicots (clover) with and without seeds, or on herbaceous monocots (ray grass or a multi-specific assemblage of grasses), modeling the different ecodietary spaces from browsers to grazers known in the wild game.

Then, we re-interpret the dental microwear textures we gathered from 141 fossil antelopes belonging to Reduncini, Aepycerotini, and Tragelaphini, all coming from the geological members E and F over a time interval between 2.4 and 2.27 Ma. From Member E to F members, there are significant variations towards more grazing habits for reduncines and more browsing preferences for tragelaphines, a pattern that cannot be explained by differences in dust but by differences in food resources. We here conclude that these two taxa of bovids occupied more contrasted habitats. Besides, aepycerotines do not show any significant changes in diet over time attesting that as their modern relatives, they were mixed feeders, both engaged in browsing and grazing.



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#### Finite Element Analysis of durophagous crab predation

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The shells of bivalves protect these organisms from their environment. One of the most dangerous aspect of their life are encounter with predators. Especially crushing (durophagous) predators pose considerable threat to the mostly immobile mollusks. Amongst putative defensive adaptation in bivalves, shell shape has often been hypothesized to strengthen the valves during a predatory attack, but not much data is available to corroborate this claim. Using Finite Element Analysis we model the crushing attack of Florida stone crab on a hard clam, a soft clam, and a blue mussel. Nanoindentation tests provide material properties of the different shells, and feeding experiments inform the location of contact areas between shell and crab claw, and direction of applied force. Our results show a close relationship between shell material and the way valve symmetry distributes the loads applied by the crushing attack. The hard clam disperse the loads of a crushing attack evenly across its heavy, brittle shell. These valves experience the lowest stresses out of all the models. The soft clam model documents that these bivalves respond to the more localized stresses with deformation rather than dispersion. The blue mussel geometries show that loads are distributed in an alternating stress distribution pattern. Dispersing stress to inside or outside of the shell allows them to absorb more energy than the more brittle shells.

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Speaker
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### Dental growth and development in Turolian hipparionine species: comparison with extant Equus and life history inferences

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Dental histology has proved to be a valuable tool for reconstructing life histories, since dental formation times and growth rates are closely related to the animal's pace of life. The timing of the first molar eruption, for instance, correlates well with the age at weaning, while the eruption of the third molar marks attainment of skeletal maturity. Current advances in dental histology of extant equids have shed light on the pattern of growth of their hypsodont teeth, providing a solid framework for studying fossil taxa. The high diversity of the Old World Hipparion s.l. lineage during the late Miocene constitutes a perfect opportunity to test for differences in life history strategies related to size changes. Here, we aim to infer the life history traits of three different-sized hipparionines from the Spanish Turolian through dental histology. To achieve this objective, we analyzed the enamel growth of the lower first-second and third molars of Hipparion concudense (95 kg), Hipparion gromovae (59 kg) and Hipparion periafricanum (23 kg) from two Spanish fossil sites, Concud (MN12) and Rambla de Valdecebro II (MN13). Moreover, we reconstructed the enamel growth pattern of the first and third lower molar of the extant species Equus guagga (245 kg) for comparative purposes. In this extant equid the growth trajectory is described by a first high-speed growth phase followed by an asymptotically decreasing rate until root formation. This process spans for almost 2 years in first molars and 5 years in third molars. Hipparion teeth, however, grow at slower rates and during a shorter time, but following a similar growth trajectory. Considering the important differences in hypsodonty between Equus and Hipparion, the higher enamel growth rates found in E. quagga suggest the need to form higher-crowned teeth. The studied hipparions, however, present similar hypsodonty indexes and little difference in tooth formation, which points to a similar pace of life for all the species analyzed. Considering the coupling between size and life history, we infer a slower pace of life for the small species as formation times and extension rates are similar to those found in the larger taxon.



Speaker

### Can seasonal climatic contrast in ancient tropical contexts be estimated from growth of tropical ectotherm vertebrates as controlled by environmental drivers? An experimental study

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During the Neogene, the intensity of the contrast between wet and dry seasons may constitute a main component of climatic variations in continental areas. Our project aims the use of the growth rates that are recorded in skeletal elements of fossil ectotherm vertebrates to depict local seasonality and its change through time. Effectively the growth cycles of the ectotherms are partly controlled by environmental conditions. However, seasonal factors that may modulate growth are multiple and it is necessary to process calibrated study to interpret consistently change in bone growth rates measured in fossil remains. Our dispositive includes an experimentation in controlled conditions. Three species that are frequently yielded by Neogene outcrops from Africa were used: the fishes Polypterus senegalus, Auchenoglanis occidentalis and the turtle Pelusios castaneus. Specimens were bought in an animal farm and the experiment got ethical agreement (n° 86050). We aimed to evaluate the relative influence of three environmental parameters known to modulate growth rates and growth rhythm in ectotherms: food abundance, temperature and photoperiod. In replicated tanks, 3 groups of specimens were submitted to seasonal variations of these parameters following the variation intensities and durations observed in tropical environments of Africa, while a 4th group was reared in constant conditions. Every change applied on parameter values to simulate seasonal fluctuations was associated with the injection of a calciumbinding fluorescent dye. Temperature of the water was measured daily and somatic growth of each specimen was measured each week. At the end of the experimentation, specimens were euthanized and their otoliths and bones were sampled and prepared (thin section) for growth pattern analyses regarding the controlled framework. As a first result, we observed that inner natural rhythm has operated at least in the fishes, independently of the conditions applied. Then, food abundance appeared as the only parameter to have pulled a significant growth difference compared to control groups. Depending on the fish social status, the growth was more or less rapid, but the rhythm was similar in all tanks under similar conditions. Finally, we also observed that depending on the taxa, reduction of the food doses did not affect growth in the same respect.



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### How ecologically sensitive is texture analysis of tooth microwear? Testing hypotheses of niche partitioning in sympatric species

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Recent work shows that tooth microwear analysis can be applied further back in time and deeper into the phylogenetic history of vertebrate clades than previously thought (e.g. niche partitioning in early Jurassic insectivorous mammals; Gill et al., 2014, Nature). Furthermore, quantitative approaches to analysis based on parameterization of surface texture are increasing the robustness and repeatability of this widely used dietary proxy. Discriminating between taxa within dietary guilds has the potential to significantly increase our ability to determine resource use and partitioning in fossil vertebrates, but how sensitive is the technique? Can microwear texture analysis detect differences between sympatric species which exhibit niche partitioning with significant dietary overlap? To address these questions we combined detailed dietary analysis with tooth microwear texture analysis of sympatric populations of shrew species (Neomys fodiens, Neomys anomalus, Sorex araneus, Sorex minutus) from Bialowieza Forest, Poland. Dietary analysis reveals that these populations exhibit varying degrees of niche partitioning with greatest overlap between the Neomys species. Sorex araneus also exhibits some niche overlap with N. anomalus, while S. minutus is the most specialised. Multivariate analysis based only on tooth microwear textures recovers the same pattern of niche partitioning, demonstrating that validated microwear texture analysis can provide very subtle dietary discrimination in fossil insectivores. Application of these results to a combined dataset of extinct and extant taxa has some surprising implications.



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#### Wear your diet on your teeth: Dental Microwear Texture Analysis as a proxy for estimating the diet of extinct South American caviomorph rodents

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Modern caviomorphs or South American hystricognathous rodents exhibit a great taxonomical and ecological diversity, with a broad spectrum of dietary habits, ranging from frugivorous to grass eaters. Their oldest record dates back to the late middle Eocene from Peruvian Amazonia. Continuous paleontological field efforts have substantially increased the fossil record of early caviomorphs, testifying of a complex early evolutionary history. The late Oligocene locality of Salla (Bolivia) has yielded a diverse assemblage of caviomorphs, including taxa representing the four extant superfamilies. The systematics of the Salla rodents is now better established, but little is known regarding their ecology and ecological interactions.

Here, we reconstructed the diet of the Salla rodents in performing a Dental Microwear Texture Analysis (DMTA) on the enamel tooth surface. Microwear analyses are proxies providing an insight not on the ability but directly on the use of teeth. The DMTA describes and analyzes automatically surface textures with a high degree of precision. We firstly analyzed the microwear texture of 79 wild specimens of extant caviomorphs showing different feeding habits that we compared with those of 241 fossil specimens from Salla. For each specimen of modern and fossil species, we performed a scan on a high resolution silicon mold of the molar occlusal surface with an optical surface profilometer (2). We then applied a scalesensitive fractal analysis with Toothfrax and Sfrax softwares to describe the microwear textures through four variables: Asfc (complexity), epLsar (anisotropy), HAsfc (heterogeneity of the complexity), and TFV (textural fill volume).

Feeding habits among extant caviomorph species provide distinct microwear textural signals for each studied variable. However, diet distinctions for the extinct Salla species are not as marked as in extant species. Dental microwear textures vary significantly among Salla species primarily on the complexity and textural fill volume. But only main tendencies regarding the paleoecology and niche partitioning can be advocated for the Salla rodent community.

Based on complexity, *Incamys, Sallamys, Migraveramus* and *Cephalomys* appear to have been generalist frugivorous (as the modern *Dasyprocta*), and *Eoviscaccia* might have fed on tougher items such as leaves (as the modern *Phyllomys*). In contrast, *Protosteiromys* and *Branisamys* seemingly included blander young leaves in their diet (as the modern *Coendou*).

\* Speaker

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# Everything matters: molar surface texture in goats fed diets of different abrasiveness

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A previous feeding experiment with sheep suggested that dust added to a diet of natural forage at a quantity of approximately 1% of dry matter had little effect on molar surface texture. Here, we maintained 28 adult female goats in four groups, fed pelleted diets of lucerne (L, without phytoliths), grass (G, phytoliths), grass/rice hulls (GR, increased phytoliths) and grass/rice hulls/sand (GRS, external abrasives at 5% of the pellet ingredients), supplemented with a necessary minimum of lucerne hay (lucerne group) or grass hay (the other groups). After 0.5 years, the animals were slaughtered and 3D surface texture analysis applied to the upper and lower second molar.

Increasing dietary abrasion in the diet (L less than G less than GR less than GRS) led to gradually increasing roughness and larger volume in surface texture features. Highest void volumes (largest pits) were found in the GRS group. This is consistent with texture results from rabbits fed the same pelleted diets. We conclude that the same diet forms similar surface textures even in two very different mammal species. Further it indicates a general diet-dependent principle of surface texture formation.

In the direct comparison of upper and lower molars, the sand diet had a significantly more pronounced effect on the upper molar, having more voluminous valleys and larger texture direction values. This contradicts the concept that gravity making lower molars more susceptible to impact from external abrasives, but supports the concept of upper and lower molars as an inverted pestle-and-mortar system.

The results indicate that external abrasives (of the size and concentration of the present experiment) do have a 3D texture effect in goats that could be relevant for dietary/environmental reconstructions based on this method.



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#### Low prevalence of molar crushing behavior in tufted capuchin monkeys, and its consequences for the investigation of seed predation in extinct mammals

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From squirrels to peccaries, seed predators are found in several mammalian orders. To access protected seeds, seed eating mammals can use their teeth in two types of ingestive i.e., non chewing behaviors. The first one involves the use of anterior teeth i.e., incisors and canines to open and remove seed shells, while the second involves the use of post canine teeth i.e. premolars and molars, to crush seed shells and get access to their content. Both can result in dental adaptations, some of which could be used to infer seed predation ability in extinct mammals. Most of the literature on adaptations to seed predation focuses on molars, which is based on the basic assumption that seed predators either (i) commonly chew hard, stress-limited food or (ii) use molar crushing to ingest food items protected by a hard shell. Both assumptions have been tested in a seed predator primate notorious for using both anterior and post-canine teeth, the tufted capuchin monkey Sapajus apella. The first assumption was tested by comparing hardness scores of seeds and seed shells reported in the literature. To test the second assumption, captive specimens (N=13) from Guangzhou Zoo were observed during feeding trials. Monkeys were fed with seeds characterized by either soft shell (peanut) or hard shell (walnut), and ingestive actions were scored using ethograms.

The first assumption was rejected, as seed shells were significantly harder with most seed classified as non challenging. Regarding the second assumption, molar shell crushing was observed for both soft and hard seed shells. However, monkeys performed significantly less molar crushing when opening hard shells, relying more on their anterior teeth. This low prevalence of molar shell crushing might be due to the difference in food size. Regardless, this study does not support either of the two basic assumptions, meaning that seed predators could rely less on their molars and more on their incisors or canines to ingest protected seeds.

The classification of several extinct mammals as 'seed predators' is further examined at the light of these results. Different conclusions could be drawn in some occurrences. It is therefore recommended to (a) assess the prevalence of molar crushing in other mammalian orders and (b) when it is possible, consider the whole denture when inferring adaptation to seed predation in fossils.

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Speaker

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#### Developing a systematic approach to virtual threedimensional avian bone histology

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Bone histology in fossil vertebrates is critical to palaeobiology as it enables reconstructions of developmental age, life history, and growth rate, as well as biomechanics. Histological studies on birds have transformed our understanding of avian evolution but the production of thin sections for histology is destructive and time consuming, typically resulting in a single plane cut from a small region of interest. Furthermore, the resulting sections are two-dimensional (2D), not representing structures in their genuine three-dimensional (3D) context.

In order to mitigate some of the difficulties inherent with the use of (2D) thin sections, a noninvasive and fully 3D imaging approach can be adopted using high-resolution X-ray-based computed tomography (CT). CT is becoming increasingly widespread throughout palaeontology, from scanning whole skulls to interrogating small regions at the cellular level. Nevertheless, limited systematic work has so far been carried out to characterise bone microstructure in extant birds in 3D, a crucial prerequisite before extrapolation to fossils.

We imaged cortical bone from the midshaft of the femur, tibiotarsus, and humerus, encompassing a complete growth series of modern domestic ducks (*Anas platyrhynchos*) using highresolution synchrotron-based CT at the TOMCAT beamline of the Swiss Light Source (X-ray energy 21 keV, voxel size 1.6  $\mu$ m, exposure time 180 ms, 1501 projections). We scanned 21 naturally deceased individuals: a range of juveniles (less than 6 months), and three adults (two years).

After segmentation of intracortical porosity by absolute thresholding, 2D and 3D visualisation revealed cortical microstructural changes during development, including bone volume fraction, heterogeneity in canal diameter across the cortex, and differences in canal orientation and delayed mineralisation in the humerus compared to the leg bones. Variation between bones reflects limb use: ducks are precocial and run immediately after hatching, but fly later in life. Our results corroborate published observations in 2D sections, but critically add further information in the true 3D measurement of canal networks and osteocyte lacunae, impossible from 2D sections. The next steps of this work will be to quantify the observed variations in bone microstructure through the life course, and across different extant species to characterise the influences of life history, bone mechanics, and phylogeny on 3D microstructure.



Speaker

#### Dental 3D surface texture in guinea pigs fed fresh or dried forages reflects phytolith content and plant material properties

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Although it is still debated whether phytoliths can abrade dental tissue, recent experimental work has repeatedly shown that this can occur, even though native phytoliths are softer than dental enamel. The resulting hypothesis is that phytolith content should be reflected in dental wear features, which allows for subtle discrimination of feeding traits along the browser-mixed feeder-grazer continuum. It has, however, been noted that phytolith characteristics depend on the extraction method, with native phytoliths showing lower indentation hardness than phytoliths extracted by dry ashing. We thus propose that the state of the plant tissue, fresh or dry, will have an effect on dental abrasion.

To assess this, we performed a controlled feeding experiment with 36 adult guinea pigs, fed exclusively with three different natural forages: lucerne (no phytoliths; low silica content of 0.0- 0.4% DW), timothy grass (phytoliths, moderate silica content of 0.8% DW), and bamboo (more phytoliths, high silica content of 8.3% DW). Each forage was either fed in fresh or - harvested from the same batch/field - dried state (6 groups of 6 animals each). After three weeks, the animals were euthanized, and 3D surface texture analysis (3DST) was performed on the upper fourth premolar.

Generally, enamel surface roughness and volume increased with higher phytolith/silica content of the feed (lucerne lower than grass lower than bamboo), confirming that 3DST reflects the amount of phytoliths in the diet. Additionally, fresh and dry forages caused distinct dental surface texture signals, with fresh grass and dry grass displaying the most pronounced differences in wear patterns. Surface textures of animals feeding on fresh grass were often similar to those on fresh or dry lucerne, supporting previous reports that 'fresh grass grazers' have a less abrasion dominated wear pattern than 'dry grass grazers'.

Our results confirm that different types of forage can cause distinct 3D surface texture patterns, but also indicate that besides phytolith content, other material properties such as moisture content can significantly affect plant fodder abrasiveness; even to such an extent that wear patterns characteristic for dietary traits (i.e. browser versus grazer) become indistinguishable.

Thus, feeding on fresh or dry grass matters and needs to be taken into account for dietary reconstructions.

<sup>\*</sup> Speaker

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### S16 - 3D imaging of fossils: novel approaches, advances and data management

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# The extra dimension of energy – Strategies for the collection and analysis of complex synchrotron data sets

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X-ray fluorescence (XRF) measurements are becoming a routine technique for the analysis of geological and fossil materials. The use of high brilliance synchrotron sources allows for the detection and characterization of trace constituents, as well as gaining spatially resolved measurements at the scale from sub-microns to millimeters. When one thinks of a three-dimensional data set from XRF, the most common result is tomography. However, in addition, with the use of synchrotron radiation, another important dimension that can be explored is that of the incident x-ray energy. The energy dimension not only allows the quantification of the element of interest on the sample, but the spatial distribution of its chemistry as well. This chemical knowledge of element can provide a remarkable wealth of information, which can inform on not just distribution, but also on the processes that have lead to distribution throughout the specimen's complex digenetic history. Several examples will be show that illustrate the utility of this type of multi-dimensional data set, and highlight advances in the both the data collection and analysis that have been implemented to make XRF measurements within the energy dimension a routine procedure.



Speaker

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#### 3D reconstruction of the brain endocast and inner ear of *Malawisaurus dixeyi* (Sauropoda: Titanosauria)

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A braincase of the Cretaceous titanosaurian sauropod Malawisaurus dixeyi, complete except for the olfactory region, was CT scanned and a 3D rendering of the endocast and inner ear was generated. Cranial nerves appear in the same configuration as in other sauropods, including derived features that appear to characterize titanosaurians, specifically, an abducens nerve canal that passes lateral to the pituitary fossa rather than entering it. Furthermore, the hypoglossal nerve exits the skull via a single foramen, consistent with most titanosaurians, while other saurischians, including the basal titanosauriform, Giraffatitan, contain multiple rootlets. The size of the vestibular labyrinth is smaller than Giraffatitan, but larger than most derived titanosaurians. Similar to Giraffatitan, the anterior semicircular canal is larger than the posterior semicircular canal. This contrasts with more derived titanosaurians that contain subequal anterior and posterior semicircular canals, supporting the position of Malawisaurus as a basal titanosaurian. Measurements of the humerus of Malawisaurus provide a body mass estimate of 4.7 metric tons. Comparison of body mass to radius of the semicircular canals of the vestibular labyrinth reveal that Malawisaurus fits the allometric relationship found in previous studies of extant mammals and Brachiosaurus. As in Brachiosaurus, the anterior semicircular is significantly larger than is predicted by the allometric relationship suggesting greater sensitivity and slower pitch movements of the head. Habitual head posture was calculated using orientation of the lateral semicircular canal of the inner ear. Based on our reconstruction, there appears to be only modest reorientation of the jawline relative to the lateral semicircular canal, comparable to Camarasaurus.

Speaker

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#### Fossils enlightened by Reflectance Transforming Imaging

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Fossil imprints are sub-plane items whose subtle differences in relief can have critical implications regarding their systematic placement and morpho-functional interpretations. However, the production of demonstrative evidence of such specimens can prove a laborious task, in particular when relevant structures have diverging orientations. Computer-assisted photographic techniques, which generally speaking are revolutionizing the field of palaeontology, offer new opportunities to provide exhaustive documentation. One of these techniques, Reflectance Transforming Imaging (RTI), used in the field of archaeology for more than a decade, but rarely in palaeontology, delivers a photograph which enlightenment can be modified at will. Several cases applied to fossil items are presented, including the earliest earwig, an early relative of cockroaches & mantises, a Mesozoic crustacean, and a Paleocene plesiadapiforme. Such files are comparatively easy to produce and disseminate and are memory-friendly. Limitations of the technique are also discussed.



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Speaker

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#### Digital endocranial reconstructions of the extinct scelidothere sloths (Xenarthra, Mylodontidae): emerging patterns in folivorans' evolution

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The latest CT-scanning facilities and 3D imagery techniques are greatly improving our understanding of animal morphology, revealing important aspects of the internal cranial anatomy for both extant and extinct vertebrates. This non-destructive methodology has the potential to greatly facilitate studies of adaptations and paleobiology for fossil species. Recent research on the extinct giant mylodontine sloth *Glossotherium robustum* allowed the documentation of many previously unknown structures, such as the inner ear, brain cavity, paranasal sinuses, and trajectory of several cranial nerves and blood vessels. It was also possible to compare these structures with their counterparts in the living arboreal sloth genera Bradypus and Choloepus, together with the extant anteaters and armoured cingulates. Their morphologies suggest the influence of different effects, such as phylogenetic imprint, as well as allometric and functional components, and reveal the importance of the application of these techniques for elucidating the evolutionary history of sloths. For this reason, we extended our observations, performing new CT scans on some representatives of another highly peculiar group of mylodontid sloths, the Scelidotheriinae. This new sampling includes several South American Pliocene and Pleistocene taxa that are not necessarily closely related phylogenetically. It includes small- and large-sized forms, and individuals of various ontogenetic stages, in order to encompass the different morphologies, respectively related with phylogeny, allometry, and ontogeny. Preliminary qualitative data reveal a conservative morphology of the brain casts (i.e., olfactory bulbs, cerebral hemispheres, and cerebellum) among Mylodontidae, despite their marked differences in their external cranial anatomy. On the contrary, paranasal sinuses show marked differences between Scelidotheriinae and Mylodontinae, in both shape and size. The observed morphology of the paranasal pneumatization seems to be affected also by ontogenetic development, and to be less related with allometry than previously expected. The current study represents the first exploration of the endocranial morphology of the scelidotheriine sloths through digitally-based methods, and a further step toward the comprehension of sloth anatomy and evolution.



<sup>&</sup>lt;sup>\*</sup> Speaker

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#### Computed Tomography for ichnological analysis of modern marine cores: palaeoenvironment and reservoir quality applications

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Ichnological analysis has been revealed as a very useful tool in palaeoenvironmental studies and hydrocarbon exploration. In the beginning, most of studies were conducted on outcrops, but during the last decades studies based on sediment cores have suffered a huge growth. Sediment cores provide an excellent record but their study has some limitations due to core features, being especially harder in cores from modern marine sediments. Some techniques as image treatment or penetrative methods have been used to solve these limitations. Concretely, penetrative methods as X-ray or Computed Tomography (CT) have been successfully applied to ichnological studies in lithified cores with pyritized burrows. However, the use of these techniques in soft cores from modern marine deposits is still poorly explored. In the present contribution, CT techniques have been used to support the ichnological characterization of modern marine cores, and the obtained results have been compared with previous studies conducted on highresolution images. Data obtained from CT allow getting a more detailed characterization of trace fossil assemblages, as well as differentiating intervals based on dominant burrow orientations. The combination of results from both techniques, CT and high-resolution image treatment, allows a more precise analysis, supporting palaeoenvironmental interpretations associated to changes in environmental (depositional and ecological) parameters as bottom-water energy or oxygen, and provides very interesting information for the characterization of reservoir properties, as porosity and permeability, affected by bioturbation.

Speaker

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### Virtual dissection and characterization of extant and fossil specimens with VGSTUDIO MAX

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Volume Graphics software is a powerful and established tool for the precise image analysis of volume data and works equally well on data, e. g., from neutron tomography, X-ray CT, synchrotron tomography, or MRI. The virtual dissection of extant specimens or the uncovering of fossils is a main application of our software in paleontological research. Various (live) segmentation tools offer the possibility to directly use the gray values of the data set, to define own customized shapes or even segment in 3D. Besides these traditional applications multiple analysis options are available to characterize the specimen and analyze its features. Here we present a selection of analysis options and features available in VGSTUDIO MAX showing the diverse utilization in a biological and paleontological context. For instance our geometrical comparison may be used to compare different individuals e.g. quantifying different wear stages of teeth or finding differences between bones of extant and fossil or male and female specimens. The implemented wall thickness analysis offers different algorithms to characterize e.g. the microstructure of wood or thickness of a nautilus shell. Simulation based directly on the voxel data allows to perform virtual stress tests to estimate e. g. bite forces on teeth or osteoderms. Our advanced surface determination - being the basis of the analyses - works subvoxel precise and additionally performs a local correction, reducing the influence of artifacts and users. Various measurement instruments help to characterize the specimens according to their dimensions for a profound description. With our high end visualization and animation tools the user is able to create appealing visualizations to present the results of research in publications or talks.

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Speaker

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#### Automatic 3D reconstruction of polygon triangulation for mounted skeleton point cloud

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In the collections of natural history, mounted skeletons, composed of hundreds of different bones, are among the most complex objects. To produce a virtual representation and have a complete digital documentation of more than 200 large mounted skeletons, the Galleries of Palaeontology and Comparative Anatomy of the National Museum of Natural History of Paris were globally scanned, which resulted in a digitized 3D point cloud.

However, the separated datasets, corresponding to each of the acquired skeletons, present noise artifacts (i.e. imprecision of the point coordinates), density defects (i.e. grey areas remaining hidden to the scanning device) and parasitic points (i.e. supporting metal structure underneath the mounted skeleton). Moreover, the use of biomechanical models to investigate the origin of large vertebrates' anatomical diversity requires a mesh triangulation that is consistent and accurate.

The aim of the present work is to develop a mathematical model of the bone surface deformation through optimization and to produce a 3D surface reconstruction, adapted to the geometric properties of a given skeleton point cloud.

Outlier points are first removed from the data, and remaining inlier skeleton points are labeled according to their membership to a specific bone structure. Each skeletal feature from the point cloud is then reconstructed using a variational model, by deforming and adjustinf a generic representative surface from a common skeleton template, based on morphological synapomorphies. This morphing leads to the definition of a closed orientable surface and to the preservation of specifically labeled components, and also allows the mathematical extrapolation of the unknown articular surfaces, which were not covered during the data acquisition. The results are validated in the context of numerical simulation from the anatomical point of view, and will be used to conduct derivative morpho-functional studies.

Collections of natural history are a huge research infrastructure, limited by their accessibility, and new digital tools, like an automatic 3D reconstruction of mounted skeleton point clouds, represent a major step forward for their massive digitalization. Moreover, the ability to model the biomechanical behavior on comparative series of complete large vertebrate skeletons would allow to improve the reliability of functional interpretations about changes in body shape for the adaptation of individuals to their environment and way of life.

\* Speaker

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#### The chemical preservation of insects in resins revisited: insight from 3D X-ray Raman scattering

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The 3D morphological fossilization of insects in amber and copal is exceptional as many localities only preserve cuticle or hollow moulds, or no fossils at all, and the processes that control this diversity in preservation (nature of the resin producer and of the inclusions, environmental conditions, maturation, reworking) are largely unknown. Chitin could be identified in sub-fossils (2-20 ka), but there is no trace of this macromolecule in the Miocene Dominican amber (> 25 Ma). Recent chemical characterization focused on the resin itself whereas very few works investigated the chemistry of the inclusions as it faces important challenges: spectral features from the inclusions are predicted to be very close to those of the resin; and, as components of the resin may have largely penetrated the inclusions, sampling and/or spectroscopy techniques may only provide average information. Here, we show the potential of inelastic X-ray Raman scattering (XRS) to investigate deeper into the chemical preservation of insects in resins. XRS is a synchrotron technique that uses high energy X-rays (~6–10 keV) to probe the speciation of light elements (carbon, nitrogen, oxygen) non-destructively, in air with bulk sensitivity avoiding surface contamination. Also advantageous is the fact that the scattering of hard X-ray photons by core electrons provides multipolar spectral features that can increase chemical contrast. Even more interestingly, as hard X-rays penetrate several millimetres in resins, the use of 2D detectors allows distinguishing signals arising from different depths (with depth, the scattering signal differently focuses on the detector), enabling noninvasive 3D study and offering an unprecedented way to distinguish between insect and resin chemistries. Preliminary data obtained at ID20 beamline of the ESRF synchrotron (Grenoble, France) on a piece of copal from Madagascar (2 ka-1 Ma) show great promise for such studies in clearly revealing, although the insect is mostly a hollow mould, chemical-bond contrast between the resin and remains inside the insect. Further processing of the spectra (one spectrum per pixel) allows recognizing pixels with a different chemistry around the mould, associated to the preservation of cuticle components.



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#### X-ray microscopy of plate assembly in Early Devonian articulated machaeridians from Australia

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Machaeridians are Palaeozoic armoured annelids that produce a calcitic dorsal scleritome comprised of two to four longitudinal series of interlocking shell plates. The disarticulated plates form a common constituent of marine fossil assemblages ranging from the Early Ordovician to Permian Periods, but fully-articulated specimens are rare. The Early Devonian (Lochkovian Stage) Garra Limestone of New South Wales is renowned for its silicified fauna, including abundant corals, stromatoporoids, sponges, brachiopods, gastropods, bivalves, polyplacophorans, crinoids and – as documented here for the first time - machaeridians. These represent the first lepidocoleid fauna (at least two new taxa) described from Australia, and include remarkably well-preserved, articulated specimens as well as abundant disarticulated plates. Using microcomputed tomographic X-ray microscopy ( $\mu$ CT), we were able to investigate biomechanical features involved in the articulation of individual plates within the scleritome, previously denied in other articulated forms due to lower resolution preservation (i.e., pyritization). Both straight and enrolled articulated specimens were scanned and virtually dissected in order to quantify aspects of their three-dimensional geometry, inter-plate overlap, and degree/continuity of curvature. This research not only provides novel insight into the sagittal flexibility of these organisms, but also allows for direct comparison with modern multi-element organisms (e.g., chitons) that employ their scleritome as a defensive strategy.

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Speaker

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#### High-resolution X-ray computed tomography of Lower Ordovician Palaeoscolecid worms

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Palaeoscolecids are an extinct class of Early Palaeozoic worms characterized by an annulated trunk bearing transverse rows of organic or phosphatic plates, an eversible proboscis and tail spines. The group ranges from the early Cambrian to the late Silurian but it is best known from Cambrian Lagerstätte such as the Chengjiang biota, the Burgess Shale and the Sirius Passet biota. Ordovician occurences of palaeoscolecids are relatively sparse. However, they have been recently reported from the Fezouata Lagerstätte (Central Anti Atlas, Morocco) which is a remarkable biota as it contains wide range of iconic Burgess Shale-type elements normally considered characteristic of the Cambrian co-occurring with forms typical for the post-Cambrian Palaeozoic. Specimens described from this locality are generally incomplete trunks occuring mostly in small clusters and were assigned tentatively to Palaeoscolex? tenensis on the basis of strong similarities in the morphology and distribution of cuticular microplates. In addition to material described previously from Fezouata Biota, one new specimen preserved with its anterior part from the same locality have been highlighted by computed microtomography (XR-  $\mu$ CT) to study its threedimensional morphology. The application of XR-µCT technology allows a non-destructive high-resolution access to hidden structures. More characters are preserved than previously thought such as longitudinal rows of tiny teeth in the pahrynx and tubular structures representing likely the fragments of a cylindrical gut tract connecting the mouth to anus. Specimens can be viewed at an anatomical level without losing data in a variety of 2D and 3D reconstructions. This study shows a few of the benefits of XR- $\mu$ CT over current optical investigation methods. This technique can be a valuable tool in the study of Fezouata Biota fossils providing better insights in their structure, internal processes and preservation.



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# MorphoDig, an open-source 3d freeware dedicated to biology

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Over the last 25 years, 3D data acquisition and computer-assisted techniques have grown increasingly popular among biologists, paleontologists and paleoanthropologists, as they have offered the opportunity to analyze the morphology of biological organisms from a whole new perspective. However, so far, no standard 3D biological model manipulation software has emerged; researchers either use commercial software which are not primarily designed for biologists, or develop their own in-house software solutions. In this paper, we present MorphoDig, a software based on the design concepts of the software FoRM-IT (Fossil Reconstruction and Morphometry Interactive Toolkit; see Zollikofer and Ponce de León 1995, 2005), the aim of which to facilitate the production and the diffusion of 3D models of biological organisms. This software provides a set of tools for editing, positioning, deforming, labelling, measuring and rendering sets of 3D surfaces. Features include: retro-deformation for un-deforming fossils/deformed specimens; point and curve primitives for placing the exact type of landmark points researchers are interested in; easy to use 3D interface for positioning and manipulating sets of surfaces and landmark primitives; advanced surface tagging, labelling and coloring possibilities (to allow for the creation of anatomy atlases); scalar computation and coloring (based for instance upon surface curvature/thickness); powerful 3D visualization features based on the VTK library. MorphoDig allows to import and export 3D meshes in standard formats such as STL and PLY. MorphoDig is based on the libraries VTK and Qt. The software can be downloaded at http://morphomuseum.com/morphodig. The sources are available at https://github.com/morphomuseum/MorphoDig.

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Speaker

# Assessing new biogenicity criteria of microfossils with high-resolution imaging techniques

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Microfossils are morphological biosignatures of microorganisms preserved in the geological record and comprise the oldest direct record of life on Earth. Their study can provide information about the palaeoenvironment and the origin and evolution of life on the planet. However, due to the high level of geological processing over billions of years, the micrometric size and the chemical composition (highly dense and homogeneous rocks), the study of such structures has been limited, and many questions about their morphology, preservation and biogenicity remain unsolved. The use of micro-analytical imaging techniques based on different physical phenomena has been proposed as a potential approach to overcome these limitations, exploring both the morphology and chemical composition of the samples in its geological and paleoenvironmental context. Here we present some challenges of using X-ray imaging to study microfossils, and also some preliminary results of Confocal Laser Scanning Microscopy, micro-CT and Ptychography in different microfossils immersed in rock matrix. Through complementary data, these techniques allowed the identification of in situ structures in a non-destructive approach, the evaluation of 3D distribution of carbonaceous organic matter, and also provided new information of the preserved cellular ultrastructure. Together, these approaches can largely contribute for stablishing more robust biogenicity criteria, that can be applied to the study of ancient controversial structures, helping refining taxonomic data and cladistics, and also recreating more accurately paleoecological and paleoenvironmental scenarios.



Speaker

# Morphofunctional 3D analysis of long bone shape variation among rhinos

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A great variation of body sizes and shapes occurs among Perissodactyla and is associated with a diversity of locomotor modes and ecological habits. This variation is reflected in the proportions of the appendicular skeleton, with strong differences between cursorial, mediportal, and graviportal forms. Here we focused on Rhinocerotoidea and explored the long bone shape variation among the five species of extant rhinos in order to highlight their specificities and to link them with the morphofunctional requirements associated with their distinct ecologies. Since extant rhinos show an important variation in body mass and size, we also analyzed and discussed the relation of shape with these parameters. This work also included closely related Perissodactyla (horses and tapirs) in order to put these data into a larger evolutionary context. The 3D geometric morphometric data were analyzed with multivariate analyses taking phylogeny into consideration. This work on modern taxa enables to better characterize the shape diversity and form-function relationships in the long bones of extant perissodactyls. The inclusion of fossil taxa then allowed exploring their resemblances in shape and proposing morphofunctional and ecological hypotheses for extinct rhinocerotoids, brontotheres, and chalicotheres.



Speaker

#### Two DIY methods for obtaining 3D images and measures of small-sized fossils

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In the computer graphics, several techniques are available to estimate three-dimensional measures of bodies. Commercial products are available for rough measures with application in prototyping and mechanical industry. A three-dimensional scanner is an expensive equipment usually precise to the micrometer level. In several fields of paleontology, estimation of surface area, volume and particular dimensions of a fossil are instrumental information. Small fossils are difficult to measure as there is no simple and cheap equipment that can achieve millimetre precision. Fossils that demand such conditions previously studied by the authors are brachiopoda from Lower Ordovician strata, Paraná Basin, Mato Grosso State, Brazil. Two adult specimens denote the presence of the lingulate brachiopods: Kosoidea (a Discinid) and Paleoglossa (an Obolid). Nonetheless, there is an extreme abundance of juvenile valves which do not show very distinctive morphological characters for the recognition of both genera. The aim of the analysis is to obtain precise information on their volumes, number of growth rings, position of the umbo and size (width, length) of the better-preserved specimens. These features could assist the differentiation between both genera. Besides, most of the specimens show deformation caused by sedimentary compaction. The analysis of the degree of the plastic deformation is also a feature that could help to determine and differentiate the genera, in their juvenile stages. In order to know these details, a threedimensional shape analysis can be obtained through several techniques, two simple of them are based on different sources of light and on different focal distances. When using different sources of light, the different shadow and light patterns can be used as intensity measure of light estimating an angle. In the focal distance technique, different distance to the focal point are estimated using edge detection. These techniques are available to be computationally applied on images in several computer packages such as Matlab and Python/OpenCV. Thus they can be used in a computer if only an simple apparatus for capturing images with different light sources and focal distances is available. The proposed work is an instruction to build an small device of this kind that poses a camera and various sources of light using light emitting diodes (LEDs) operated using an Arduino board. Such a device is made simple in order to be easily reproduced and of low cost assembly using wood, wiring, welding and basic electronics. The definition of the images (and of techniques) remains limited by the digital camera used. The devices will be tested with paleontological specimens and three-dimensional shapes are evaluated for the usability of futures studies.



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#### Tyrannosaurid-like osteophagy by a Triassic archosaur revealed through synchrotron tomography of coprolites

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Coprolites (fossil faeces) and their contents can reveal important information on trophic relations, but until recently it has been difficult to analyze the inclusions in an adequate manner. Propagation phase-contrast synchrotron microtomography (PPC-SR $\mu$ CT) has been shown to permit high-quality virtual 3D-reconstruction of the inclusions from entire coprolites, which has led to discoveries of new palaeoecological interactions. One fascinating example is from three coprolites from the Lipie S laskie clay-pit at Lisowice (Poland). The coprolite contents are dominated by fragmented bones (up to 50% of the total coprolite volumes) and crushed, serrated teeth. The coprolite sizes together with the fossil record of the site, suggest that *Smok wawelski* was the producer. Also several of the fragmented teeth are attributable to *S. wawelski* and most likely derived from the coprolite producer itself. The abundance of fragmented bones in the coprolites, bone-rich regurgatilites and bones with bite marks, all attributed to actions of *Smok wawelski*, suggest that the animal was osteophagous (bone exploiting). Osteophagy is rarely connected to extinct archosaurs, with the exception of the Late Cretaceous tyrannosaurids. Consequently, it appears that this behavior is convergent between the tyrannosaurs and this early archosaur, which lived some 140 million years earlier than the former.



Speaker

# Using neutron tomography to study fossils with poor X-ray attenuation contrast

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The advent and widespread use of X-ray computed tomography (CT) has led to a paradigm shift in our understanding of past life by providing a non-destructive means to visualize the internal anatomy of three-dimensionally preserved fossils. However, certain specimens are poorly suited to CT and its variants because they have a very similar chemical composition to the host rock. In such specimens, fossil and rock cannot be clearly differentiated because X-ray attenuation scales with atomic number and, hence, material density. As a result, this material has typically been studied using destructive approaches (i.e. serial grinding), which are both time consuming and necessitate the complete or partial destruction of the original specimens. Neutron tomography (NT) is an alternative non-destructive approach for studying CTpoor fossils. Neutron attenuation-caused by nuclear scattering or absorption-varies haphazardly across the periodic table and between isotopes, and is thus not correlated with density. Consequently, NT can potentially enable us to visualize the internal structures of chemically homogeneous samples that are not suitable for X-ray CT. To test the efficacy of NT for studying fossils, we used the new imaging and materials instrument (IMAT) at ISIS Neutron and Muon Source, UK, to image specimens belonging to a range of taxonomic groups and preservation types. The results demonstrate that NT can distinguish between fossil and matrix even in material with limited internal density contrast, revealing key details that are not apparent in CT scans. However, the maximum resolution of NT is currently inferior to that of many CT instruments, and this makes it difficult to resolve very fine structures. Future experiments will help clarify NT's strengths and weaknesses versus more traditional CT scanning, and this will aid palaeontologists in selecting the optimal technique for the specimens under study.



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#### Development of a 3D Point-based visual analytics methodology to enable virtual access and taphonomic analyses of submerged Late Pleistocene and Early Holocene cave deposits of the Yucatan, Mexico

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Researchers involved in the Hoyo Negro Project are developing and implementing novel software tools – as well as optimal workflows for digital documentation and analysis – to virtually access and interact with submerged paleontological cave deposits in Mexico. The approach enables transdisciplinary, collaborative study and interpretation of 3D data by a diverse group of scholars and stakeholders across borders and free of existing computing limitations.

Recent efforts involve the use of an extraordinarily powerful, point-rendering and visualization software platform and multiuser cyber-infrastructure, which facilitates real-time analysis and annotation of image-derived pointdata. Domain experts can conduct a range of deposit- and site-scale taphonomic or spatial analyses via a digital surrogate of the site. Rather than simply serving as models of a site and its ancient faunal remains to view and share, the full-resolution point-clouds can be manipulated by a variety of user-scripted tools. Paleontologists can, for example, mark points in 3D space and virtually extract skeletal elements to make necessary measurements or remove surrounding objects to better assess element articulation and distribution. Native image files corresponding to point regions can be readily called up for simultaneous viewing and evaluation.

The interactive, point-based visual analytics workflow has proven to be especially empowering for researchers unable to otherwise access deep and remote underwater sites. In practice, team researchers have used the models to select specimens for recovery, collaboratively plan the recov ery process, and design successful recovery vessels and tactics without ever seeing the deposits in person.



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#### Analysis of 3D comparative data for paleobiological inference: the circulatory system of a giant fossil crinoid as a case study

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While 3D imaging provides useful qualitative information on the morphology of living and fossil organisms, this approach can also facilitate the rapid collection of quantitative morpho- metric data, which can eludicate important biological processes. Here we describe an approach for investigating the allometric consequences of large body size, using the circulatory system of crinoids (Echinodermata) as a case study. Cilia-driven circulation of coelomic fluid in crinoids has been previously suggested to function in exchange processes, such as respiration or nutrient transport, for which rates are proportional to surface area. New, exquisitely-preserved specimens of the giant stalkless crinoid Decameros ricordeanus (d'Orbigny, 1850) from the Aptian of Spain reveal that the circulatory system in the central skeletal unit, the calyx, is complex and reticulate, occupying all surfaces between skeletal elements. Using X-ray microcomputed tomography ( $\mu$ CT), we reconstructed the internal anatomy of over 30 extant species of crinoid in 21 phylogenetically widespread families in order to evaluate scaling in the crinoid circulatory system. We find that coelomic surface area exhibits positive allometry with respect to body size: larger crinoids have more complex circulatory anatomy, consistent with a role of coelomic circulation in surface-area dependent processes such as gas exchange and hormone transport. Our results imply that maximum calyx size in crinoids may be limited by the capacity of the internal circulatory system. Our results highlight the usefulness of large databases of 3D morphological data for investigating limitations on body size, and more generally for rapidly accessing and analyzing previously inaccessible morphological variation.



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#### Quantifying morphological change across a mass extinction: a test of a 3D photogrammetry method using strophomenide brachiopods

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The morphology of Paleozoic strophomenide brachiopods varied with water depth and across the Late Ordovician mass extinction, but more data are needed to assess these trends and adequately evaluate evolutionary and ecological change. Quantifying this morphological variability will allow for better assessment of the characters that promote success under different environmental pressures and evolutionary regimes. Because brachiopods are predominantly sessile organisms that interact with the environment via external shell morphology, 3D data are needed to accurately capture characters such as overall shape, globosity, and ribbing.

For this project, we collected 3D morphological data from strophomenide brachiopods using the photogrammetry method Structure-from-Motion (SfM). SfM creates a high-resolution 3D model from a series of overlapping 2D digital photographs. It has been used in geomorphology, stratigraphy, geography, and archeology, but has not yet been widely applied to paleontology. We applied SfM to 300 well-preserved brachiopod specimens from 7 abundant genera within the order Strophomenida, borrowed from the Yale Peabody Museum. Tests of the method demonstrate that SfM models based on quality digital photographs can robustly resolve important external shell features in 3D. Preliminary ordination results show separations and groupings in morphospace that correspond to water depth affinity and survivorship at the Late Ordovician mass extinction.

These results improve our understanding of the relationship between morphology and environment for strophomenide brachiopods, which survived a mass extinction that removed evolutionary clades and reduced morphological variability. Brachiopods were among the most ecologically dominant organisms in Paleozoic oceans. Thus, quantifying their 3D morphology is important to interpreting the impact of extinction and evolutionary events. Using a simple, inexpensive, and field-accessible, method like SfM will make generating large data sets for robust statistical analysis possible. This will help improve our understanding of the impact of past extinction and evolutionary events on brachiopods, particularly in terms of the extent to which morphological change reflects spatial and environmental variability.



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#### Intraspecific variation in cephalopods conchs changes during ontogeny: new data from 3D morphometry of *Nautilus pompilius*

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Knowledge of intraspecific variation of organisms is of great importance because it is a prerequisite for correct taxonomic assignments, and thus biostratigraphy, biogeography, biodiversity as well as evolutionary studies. Externally shelled fossil cephalopods such as ammonoids and nautiloids have often been used for research in these fields. However, their intraspecific variation is rarely examined in detail when a new species is introduced, which often results in oversplitting. Naturally, this can produce biases affecting the above-mentioned fields of palaeobiological research. Although ammonoid intraspecific variation is sometimes discussed by palaeontologists, the number of specimens is often too low to yield statistically sufficient data. Also, many studies on intraspecific variation use only one or a few measurements per specimen without considering ontogenetic change. Furthermore, time-averaging may bias the interpretation of intraspecific variation of fossil organisms. Therefore, a no time-averaged example should be examined as a first step to understand this phenomenon in externally shelled cephalopods. In this study, we examined the intraspecific variation of Recent Nautilus through ontogeny. We applied computed tomography to 93 conchs of Nautilus pompilius from three geographically separated populations (Philippines, Malaysia and Indonesia). Measurements of whorl expansion rate (WER) and whorl width index (WWI) were taken at about 14 different ontogenetic stages from each specimen. Additionally, phragmocone chamber volume (PCV) was measured (a measure that can only be quantified using tomographic methods). Standard deviation of WER and WWI and coefficient of variation of PCV were calculated through ontogeny as measures of intraspecific variation. Our data revealed that intraspecific variation is high early in ontogeny and decreases subsequently until short before maturity in all three populations. This data was compared to those obtained from ammonoids and belemnites, it turned out that this pattern of variation is also present in the examined ammonoids and belemnites.

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# 3D tomography on an Early Jurassic coral: solving a paleontological question by non-destructive investigations

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"Mesophyllum" pseudocolumellatum, a Pliensbachian/Sinemurian coral is of scientific interest as it is a fossil that went extinct during the Pliensbachian/Toarcian transition. In addition, this cnidarian is important because of a distinctive skeletal organization; the axial structure of the corallite, with no equivalent in Mesozoic taxa, is reminiscent of the skeletal organization of some Palaeozoic rugose corals based on the occurrence of a calicular boss. Thus, two questions arise: is the apparent similarity between these two structures due to an evolutionary convergence or is this organization inherited by "M". pseudocolumellatum from a Palaeozoic ancestor? As two distinct pseudocolumella shapes can be distinguished in "M". pseudocolumellatum populations, are the two pseudocolumella shapes a result of two distinct species within the genus ? The morphological aspects of the skeleton have been assessed in order to understand the function and growth of this axial "calicular boss" as well as to describe more precisely the genus and species characters. To answer these questions, we analyzed samples with Computed Tomography X-ray scans (CT scans). The X-ray tomograph is a Nanotom Phoenix (GE) of GeoRessources laboratory in Nancy. CT scanning is a non-destructive technique used to inspect the internal structure of solid specimens based on recording attenuation levels of X-rays after passing them through a specimen. After acquisition the digital sample can be analysed (e.g., digital cross sections can be made, phases can be separated and surfaces, volumes, and orientations measured). Two samples (A57331-1 and AM16161) have been chosen for their sufficient density contrasts between skeleton and matrix. These analyses revealed the coexistence of the two distinct pseudocolumella morphologies in one sample, corresponding to two distinct stages in the life of the animal. This observation excludes the distinction of two distinct species under the genus on the basis of the different apparent pseudocolumella shapes. Moreover, the question of the link between "M". pseudocolumellatum and Palaeozoic corals is answered by the organization of the septal apparatus observed in tomography and thin sections, which points to a Scleractinian Bauplan. This is also supported by the aragonitic nature of the initial skeleton. Together, these data suggest a convergence phenomenon, leaving open the question of the functional significance of such a calicular organization.

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#### XRF imaging and spectroscopy applied to ancient life at SSRL

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Recent investment into the XRF imaging beamline 6-2 at SSRL has allowed us to significantly upgrade this rapid-scanning facility. Here, we will present an overview of the development of large object XRF imaging at SSRL, focussing especially on the most recent upgrades and improvements to beamline 6-2. This beamline has several characteristics which initially made it ideal for the XRF imaging of large objects with biochemical trace components, these include: a 54-pole wiggler source giving useful flux throughout the range 2-14 keV, a large hutch area to enable installation of a heavy duty scanning stage, custom-built electronics read-out system to enable rapid scanning, a pair of focussing mirrors with pinhole aperture to allow decimetre-sized objects to be scanned easily at 20, 50, or 100 micron resolution, and a double-crystal monochromator to allow excellent incident beam energy control which enables both the collection of X-ray Absorption Spectra at points within regions mapped and also provides the capability to map at certain critically important resonances. Because the original set-up had these characteristics, this beamline led several of the first archaeological and palaeontological studies that used rapid scanning, including the Archimedes palimpsest, Archaeopteryx, and Confuciusornis sanctus studies. An eleven year partnership between Stanford and Manchester has enabled us to plan and implement upgrades to this system that improve data quality, make the beamline more flexible, and optimize sample throughput. The upgrade was funded in 2016 and the work is now nearly complete. Upgrades include: improved X-ray detection, dynamic image resolution change, improved user interface for scan control, improved sample chamber for analyses at low incident energies, and the ability to collect a full data cube while maintaining a rapid scan rate. A set of images and spectra from the first uses of the instrument will be presented along with details of the equipment parameters corresponding to that data. These will include data from key past publications which will then be compared to the most recently collected data from this beamline in order to give practical examples of how specific instrument changes have improved data quality. Examples will include parchment with ink, sedimentary rock which retains information concerning the sediment-water interface, and fossil organisms from deep geological time.



<sup>&</sup>lt;sup>\*</sup> Speaker

#### Three-dimensional non-destructive imaging method of structural and elemental information using scattering X-rays

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1. Introduction:

The need of three-dimensional non-destructive inspection is high in the field of paleontology. Three-dimensional images of fossils can be acquired using conventional X-ray CT. However, it is difficult to analyze detail internal structures because of its low contrast, and elemental information cannot be obtained. It is expected to establish a novel imaging method which enable to measure both of the structure and the element of the fossil.

2. Purpose

The purpose of this study is to develop a three-dimensional non-destructive imaging method of the structural and elemental information of fossils using the scattering X-rays.

3. Methods

Our novel imaging method uses scattering X-rays from a sample. An experimental system with monochromatic X-rays of synchrotron radiation and a silicon drift detector (SDD) is developed to accurately observe characteristics of the scattering X-rays. The fluorescent X-rays can be measured simultaneously by setting a region of interesting (ROI) on the energy of the backscattering X-rays. Therefore, the elemental information is acquired by the back-scattering X-rays and the fluorescent X-rays. Finally, three-dimensional distribution of each element is estimated by superposing the elemental image on three-dimensional structural images by laminography CT.

4. Results

For feasibility study of the method, a fossil plate containing several fusulines was observed with our experimental system using monochromatic X-rays of 10-20-keV energy. The elemental images of the fusulines in the plate were acquired using the back-scattering X-rays and the fluorescent X-rays. In addition, three-dimensional distribution of each element was obtained by superposing the structural three-dimensional images obtained by laminography CT. The spatial resolution of elemental image by the scattering X-rays and the fluorescent X-rays was about 200 micron, and that of laminography CT was 10 micron.

5. Conclusion

The result shows that the novel method using the scattering X-rays and the fluorescent X- rays would be used for non-destructively detecting the internal three-dimensional structural and elemental information of the fossil.



Speaker

#### Virtual 3D biostratigraphy: Applications from micro-CT scan data

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In micropalaeontological studies, the recognition of the internal and/or external morphological features of microfossils is essential. However observations in light microscopy have some limitations: (1) it is often impossible to extract microfossils from indurated facies, (2) the manufacturing of oriented thin sections is time consuming, and (3) the process results in the destruction of the sample. The microCT scan provides a promising alternative, which is already employed for the study of foraminifera released from the rock by disaggregation. It is non-destructive, and provides a large range of 2D and 3D images.

The present study focuses on the analysis of rock samples containing various microfossil groups (ostracods, benthic foraminifera and Dasycladales algae). The objective of the study was to develop and improve the imaging and the taxonomic determination capabilities of our in-housesoftware SISMAGE® of selected microfossils contained in indurated rocks, and get an overview of the impacts of various lithologies on microCT scan imaging.

By testing different imaging methods, the most effective techniques to visualize the morphological characteristics are proposed for each group of fossils and each facies type. Internal and external structures can be distinguished in CT scan imaging with a  $2\mu$ m resolution, as long as they are larger than  $5\mu$ m. When mineralogy (~density) of fossil and matrix are similar, only the extraction by manual segmentation is effective. In the other cases the use of automatic segmentation methods is more relevant. The microscopy study of thin sections shows that siliceous cements are clearly discriminated from calcitic areas in CT scan Imagery, so they do not affect the extraction of fossil unlike calcitic cements. The possibility to easily orientate 2D sections and/or extract 3D morphology allowed to confirm the ability to recognize key morphological criteria for a determination at specific levels resulting in accurate age determination.

The perspectives of the Virtual 3D biostratigraphy project include: (1) dedicated analyses of benthic foraminiferal assemblages with complex internal features in indurated rocks (oriented sections), (2) semi-automatic recognition of bioclasts to contribute to the characterization of facies and/or depositional environment (3D Fossil Atlas), and (3) the capitalization of collection material to be shared with the scientific community.



Speaker

#### Deep insight into natural history specimens: The 3D Lab of the ISYEB Institute (MNHN/Sorbonne Universités)

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The rise of analytical techniques related to the use of 3D methods in natural history and paleontology led us to develop a 3D imaging reconstruction lab in the MNHN Systematics Institute (ISYEB). This rise is due to the increased use of scanning platforms such as CT-Scan, as that of MNHN (AST-RX) and the implementation of 3D methods in microscopy (fluorescence, confocal laser, OCT, structured light-Apotome), some of which are accessible in MNHN platforms, and a large part of the tomography methods derived from synchrotron light (synchrotron SOLEIL and ESRF Grenoble in France).

The work of this 3D lab mainly concerns fossils in amber or compression (insects and plants) but also multidisciplinary work on the evolution of wing structures in insects, plant conservation, etc.

We present some published and ongoing results of research programs in paleontology of invertebrates using 3D reconstruction techniques, whether in the amber collections or the compression fossils collections of the MNHN. The future of these methods is also discussed including a program of digitalization of collection specimens and the study of key specimens of the MNHN's collections, pedagogy through E-learnig programs and virtual museography.

We believe that these methods are important bridges between biosciences and geosciences, of which paleontology is the interface par excellence.



Speaker

#### First digital cranial endocast of the "horned armadillo" *Peltephilus* (Mammalia: Xenarthra): Neuroanatomy and morphology of the caudal cranium

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The Peltephilidae or "horned armadillos" were a group of cingulates ("armored xenarthrans") that notably differ from typical dasypoid armadillos. Peltephilids are recorded exclusively in South America from the Eocene to the Miocene; skulls are known from the Oligocene and Miocene. We provide the first description of the cranial endocast of Peltephilus Ameghino YPM PV 15391 (early Miocene of Patagonia, Argentina), based on a three-dimensional reconstructions of the brain and ear region extracted from highresolution X-ray computed microtomography imagery. We describe the olfactory bulbs, cerebrum (including fissures and sinuses), cerebellum, and we calculate their relative volumes. We identify the morphological origins of cranial nerves I, II, V, VII, VIII and IX. The neuromorphology of Peltephilus is similar to that of Dasypodidae as revealed by endocasts. However, the cerebral hemispheres of Peltephilus exhibit a pronounced convexity towards the parietal region and a marked widening caudally, indicating a more expanded neocortex and pyriform lobe. We also describe the inner ear (bony labyrinth, including cochlea, vestibule and semicircular canals) and the middle ear (malleus, incus and stapes). We describe the caudal cranium (basicranium and overlying cranial vault) in regard to suture placement and trackways for blood vessels and nerves. According to current phylogenetic reconstructions, peltephilids are the earliestdiverging cingulates for which cranial information exists. Our detailed description of this taxon will help to illuminate character evolution within Cingulata.



<sup>&</sup>lt;sup>'</sup> Speaker

# ATLAS 3D: a bridge project between research and teaching in palaeontology

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The use of 3D imaging techniques is nowadays widespread in palaeontological research and offers new opportunities to prepare demonstrative figures for publication, and tools to animate images for communication. Although the value of 3D technologies is fully demonstrated in research, it remains poorly explored for teaching biology, geology and palaeontology in the University undergraduate programs.

We developed the project ATLAS 3D (Sorbonne Université, FormInnov project): an interactive pdf of 3D objects commonly studied when teaching Natural Sciences including palaeontology. The transfer of research expertise to education is expected to improve the way students can learn and increase their skills. Examples of objects already available in ATLAS 3D include microfossils (foraminifers), cephalopods, cnidarian, brachiopods. ATLAS 3D can be used with an open access software (Adobe Acrobat Reader), allowing the user to navigate through the object using slicing tools. The anatomical structures can be selected and therefore viewed independently, allowing for example to highlight differences between the external skeleton/shell and internal cavities or structures. Pre-selected views can also be recorded by the teacher in order to label or comment anatomical features.

At the hinge of recent research in palaeontology and museography, this tool is designed to increase the autonomy of the students and ease the understanding of anatomy.

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Speaker

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#### Understanding the systematic relationships of Devonian spores from integrated studies using light microscopy, SEM, TEM ultrastructure and nanotomography

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Nanotomography has been widely applied in palaeontology although mostly on mineralised material that is still within the rock matrix. There have been a few initial applications that have used these methods in palynology but generally not as a systematic tool. Here we show how nanotomography is best utilized in conjunction with classical light microscopy and TEM. Nanotomography permits a 3D imaging of the structure, whilst the TEM enables comparison of ultrastructure at a finer scale. All of this imagery can be integrated with classical light microscopy and SEM.

The application will be demonstrated using exceptionally well preserved and low thermal maturity Late Devonian material from the Russian Platform. This includes material from the type locality of *Kryshtofovichia* which has megasporangia containing *Nikitinsporites* and microsporangia with the monolete microspore *Archaeoperisaccus*. This material had been thought lost but has been rediscovered in the collections of the Komarov Botanical Institute. The nanotomography has provided images of sufficient resolution and contrast make 3D interactive images and reveals a structure unique to Devonian megaspores- the androtheca. The TEM ultrastructure of *Nikitinsporites* and *Archaeoperisaccus* is different. The megaspores have an ultrastructure similar to that of *Archaeopteris*. In contrast, the microspore *Archaeoperisaccus* has a different ultrastructure of lamellae that become more loosely packed in the outer wall layer. This also differs from the ultrastructure in other species of *Archaeoperisaccus*.

It is that integration of these microscopical methods that has now enabled us to go beyond the limits of light microscopy and reveal the complexity of relationships with Devonian plants groups including hitherto unrecognized morphological convergence.



Speaker

#### Digital cranial reconstruction and intraspecific appendage variability in *Decennatherium rex* (Ruminantia, Pecora)

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Non-destructive 3D reconstruction techniques allow for visualization and interpretation of distorted, damaged, or even incomplete specimens. Digital 3D models are widely utilized in paleontology. The remarkable fossil collection from the Vallesian of Cerro de los Batallones fossil complex (Los Batallones butte; Madrid Basin, Spain) includes a large number of associated skeletons, posing it as a unique opportunity to study intraspecific variability. Here we report an updated 3D reconstruction of the cranial anatomy of Decennatherium rex. D. rex is the only giraffid described from the butte thus far and is considered the earliest known species with evidence of the Sivatherium ossicone plan formed by a pair of long and curved posterior ossicones and a couple of smaller anterior ones. The cranial remains, collected in Batallones-10, includes three complete skulls and six calvaria, and can be associated with two sexuallydimorphic groups. The sample includes individuals with extensive taphonomic deformation along with others that are nearly incomplete. Each skull element was 3D digitized with a laser surface scanner. The obtained meshes were retrodeformed and modified in Blender and ZBrush. The presented methodology uses bilateral symmetry to correct affine non-isometric deformations and mesh mirroring of missing parts. Finally, a 3D geometric morphometric analysis has been performed to describe the morphospace across the studied sample and estimate their original morphology by correcting non-affine non-isometric deformations. Integrated 3D digital reconstruction is reproducible, non-invasive, and shows the potential utility for anatomical descriptions in fossil species



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<sup>&</sup>lt;sup>'</sup> Speaker

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# Novel observations on the economic significance of radiolarians

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During the recent intensification of shale gas exploitation in China a close association between radiolarians and hydrocarbon-bearing black shales has been noticed. The siliceous skeletons of radiolarians, along with their organic matter and symbiotic algae are all of economic importance, as they can become essential components of gas-producing shales. Radiolarian skeletons are brittle and their biogenic quartz increases the fracability of these tight shales. The abundance of radiolarians not only serves as a proxy for the primary production, but also contributes to the organic content. However, there has been little study exploring the controlling factors behind the co-occurrence of radiolarians and hydrocarbon-bearing shales globally. Sixteen samples containing abundant radiolarians were collected from the Upper Ordovician Wufeng Formation in the Sichuan Basin. This unit is currently a primary target for shale gas exploration in China. Radiolarians preserved as siliceous spheres constitute up to 40% of rocks observed in thin section. Many skeletons infilled with carbonaceous material showing exceptional preservation of internal skeletal features can be observed in the thin sections. The siliceous black shales of Wufeng Formation were deposited around the Ordovician-Silurian boundary and represent a prolonged oceanic anoxia event. Radiolarian-bearing black shales from the Wufeng Formation provide us with a valuable opportunity to investigate how tectonics, sea level change and oceanic chemistry may have affected the bloom of radiolarians and the formation of siliceous hydrocarbon-rich black shales. Moreover, the well-preserved radiolarians with unusual carbonaceous infillings provide us with an excellent opportunity to experiment with micro-imaging techniques such as in-situ 3D X-ray micro-computed tomography ( $\mu$ -CT) and confocal laser scanning microscopy.



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<sup>&</sup>lt;sup>•</sup> Speaker

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#### μ-CT investigation of well-preserved Middle Cambrian radiolarians

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A radiolarian assemblage was extracted using acetic acid from limestone concretions of the Inca Formation, Georgina Basin, Australia. This unit is of Middle Cambrian (Epoch 3) age and contains one of the best-known occurrences of the earliest well-preserved radiolarians. Due to the complex spicular composition of many radiolarians in the Middle Cambrian, detailed observations with traditional scanning electron microscope (SEM) and transmitted light micro- scope (TLM) imaging methods can be challenging. Exceptional preservation presented us with a rare opportunity to perform a detailed investigation with 3D X-ray micro-computed tomography ( $\mu$ -CT) in order to examine fundamental structures amongst the primitive morphology of these first radiolarians. Here we report the  $\mu$ -CT results of two well-preserved Middle Cambrian radiolarians Archeoentactinia incaensis and Archeoentactinia tetractinia, previously assigned to the family Archeoentactiniidae by Won and Below (1999). The individual spicules that make up the skeletons were separated and analysed in detail. The skeletal units can be identified exclusively as tetractine spicules, which conforms to the diagnosis of the family Echidninidae. Both specimens consist of a subspherical basal framework made of fused robust to relatively robust tetractine spicules and a threedimensional meshwork constructed by the fusing of smaller tetractine spicules of various sizes and orientations. The sphericity of each specimen was tested digitally and using 3D printed models. In both specimens, among the spicules that make up the basal framework, central points of the robust primary spicules lie perfectly on a spherical surface. Relatively robust secondary spicules lie slightly above this spherical surface. In Archeoentactinia incaensis, no skeletal elements intrude the spherical cavity. In Archeoentactinia tetractinia, due to the more angular configuration of the framework, more skeletal elements lie within the internal sphere. Observations made using  $\mu$ -CT techniques clearly provide new opportunities to better understand the family Archeoentactiniidae and the evolution of the earliest radiolarians.



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#### Detailed three-dimensional modeling of paleontological samples using combination of synchrotron-based fine CT and 3D printings techniques

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Synchrotron-based micro computed tomography (Micro CT) provides a way to perform detailed non-destructive three-dimensional observation of samples with micron-order, because the intensity is much higher than that of conventional X-ray sources. In addition, phase-contrast X-ray imaging having 1000-times higher sensitivity compared with that of absorption (conventional) imaging can be performed by using the small divergence and monochromatic synchrotron X-ray. Aiming at detailed three-dimensional analysis and modeling of paleontological samples, we combined the synchrotron-based imaging and 3D printing techniques.

Micro CT measurements were performed using pink X-rays monochromatized by metallic filter at the beamline BL 07 of Saga light source in Japan. The average energy of X-ray was 25 keV, and the band width of the energy was 5 keV. X-ray imager composed of a scintillator, optical lens system, and sCMOS image detector was used to detect transmitted images. Fine three-dimensional images of microfossils were successfully obtained with only 100-sec total measurement period. The spatial resolution calculated from the line profile in the sectional image was estimated as 2-micron. Finally, a three-dimensional model created by conventional 3D printing machine with obtained data showed detailed surface and inner structure.

Phase-contrast X-ray imaging was performed using monochromatic X-ray at the same beamline of the Saga light source. Phase map showing the spatial distribution of phase-shift caused by sample were detected by diffraction-enhanced method using many images (DEIM). Fine threedimensional image of an insect embedded in amber was successfully obtained nondestructively. Finally, we also modeled the detailed insect by 3D printing technique with the phase-contrast CT data set. These result indicate that the modeling technique will be a powerful tool for three-dimensional analysis of paleontological samples.



Speaker

# S17 - Fossils and Recent, molecules and morphology: dialogs in phylogenetics

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# "The One Tree": Testing for bias in paleontological systematics

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There are more possible bifurcating trees for even small numbers of species than there are atoms in the visible universe. Yet an evolutionary process behind biodiversity hypothesizes that only one or few of these accurately represent the historical patterns of ancestry shared among living and fossil species. Subsets of this tree of life (e.g., vertebrates and in particular mammals) are now better understood and well-corroborated by diverse lines of evidence than ever before. In this presentation, I take advantage of well-corroborated phylogenetic hypotheses for living and fossil vertebrates to test the extent to which certain kinds of data (e.g., hard-tissue) are subject to bias. For example, do hard-tissue characters typically available among fossils mislead paleontologists to place taxa closer to the root than they actually are? This can in principle occur, but the uniquely well-corroborated topology now available for at least some vertebrate groups (e.g., mammals) contradicts claims that such effects are ubiquitous. Fossilization does indeed strip away valuable phylogenetic information. However, its ubiquitous effect on topologies with fossil taxa is uncertainty, not bias.



Speaker

# Proteomics and systematics in paleontology-going backward, looking forward

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Systematic paleoproteomics-reconstructing phylogenetic relationships utilizing ancient protein sequence information-is emerging as a new molecular tool in paleontology. In theory, structural proteins should degrade and lose sequence integrity at a slower rate than DNA, thus extending in principle the time range within which authentic molecular information might be recovered. However, although claims continue to be made regarding identification of endogenous proteins in truly old fossils (e.g., Cretaceous dinosaurs), most verifiable success stories involving recovery of high-quality sequence information come from material no older than mid-Pliocene (current proteomics record, 3.5 My). Although this is a considerable advance over the current aDNA record (~700 kyr), the goal is to achieve much greater time depth. Using examples from current research, the problems and possibilities of systematic paleoproteomics will be discussed, with special reference to: (1) issues relating to extraction methods and analytical tools (e.g., lack of standardization), (2) significance of preservational contexts (e.g., ostrich eggshell, bones in permafrost, tar seep fossils); (3) application of collagen Ia 1 and Ia 2 sequence information to higher-level systematic problems (e.g., meridiungulates, afrotherians, folivorans); and (4) future prospects (more databases, faster processing, better grasp of taphonomy). In connection with this last point, for systematic paleoproteomics to realize its potential it will be important to build databases for a variety of bone proteins, not just collagen.



Speaker

## Estimating diversity and diversification using fossil occurrence data

Tobias Andermann \*<sup>+1</sup>, Rachel Warnock<sup>2</sup>, Alexandra Gavryushkina<sup>3</sup>, Tanja Stadler<sup>2</sup>, Alexandre Antonelli<sup>1</sup>, Daniele Silvestro<sup>1</sup>

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Present biodiversity represents a snapshot of a very long and complex evolutionary history, during which species and entire clades have originated, diversified and -to a large extent- gone extinct. Reliable estimates of the processes that have shaped diversity through time are crucial to understanding present biodiversity patterns and the factors that may affect global and local species richness. Both fossil data and phylogenies of extant taxa are commonly used to quantify diversification processes, particularly speciation and extinction rates. However, the speciation and extinction rates inferred from paleontological versus neontological data are often strikingly different. This is remarkable, since the fossil record of a clade and the phylogeny of its living species are samples of the same underlying evolutionary process. In particular, past diversity is commonly underestimated from empirical phylogenies in comparison to the true extinct diversity observed in the fossil record. We show here that these discrepancies are partly driven by different implicit assumptions about the processes of species diversification, which alter the interpretation of speciation and extinction rates inferred from fossils or phylogenies. We argue that this often- neglected discrepancy should be modeled explicitly when attempting to integrate the two data types in a single framework, for instance, when using a single birth-death process encompassing both extant and extinct species. In addition, biases in taxon sampling may complicate the comparability of fossil and phylogenetic estimates of diversification rates. We demonstrate the implications of these issues by analyzing the complete mammalian fossil record. We use a Bayesian method to infer extinction dynamics of mammals during the recent past (since the Late Pleistocene), and find strong evidence of a recent dramatic increase of extinction rates across all major lineages of mammals, although different extinction dynamics characterize each clade. These results suggest that current birth-death models, which generally assume constant rates and positive net diversification, may be inadequate to infer divergence times and diversification in the phylogeny of extant mammals, and potentially many other clades.



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# Homoplasy and correlation of morphological characters in birds and reptiles relative to molecular phylogeny

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Despite increased use of genomic data in phylogenetics, morphological information remains important for resolving evolutionary relationships, in particular for fossil species for which molecular data is unavailable. However, selection and evolutionary lability can make some morphological characters more prone to homoplasy than others. Moreover, when these characters evolve in semi-autonomous modules, they have the potential to overwhelm genuine phylogenetic signal contained within the data. Here we investigate homoplasy and correlation of morphological characters relative to molecular trees. Meta-analysis of 27 avian and squamate morphological datasets finds that finds that non-osteological characters (plumange, myology etc.) are less consistent with molecular data than osteological characters (p< 0.001). We also identify differences in the distribution of pairs of correlated characters across the morphological partitions. This finding offers reassurance to palaeontologists building phylogenies of birds, dinosaurs and other reptiles, as the more readily fossilizable characters are those found to be more consistent with molecular trees.



Speaker

#### First skeleton of a flying squirrel and a new timecalibrated phylogeny of the group combining molecular and morphological data

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Gliding has evolved independently several times in mammalian evolution. However, flying squirrels (Sciuridae, Sciurinae, Pteromyini) are the only group of gliding mammals to have achieved a significant diversity (52 species in 15 genera) and wide geographical distribution, occurring in Eurasia and North America. Yet their evolutionary history is insufficiently known, to the point that estimates on their time of origin as derived from paleontological and molecular data blatantly disagree. While for most mammal clades molecular-based estimates yield older dates, for flying squirrels fossil evidence exceptionally suggests a much older divergence time (ca. 36 Ma) than most molecular phylogenies (23±2.1 Ma). This discrepancy might derive from the identification of extinct flying squirrels exclusively based on dental features, which, contrary to certain postcranial characters, are not unique to them. Therefore, postcranial material of fossil taxa is of utmost importance to clarify the assignment of extinct 'flying' squirrels and calibrate their divergence date from other sciurids. Recently, a partial skeleton attributed to the Miocene flying squirrel Miopetaurista neogrivensis was recovered from Catalonia (Spain), with an estimated age of 11.6 Ma. The recovered remains were found partly articulated and comprise elements of the limbs that display the diagnostic gliding adaptations shared by extant pteromyins. The wrist bones show the unique features related to extend and support the patagium and further indicate that Miopetaurista belongs to the large-sized flying squirrel clade. This new fossil evidence allows for a recalibration of the divergence date between tree and flying squirrels using two independent phylogenetic approaches, total evidence and node dating analysis. Both methods provide older estimates for this event (more likely around 31–25 Ma) which are still consistent with previous molecular studies and further suggest that fossils older than 31 Ma likely do not belong to the flying squirrel lineage. Perhaps not surprisingly, these oldest fossil occurrences are separated by a gap of several million years from other putative flying squirrel records, which date back to the Oligocene/Miocene transition. In addition, total evidence analysis recognizes Miopetaurista as the sister taxon of the extant Petaurista, their striking morphological similarity further showing that giant flying squirrels have undergone little evolutionary change for almost 12 million years.

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# Fossils, molecular dating and arthropod terrestrialisation

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Modern phylogenies of the arthropods predict that terrestrialisation has independent origins in the most recent common ancestors of all extant myriapods, arachnids and hexapods, as well as within the "crustaceans". Phylogenomic-scale analyses strongly support the monophyly of Myriapoda and Hexapoda, and arachnid monophyly, though sensitive to analytical methods, is also recovered under optimal conditions. Myriapod and arachnid monophyly imply a single origin of terrestrial adaptations shared by extant members of those groups. Transcriptome- based phylogenies have offered support to new hypotheses for some of these adaptations, such as homology of book lungs in scorpions and tetrapulmonate arachnids, and has allowed some unexpected groupings from early molecular analyses (such as Edafopoda within the myriapods and Nonoculata within the hexapods) to be rejected in favour of classic morphological clades. Fossil-calibrated time trees reconstruct Cambrian divergences between the major crown-group myriapod and arachnid lineages, substantially predating the appearance of body fossils in the Silurian. The Cambro-Ordovician trace fossil record partly fills this gap, as do candidates for aquatic or amphibious stem groups in the Cambrian. Recent time trees for land plants that infer Cambrian origins allow that terrestrialisation of arthropods may have been possible earlier than the spore or body fossil records have predicted.

Speaker

#### Patterns of morphological variation of the skull in extant Manidae (Pholidota) and phylogenetic implications for extinct pangolins

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Pangolins are one of the most endangered groups of living mammals. The order Pholidota comprises only eight extant species, divided into three genera, restricted to Africa (Smutsia and Phataginus) and Asia (Manis). However, several fossil representatives of the group are known from the Holarctic region, including remains of skulls of Patriomanis americana, Eomanis waldi, Eurotamandua joresi or Leptomanis edwardsi. Despite several works dedicated to skeletal anatomy, the morphological variation of the skull in extant Pholidota is yet to be assessed with modern geometric morphometric methods. Here, we present the first comprehensive study on the morphology of the pholidotan skull comprising seven out of the eight living species. With 241 museum specimens, our sample is the most comprehensive ever assembled, and it almost entirely covers the historical geographical range of these species. We performed geometric morphometric analyses based on 75 homologous landmarks on the skull. Missing landmarks were estimated with thin-plate spline reflection. The landmark set was then Procrustes-aligned and regressed against centroid size to check for contrasting allometric trajectories. Aligned landmarks were projected into principal component morphospace to visualize the variability of the skull shape. Our analysis reveals clear morphological discrimination between recent genera, with Asian species being closely grouped while tree and ground African pangolins present rather distinct shapes. We found evidence supporting inter- and intraspecific variation patterns recovered by molecular analysis. We further integrated a molecular phylogeny in the morphospace to estimate the shape of ancestral nodes within Manidae. An additional principal component analysis including fossil specimens (e.g., L. edwardsi) was run with a reduced landmark dataset. Additionally, we compared extant and extinct taxa and identified several new diagnostic discrete characters to differentiate between closely allied clades. Overall, our study allowed the detection of a number of diagnostic features that shed new light on the potential phylogenetic affinities of extinct pangolins. We discuss the affinities between extant and extinct Holarctic, Afrotropic and Indomalayan pholidotan taxa, and explore the morphological evolution of the group from the Middle Eocene to present days.

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IPC 5

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#### A new gobiiform phylogeny - integration of morphological and molecular data

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Gobiiformes are one of the most species-rich groups among the bony fishes, with countless adaptations and specializations, such as the symbiosis of certain gobies and shrimps or the mudskippers' amphibious lifestyle. They constitute a significant component of fish faunas in freshwater, brackish and marine habitats all over the world. Relative to their high current diversity, with more than 2300 species, the fossil record of this group is comparatively limited, with only about 130 described species. The phylogeny of extant gobiiforms is well resolved, based on molecular genetic data. In contrast, morphological data have never been used to reconstruct the phylogeny of the whole group. However, the assembly of a morphological matrix and recognition of synapomorphies is crucial for the placement of fossil gobiiforms on the phylogenetic tree. We have therefore constructed a morphological character matrix containing data for fossil taxa and representatives of all eight recent families. We analysed this dataset separately, and in combination with molecular sequence data (the "total evidence" approach). Our results show that the phylogeny based solely on morphology supports some of the patterns seen in molecular phylogenies, suggesting that some gobiiform families are supported by morphological synapomorphies. Below the family level, morphological data alone did not provide sufficient resolution in all cases, possibly due to similarities in lifestyle and associated evolutionary convergence. Results of our total evidence analysis show that this approach allows one to integrate fossils into the phylogeny of extant taxa with confidence at the family level.

Speaker

# On the use of the Mkv model for inferring phylogenies from discrete morphological data

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The increasingly common use of the Mkv evolutionary model to infer phylogenies from morphological data has often resulted in disagreement with results previously established via parsimony. A key difference between the Mkv model and parsimony is the homogeneity assumption: in the Mkv model, the probability of change for every character increases at the same branches of the tree by the same exponential factor (the "length" of the branch). Such an assumption may be justified for molecular data, but in the case of morphology it has never been explicitly justified or tested, and consideration of synapomorphy distributions in different taxonomic groups suggests that it does not apply to real morphological datasets. The present paper discusses this issue, and illustrates it by reference to a set of 13 empirical datasets. Statistical hypothesis testing allows rejecting the Mkv model with a high degree of confidence for most of these datasets. These results suggest that the Mkv model is not a good assumption for these datasets, and it should not be used for analysis of morphology.



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# High ratios of morphological:molecular evolutionary rate post-dating the origin of crown Placentalia

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A consistent and thorough understanding of the macroevolutionary patterns surrounding early placental mammal evolution has been hampered by conflicting reconstructions from different data sources. Despite almost all dating analyses, whether derived from molecular clocks or statistical interpretation of the fossil record, supporting a Cretaceous origin for the crown group, no unambiguous Cretaceous placental mammal has been discovered to date, and contention remains over the timing of the origin of the crown orders within Placentalia. If different data sources are demonstrating different signals, investigating the relationship between these signals might clarify some aspects of early placental evolution. Here, using a combined morphological (748 characters) and genomic character matrix for 248 therian genera (57 extant), we conduct a total-evidence phylogenetic analysis. Partitioned rates of evolution among the morphological and molecular partition show distinct patterns across the tree and demonstrate that, independent of reconstructed divergence times, morphological rates of evolution were exceptionally slow relative to molecular rates on those branches leading to Placentalia and several subgroups (eg Atlantogenata, Euarchontoglires, Eulipotyphla, Scrotifera), while those leading to several of the crown orders, as well as to the superorders Afrotheria and Xenarthra, exhibit very high morphological:molecular rate ratios. On the basis of recent independently-derived divergence date estimations, these patterns are broadly congruent with low morphological:molecular rate ratios in the Cretaceous and higher ratios on those branches crossing the end-Cretaceous mass extinction. By allowing rapid anatomical change without an unreasonable increase in molecular evolutionary rate, and by supporting the idea that Cretaceous crown eutherians may not have been easily morphologically distinguished from their near stem relatives, this observation provides an avenue for reconciling the fossil record with molecular divergence estimates for Placentalia.



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<sup>&</sup>lt;sup>°</sup> Speaker

#### A Cambrian weird wonder suggests a sessile, filter feeding, polyp-like origin for ctenophores

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Ctenophores are a phylum of mainly pelagic, predatory metazoans. Their bodies are clad with eight rows of large compound cilia, called comb rows or ctenes, which are used in locomotion and have no counterpart elsewhere in the animal kingdom. Despite being clearly delineated from other metazoan groups and unequivocally monophyletic, the origin of ctenophores and their body plan remains obscure. This is due to their uncertain position in the animal tree of life, heterogeneous amino acid compositions, relatively recent (latest Palaeozoic or early Mesozoic) crown group origin and sparse fossil record. Fossil ctenophores from the Cambrian reveal disparity early in their history, including numbers of comb rows exceeding that in extant taxa and the presence of an organic skeleton in 'scleroctenophores'. We describe material of a new taxon, similar to Dinomischus, from the early Cambrian Chengjiang Lagerstätte of Yunnan Province, South China. Preservation in oral view reveals a single central mouth opening as well as a blind gut that is partitioned by mesenteries in lateral specimens. The radially arranged circum-oral tentacles are clad with soft, paired sets of pinnules; each with a row of stiff filamentous structures interpreted as large compound cilia (diameter = 19-25  $\mu$ m). Ciliary structures of this size are unique to ctenophores in the tree of life. We demonstrate that together with a greater suite of Cambrian taxa we can infer homology of the dinomischiid tentacles and the ctenophore comb rows, which display a consistent anatomical arrangement across taxa with otherwise divergent morphologies. Recent phylogenomic analyses of animal relationships have recovered ctenophores in numerous phylogenetic positions including as the sister group of all other animals and as the sister group of a clade of cnidarians and bilaterians. Our new discovery highlights potential cryptic homologies shared by cnidarians and stem-group ctenophores, including circumoral feeding structures and a gut partitioned by mesenteries. In our phylogenetic analysis we recover a cnidarian ctenophore clade (Coelenterata), and infer a polyp-like body plan in their common ancestor. However, Coelenterata is not commonly recovered by molecular analyses and depending on the precise placement of ctenophores relative to other eumetazoans, some of the features we identify could instead be eumetazoan plesiomorphies. Despite this uncertainty, if these characters represent true homologues shared with cnidarians they would be difficult to reconcile with a placement of ctenophores as the sister group of all other animals.



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#### Novel approaches for phylogenetic inference from morphological data and total-evidence dating in squamate reptiles (lizards, snakes, and amphisbaenians)

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Here, I combine previously underutilized models and priors to perform more biologically realistic phylogenetic inference from morphological data, with an example from squamate reptiles. When coding morphological characters, it is often possible to denote ordered states with explicit reference to observed or hypothetical ancestral conditions. Using this logic, we can integrate across character-state labels and estimate meaningful rates of forward and backward transitions from plesiomorphy to apomorphy. I refer to this approach as MkA, for 'asymmetric.' The MkA model incorporates the biological reality of limited reversal for many phylogenetically informative characters, and significantly increases likelihoods in the empirical data sets. Despite this, the phylogeny of Squamata remains contentious. Total-evidence analyses using combined morphological and molecular data and the MkA approach tend toward recent consensus estimates supporting a nested Iguania. However, support for this topology is not unambiguous across data sets or analyses, and no mechanism has been proposed to explain the widespread incongruence between partitions, or the hidden support for various topologies in those partitions. Furthermore, different morphological data sets produced by different authors contain both different characters and different states for the same or similar characters, resulting in drastically different placements for many important fossil lineages. Effort is needed to standardize ontology for morphology, resolve incongruence, and estimate a robust phylogeny. The MkA approach provides a preliminary avenue for investigating morphological evolution while accounting for temporal evidence and asymmetry in character-state changes.



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#### Morphology and homoplasy down-weighting performs selectively across turtle clades in combined molecular phylogenetic analyses

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The first total evidence analysis of tortoises (Pan-Testudinidae) is presented here, combining previous and novel morphological datasets with fossil data and published molecular information. Parsimony analysis of this dataset and identification of wildcard taxa between molecular and morphological topologies demonstrates that the conflict between these topologies is largely due to two aberrant taxa in which the deviant features make certain characters either inapplicable or conflicting with more conventional taxa. This indicates that morphology is otherwise a powerful tool for phylogenetic reconstruction within extant and extinct Testudinidae. The total evidence topology is congruent with the molecular topology and recovered two clades of crown- Testudinidae: Testudona and Geochelona. The inclusion of extinct species revealed that fossil and published molecular divergence dates agree: Testudona and Geochelona diverged at latest by the Late Eocene and the age of crown Testudo is Late Miocene. The inclusion of fossils allowed a refined ghost lineage analysis which estimates high rates of diversification during the Late Eocene and Miocene onwards and implies no major decline during the Neogene and Quaternary. Analysis of continuous carapace-length data demonstrates that giant body size independently evolved in multiple continental mainland taxa and is not linked to insular effect. These patterns appear to be independent of topological changes resulting from homoplasy down-weighting (implied weighting). In contrast, phylogenetic resolution with morphology in other clades of turtles (e.g., extant and extinct trionychids, geoemydids, and cryptodires in general) using expanded datasets remained in major conflict with molecular topologies but only when the full skeleton is sampled for characters. In pan-trionychids (softshell turtles), implied weighting combined with molecular backbone constraint yielded better estimates of phylogeny than equal weighting because of significantly greater congruence with stratigraphy. The utility of morphological data and homoplasy down-weighting is therefore clade-specific even within a moderately diversified group, such as that of turtles (ca. 300+ extant species).



<sup>&</sup>lt;sup>'</sup> Speaker

# Frog shells through time: a dialogue between mitogenomics and Palaeontological data

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Frog shells (Bursidae, Tonnoidea,) are a rather small monophyletic family (59 species) of highly dispersive marine gastropods with poorly known phylogenetic relationships and a poorly defined fossil record, with an origin around the Bartonian (~40Ma). Strongly ornamented, hence potentially bearing numerous shell characters, contrary to many other molluscs, bursids are a good model for comparing and combining morphological and molecular data in a phylogenetic context. We reconstruct a phylogeny covering 70% of the accepted Recent and fossil species. At first we analyze separately a molecular dataset (partly based on complete mitochondrial genomes) and a shell character dataset, then combine both in a single total-evidence analysis. This analysis leads to reconsider the genus limits in the Bursidae, in particular to eliminate the non-monophyly of Bursa, necessitating the erection of four new genera. A calibrated timetree is reconstructed using 21 node and tip calibrations. Comparison of divergence events with climatic curves suggests a link with Paleogene thermal maximum (both hot and cold). Additionally, the inclusion of the fossils sheds new light on the historical biogeography of the family, otherwise hidden by considering extant species only. One of the particularities of this work lies in the constant dialog between morphological and molecular approaches and between extant and extinct taxa. At each step, taxonomic hypotheses emerging from molecular analyses allow a reinterpretation of morphological characters, especially by modifying primary hypotheses of homology. Conversely, morphological approaches, especially on fossils, consolidate hypotheses resulting from the analyses of the molecular characters, allowing us to propose a timetree based on a robust analysis of bursid paleodiversity.



Speaker

#### Improved phylogenetic inference from morphology: data from recent crocodilians

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Estimating phylogenies correctly is vital in modern macroevolutionary palaeobiology. For extant taxa, DNA sequences can be increasingly reliably and accurately used for phylogenetic inference: datasets are ever larger, analytical techniques improved, and phylogenies correspond to other data (e.g. biogeography). For fossil taxa DNA is absent, so morphological hypotheses of apomorphy in the form of discrete character matrices continue to be used to infer phylogeny. However, the accuracy of these methods is questionable: DNA and morphological phylogenies often disagree for extant taxa, and convergent and strongly divergent morphological evolution often mask phylogenetic signal. To address this problem, the correspondence of morphological characters from a recent dataset to a DNA-based phylogeny for extant crocodilians is investigated, and a new phylogenetic tree based on an improved morphological dataset presented. The homoplasy of different groups of morphological was compared using a Mann-Whitney U test on three homoplasy metrics (consistency, retention, and rescaled consistency index). Cranial characters were found to be significantly (p=0.05) less homoplastic than postcranial characters; this may be due to lower functional selection on the cranium, but may also represent scientific effort having focused on the cranium. Braincase characters were not significantly less homoplastic than other characters, but sample size was small. Characters were grouped as "robust" and "non-robust" following first hand observation, based on whether they (1) fitted the matrix scoring, and (2) their states were clearly distinct/homologous. Robust characters were significantly (p=0.01) less homoplastic than other characters, indicating that if morphology is analysed carefully and appropriately it can yield phylogenetic signal. Reanalysis of the dataset using only robust characters placed Tomistoma (false gharial) with Gavialis (gharial) together as the sister group to other extant taxa. Although closer to the DNA phylogeny, this position still differs from it, and may be due to lack of an appropriate outgroup; neighbor-joining analyses demonstrate that Gavialis and Tomistoma are morphological closer to Crocodylinae than to alligatoroids. Tentative conclusions for improving phylogenetic inference from morphology are drawn. Further analyses using rescored non-robust characters, different outgroups, and morphometric data are required.



Speaker

#### Application of proteomic techniques to the identification of quaternary mammalian bones from prehistoric sites

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Traditional palaeontological approaches to quaternary vertebrates can identify much of the bones from Paleolithic or natural deposits. It is possible to follow over hundreds of thousands of years the wildlife renewals related to climatic variations at large or shorter timescale. However, several species pose many problems, either because without a current equivalent such as the woolly mammoth, the woolly rhinoceros, the cave bear and the cave lion or the saber-toothed cat, or because of the variability that masks their anatomical evolution. Despite the use for several years of the tools of paleogenetics, it turns out that the scope is very limited by the very poor retention of DNA over time. The constitutive proteins of the bone tissues have demonstrated remarkable conservation capacities opening new fields of exploration relative to the study of the evolution of the species. Protein analysis also has the major advantage of accurately identifying sequences of unknown, extinct or non-sequenced species while consuming very small amounts of samples. Thus proteomic analysis becomes a tool of choice for the identification of species but also to study their evolution. The project will rely on several types of samples that will be used to initialize the repository of species targeted by proteomic analyzes. Bones from recently excavated sites in northern France belonging to well-identified herbivore species, contemporaneous with glacial periods (woolly mammoth and woolly rhinoceros) and interglacial periods (red deer, fallow deer, aurochs, beaver) were sampled and analyzed. . Carnivores were also selected (cave bear, cave lion, saber-toothed cat). The preliminary results obtained demonstrate the relevance and effectiveness of proteomic analyzes applied to Pleistocene bones dating from tens to hundreds of thousands of years.



Speaker

#### Investigating the phylogenetic relationships of extinct taxa among close extant relatives: an integrative case study within the long-nosed armadillo species complex (genus *Dasypus*)

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In mammalian studies, conflicts between morphological and molecular phylogenies are common, which often prevents a confident placement of fossil taxa. Here we present a case study on the phylogenetic relationships among the long-nosed armadillos (genus Dasypus, Xenarthra, Cingulata), which contain both extant and recently extinct species and whose systematics remains, as of today, very confuse. Based on an integrative study combining results from comparative anatomy, geometric morphometrics, and phylogenomics, we thoroughly revised the systematics of the group and challenged the traditional species delimitation within the genus Dasypus. Most importantly, the high level of congruence reached by genomic and morphological data on their phylogeny enabled us to establish a robust framework on which to test the affinities of recently extinct members. The present work is focused on the phylogenetic relationships of the extinct and large-sized beautiful armadillo Dasypus bellus. We first used X-Ray microtomography, which allowed finding new characters on internal cranial structures as well as extracting 3D models of skulls. Second, we highlighted main cranial shape differences between taxa in our sample thanks to geometric morphometrics. In order to use this information for phylogenetic reconstruction, we developed an innovative coding protocol using standardized distances between selected landmarks as continuous characters. Our phylogenetic analyses of a pre-existing matrix completed with these newly defined traits and with new observations on internal structures revealed that Dasypus bellus is nested within the debated Dasypus novemcinctus species complex. Analyses were performed with and without molecular backbone, which only moderately influenced the inferred topology. This highlights the importance of using a protocol that allows searching and coding characters based on subtle morphological variations using geometric morphometrics, which would be unlikely detected otherwise. This approach is of utmost importance when dealing with closely related species and presents the advantage to provide clearly-defined and repeatable continuous characters, and to limit some methodological issues identified in other landmark-based phylogenetic methods.



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# S18 - Functional morphology of the cranium in vertebrates

#### **Oral communications**

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#### Predicting competition between *Pycnodontiformes* and Ginglymodi (Osteichthyes, Neopterygii) through geologic time based on quantitative analyses of lower jaw features

Jürgen Kriwet \*+<sup>1</sup>, Giuseppe Marramà<sup>1</sup>, John Cawley<sup>1</sup>

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Ginglymodians and extinct pycnodontiforms represent non-teleostean neopterygian groups that originated in the Middle and Late Triassic, respectively with pycnodontiforms occupying a basal phylogenetic position while ginglymodians are members of Holostei, which is the sister group of Teleosteomorpha. Neopterygians are characterized inter alia by significant modifications in the skull including the feeding apparatus in comparison to non-neopterygians, which triggered the evolution of different feeding mechanisms and subsequently the colonisation of new ecological niches. Pycnodontiforms and ginglymodians represent major components of Mesozoic marine vertebrate faunas that often co-occurred in the same environment throughout their evolutionary history but both display different evolutionary trends. A first major diversification event in pycnodontiforms is recognizable in the Early Jurassic, whereas ginglymodians already rapidly diversified in the Middle to Late Triassic. This also resulted in different diversity patterns with ginglymodians being more diverse in the Jurassic while pycnodontiforms display their largest diversity and disparity in the Cretaceous. Both groups attained a nearly global distribution early in their evolutionary history based on presumably different patterns (dispersal versus vicariance). Despite the distinct evolutionary trends, both groups display similar morphological features in the feeding apparatus with most species indicating durophageous feeding habits (except in lepisosteoids). Body shape and dental morphologies have been proposed to be key factors for their success in competing with teleosts. However, possible competition patterns between pycnodontiforms and ginglymodians have not yet been analysed and compared to possible competition by teleosts, especially in the Cretaceous when many ginglymodians adapted to freshwater. To establish possible competition patterns between pycnodontiforms and ginglymodians, we selected the lower jaw as a structural feature, because morphological variations in this system have biomechanical consequences linking structure and performance. The major goal is to identify if morphometric and meristic data can be useful to detect possible competition patterns between morphotypes and thus taxa. For this, we employed geometric morphometric approaches and non-parametric tests to quantify morphospace occupation of taxa through time.



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#### Independent evolution of multicuspidness precedes the acquisition of plant consumption in squamates

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Teeth represent excellent subjects for macroevolutionary studies of vertebrates thanks to their extensive fossil record. Strong selective pressures affect many dental characters, since such features can determine possible diet ranges. This is the case for tooth complexity, which varies mainly due to the number and position of positive reliefs on the tooth occlusal surface - the cusps. Through cusp addition, mammals achieved considerable variation in terms of multicuspid tooth morphologies during their evolution. However, little is known about the evolution of teeth in vertebrate groups such as squamates. Here we present a large-scale assessment of squamate tooth morphologies, comprising over 500 extant and fossil species representatively sampled from all major lineages. Using maximum-likelihood ancestral state reconstruction, we traced the evolution of cusp number in squamate teeth across their recorded history. We also analysed the diversity of multicuspid tooth morphologies with 2D geometric morphometrics to test links between tooth shape and dietary evolution. We show that over a third of squamates sampled possess multicuspid teeth. Dietary analyses show both cusp counts and tooth shape reflect diet in squamates, with herbivores having statistically significantly more cusps and occupying a distinct region of tooth morphospace. Excluding Gekkota and Serpentes, which are strictly unicuspid, the majority (85%) of phylogeny branches show stasis in cusp number: about

10% show an increase and 5% a decrease. Single cusp addition is the most frequent type of complexity increase (90%), whereas single cusp decreases are relatively rarer (68%). While multicuspidness independently evolved as synapomorphies of four major clades (Teiioidea, Lacertidae, Acrodonta, Pleurodonta) in the Cretaceous, the majority of cusp number increases and decreases are in the Cenozoic. Most such changes are within the four basally multicuspid clades, though multicuspidness originated independently at least a further 10 times. We reconstruct the last common ancestor of all squamates with unicuspid teeth and insectivorous diet, and the majority of independent multicuspid lineages are basally insectivorous. Plant consumption evolved during the Mesozoic principally only in Polyglyphanodontia, prior to their end-Cretaceous extinction. Only during the Cenozoic did widespread plant consumption evolve in current lizard groups, substantially delayed from each of the origins of multicuspidness.



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# Morphofunctional diversity in Toarcian (Early Jurassic) ichthyosaurs

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The Early Jurassic has the highest raw diversity of ichthyosaur taxa in the Mesozoic, yet not the highest disparity or ecological variation. Two great lagerstaetten – the Lias Group and Posidonia Shale – have preserved abundant specimens representing this diversity, however, three-dimensional specimens are rare. Morphological differences in the ichthyosaur taxa present at this time have been noted, but testing of ecological adaptation and niche occupation has heretofore been infrequent. We use micro-CT scans of two highly complete, three-dimensionally preserved ichthyosaur skulls from the Upper Lias (Toarcian) Strawberry Bank lagerstaette of Somerset, U.K. - referred to Hauffiopteryx typicus and Stenopterygius triscissus respectively - to reconstruct the internal cranial hard and soft anatomy. Hauffiopteryx typicus possesses a narrow, elongate snout and jaw, and anteroposteriorly short postorbital region and supratemporal fenestra – comparable to coeval Leptonectidae. The adductor cavity is large providing broad areas for muscle attachment. In Stenopterygius triscissus the snout is broader and more robust; the postorbital region longer and supratemporal fenestra larger than in *H. typicus* – as in other Thunnosauria. A feature of Neoichthyosauria is the posterior position of the paracoronoid process on the surangular, close to the jaw articulation. We find this - coupled with extensive muscle attachment in this region - gives a high moment action on the lower jaw, allowing the jaw to be closed rapidly even in the viscous medium of water. Morphofunctional differences in the jaw action, particularly relating to movement of the lower jaw through water, is considered important in the form of the skull. The teeth of S. triscissus are longer and greater in diameter than in H. typicus, and retained in both taxa through ontogeny. We suggest that these morphologies evidence niche partitioning between the taxa. No direct evidence of diet was found in the specimens, however, the lagerstaette preserves numerous fishes and insects of small to large size; the deposit has been interpreted as a 'nursery' for ichthyosaurs. The similarity of the snout and tooth morphological in *H. typicus* and the crocodyliform *Pelagosaurus typus* may indicate similar ecologies.



Speaker

#### Massospondylus inner ear ontogeny suggests a decoupled form-function relationship with locomotory performance in dinosaurs

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The vertebrate inner ear, or labyrinth organ, is an important structure that provides balance and orientation, and plays a key role in head stabilisation. The geometries of the semicircular canals are generally hypothesised to be heavily influenced by sensory inputs imposed by locomotor styles and behaviour, and are thus important subjects for form-function studies. However, it is still not understood how semicircular canal geometries respond to locomotory changes during ontogeny in a single species. The dinosaur Massospondylus was relatively common during the Early Jurassic of southern Africa, and is hypothesised to have undergone a pronounced gait- change from a quadrupedal juvenile mode to a bipedal adult one, making it an ideal palaeontological study system in which to examine this issue. We used microcomputed tomographic ( $\mu$ CT) scanning to reconstruct the endosseous labyrinths (endocasts of the bony canals that house the inner ear) of eight specimens of Massospondylus, ranging in age from hatchling to adult. Labyrinths scale isometrically with skull size throughout ontogeny. Geometric morphometric analyses using a sliding semi-landmark approach show that, despite the gait change, no significant morphological differences occur to the endosseous labyrinth during growth. This indicates that changing functional input from disparate gaits does not affect the geometry of the labyrinth after braincase ossification. The possible explanations for this are: i) Massospondylus did not undergo a gait change during ontogeny after all; ii) geometries may indeed have changed in the membranous labyrinth organ but are not reflected in the bony canals that house it; iii) adult labyrinth geometries actually reflect ossification at ontogenetically earlier, quadrupedal locomotory stages and do not record the shift to bipedalism. These results also indicate that, in Dinosauria at least, the maturity of an individual may have no impact on palaeoecological or phylogenetic interpretations ascertained from labyrinth geometries, and is thus important for future studies.



S18 // Oral

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#### Working in 3D space – 3D measurements vs. 3D landmarks in functionalmorphological analyses of the inner ear of vertebrates

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Since Hyrtl started in 1873 his invasive and destructive analyses on the anatomy of inner ear of vertebrates, many studies were focussing on the functionalmorphological signal of this mechanosensory system. However, the results of these studies were as contradictory as the groups of investigation ranging from aquatic to land-living to flying species. Located and enclosed in the petrosal bone at the base of the occipital region, the vestibular system and its anatomy can be analysed in extant species but also fossil taxa. Even though the vestibular system is responsible in detecting the equilibrium and spatial orientation of an organism during locomotion, it is not clear which anatomical signal represents the mode of locomotion (height and width vs. diameter of the three semicircular canals) and also, if and how the phylogeny influences this morphology. Besides the changes of the visualization technique (invasive vs. micro-CT scanning), also the analyses techniques were changing in recent years. Common to all and basis of all studies are the three-dimensional models of the bony labyrinth. Traditional morphometrics are taking three-dimensional measurements of these models and, in some cases, standardize the values prior to statistical analyses. In contrast to that, geometric morphometric approaches, which are new methods since the 90s with the expansion of computers, are using homologous points (landmarks). Both techniques analyse the data through multivariate statistic tools (e.g., PCA, Procrustes analyses). This study tries to compare those two methods with the same dataset of vertebrates and discuss their advantages and disadvantages as a basis for upcoming studies.



Speaker

#### Extinct and extant predators – hunting style reconstruction and phylogenetic distinction of carnivorans based on the vestibular system

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Extant carnivorans established an array of well-documented hunting strategies and behaviours. Well known social hunters, such as wolfs, dholes and the African hunting dog, generally pursuit their prey over wide distances in groups. Most felids are perfectly adapted to ambush or stalk their prey, due to their gracile body, flexible forelimbs and retractable claws. In contrast, small to medium sized carnivorans, such as foxes or the common genet, developed a more generalistic feeding behaviour. Their search for prey usually ends with a pounce to catch it. Besides these actively hunting carnivorans, others, such as the African palm civet or the bat-eared fox, specialised their diet on either fruits or insects and hence rarely hunt at all.

However, one major question remains: how to reconstruct such varying hunting behaviours and strategies in extinct carnivorans? The petrosal bone comprises one of the best preserved anatomical systems in the fossil record, the bony labyrinth. As a cavity, it comprises the membranous system of the inner ear and represents the key feature to detect head posture and balance during body movement. The three semicircular canals of this mechanosensory organ detect angular acceleration and gravity, whereas the vestibule is responsible for linear acceleration. Consequently, the morphology of the bony labyrinth reflects locomotion, behaviour and agility adjustments and is appropriated for reconstructing the ecology, lifestyle and evolution of extinct vertebrates.

Three dimensional bony labyrinth models, of a broad sample of extinct and extant carnivoran taxa were generated based on non-invasive high resolution  $\mu$ CT scans. Using PCA and 3D measurements, different aspects of bony labyrinth morphometry indicate a functional morphological signal, just as phylogenetic adaptations. The height, width and length of the three semicircular canals perfectly correlate with hunting behaviours and strategies (pursuit, ambush, pounce, occasional). Besides these ecological adaptations, several carnivoran families are clearly distinguishable based on the height of the cochlea, just as the diameter of the semicircular canals, reflecting a phylogenetic signal.

The morphology of this remarkable sensory organ can be perfectly availed to solve the question on the evolution of hunting styles in extinct carnivorans. However, besides these ecological adaptations, even phylogenetic correlations are observed in the auditory system.

\* Speaker

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# Can the inner ear morphology bring clues to the hypothesis of a survival of fossorial therapsids during crises?

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The underground way of life is regarded to have played an important role in the survival hypotheses of therapsids (including mammals) during major biological crises. However determining the fossorial ecology of extinct animals is not always possible (fragmentary skeletal remains and taphonomic evidences) and makes it difficult to verify these assumptions.

The underground way of life imposes mechanical constraints and a restricted sensory environment on fossorial -and more particularly subterranean-mammals. The inner ear, a sensory organ that manages balance, head movement, and spatial orientation with the semicircular ducts system, plays a key role in this environment and could be an effective new proxy for determining the underground way of life of fossils.

The first step is to prove the relationship between the inner ear morphology and the underground way of life in extant animals, and then to apply it to fossils. Based on a sampling documenting the clades of mammals comprising subterranean mammals (Marsupialia, Xenarthra, Eulipotyphla, Afrotheria, Rodentia), statistical studies of the morphology of the osseous and membranous inner ear show that there is no characteristic morphology related to the underground way of life. The functional parameters of the organ finally allowed to differentiate the underground mammals from the non-underground ones and to conclude that different morphologies can provide the same functions. This work highlights a new convergent and functional adaptation of the inner ear to the underground way of life: the subterranean mammals have a greater sensitivity of detection of the movements of the head and thus a better spatial orientation, which compensates the loss of eyesight.

Can this relationship, now determined in the extant, be applied to fossils to clarify the importance of this way of life in the history of mammals, especially in the passage of major biological crises?



18 // Oral

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#### A re-examination of identification of small carnivore fossils using brain endocasts

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Generally, for identifying mammals, the use of molar forms is effective for both extant and extinct species. In addition, one classification trait that distinguishes species is brain morphology; more specifically, morphology/pattern of the sulci differ among carnivore types (Radinsky, 1980). Because of these differences, this brain morphology classification method may be used to identify fossil species. Indeed, in their attempts to identify cranial fossils of small carnivores (unidentified specimens), researchers at the Okayama University of Science, suggested that studied fossils are those of skunks by outer cerebral morphology, especially that of three sulci: the lateral sulcus (la), located in the superior temporal lobe of the cerebral hemisphere; the suprasylvian sulcus (ss), located in the middle temporal lobe of the cerebral hemisphere; and the sylvian sulcus (sy), located in the inferior temporal lobe of the cerebral hemisphere. This is consistent with previous results, who identified the same fossils on the basis of molar forms, suggesting that identification using brain morphology in small carnivores is effective. However, when comparing sulci of some extant small carnivores, identification using only brain morphology could be difficult. Therefore, in this study, we compare the dentition, the molar forms and the brain forms of small carnivores, and examine the taxonomical level that can be identified by visual observation. Using extant species of the Mustelidae (Mustela itatsi, Martes melampus, Meles meles) and Mephitidae (Spilogale putorius, Mephitis mephitis, Mydaus marchei) families, identification by extracerebral forms using three sulci was possible at the family level. However, information regarding molar forms was also required for identification up to the genus level.



18 // Poster

Speaker

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# S19 - How to build a palaeontological collection?: expeditions, excavations, exchanges

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# Paul Carié and the dodo: unexpected new specimens

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The story of the discovery of subfossil bones of the dodo (*Raphus cucullatus*) - and many other vertebrates - at the Mare aux Songes marsh, in the southeastern part of Mauritius, has been told many times. Well-known collectors include the original discoverer, George Clark, and Théodore Sauzier. The Portlouis hairdresser Louis Etienne Thirioux has also received some attention, notably because he collected subfossil remains from caves in northern Mauritius rather than from the Mare aux Songes.

Until 2011, when dodo specimens kept at the Elbeuf Museum (Normandy, France) attracted some attention, Paul Carié (1876-1930) seems to have been partially forgotten, although he was an active naturalist who donated important collections, including dodo bones, to various European museums (Paris, Lausanne, Elbeuf). He belonged to an old French Mauritian family and inherited from an uncle the Mon Désert sugar estate, which included the Mare aux Songes, where he collected subfossil remains. An active zoologist, he spent a large part of his life in Paris, and became an associate member of the Muséum National d'Histoire Naturelle. From 1910 to 1913, he conducted a scientific mission to the Mascarenes for that Museum, and brought back large collections.

Many of the dodo bones donated by Carié show the typical preservation and brownish colour of specimens from the Mare aux Songes. Others, however, are differently preserved, being a whitish colour and more friable. The explanation, given in a list of the bones sent by Carié to Lausanne in 1907, is that the white bones were collected by Thirioux from screes and caves in the vicinity of Port-louis, whereas the brown ones come from the Mare aux Songes. Carié purchased molluscs from Thirioux and must have acquired dodo bones as well.

In 2015, a forgotten collection of specimens collected by Paul Carié was rediscovered thanks to the interest of his descendants for his scientific activities. It was stored in the old family house near Paris for decades, and was found when the family decided to clear the house. This 'new' collection, which has been donated to the Elbeuf Museum, includes molluscs, insects, and vertebrates. Subfossil specimens from the Mare aux Songes and other sites on Mauritius include turtles, mammals, and birds, among which a large number of dodo specimens. Some of them, being fragmentary, could be used for histological investigations that have considerably increased our understanding of dodo biology.



19 // Oral

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# A Frenchman in Patagonia: the palaeontological expeditions of André Tournouër (1898-1903)

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Although not a professional palaeontologist, André Tournouër (1871 – 1929) led several expeditions to Argentinian Patagonia, between 1898 and 1903, to collect Tertiary vertebrates for the Paris Muséum National d'Histoire Naturelle, at a time when the Patagonian fossils attracted much attention both in Argentina and abroad. Although he brought back vast collections, which were the basis for papers by Albert Gaudry and subsequent researchers, relatively little is known about Tournouër's expeditions, partly because he never wrote a detailed account of them. Unpublished documents kept at the palaeontology laboratory of the MNHN and little known papers by André Tournouër shed some light on his expeditions and the way they were organized and funded (at least partly by the French government). He belonged to an affluent French family, and his father, Raoul Tournouër, had been an eminent invertebrate palaeontologist, although he never held an official position as such. Albert Gaudry, then head of the palaeontology department at the MNHN, was a friend of the Tournouër family, and it is upon his request that André, who was then raising cattle in northern Argentina, started on his first expedition to Patagonia. Unlike other palaeontologists working there at that time, he did not reach Patagonia by sea, but travelled all the way from Mendoza to southern Patagonia by land, with mules and workers. He collected abundant fossil material, mainly from the Deseado (Oligocene) and Santa Cruz (Miocene) Formations, that was shipped to France from Punta Arenas. Having observed a mysterious animal in a Patagonian river, he got involved in the debate about the Hyimché, supposed by some to be a surviving giant sloth, but finally concluded it was an otter. Unlike many other foreign palaeontologists working in Argentina, Tournouër was on good terms with the Ameghino brothers and exchanged information with them; nevertheless, his interpretation of Patagonian stratigraphy differed significantly from Ameghino's. After his return to France, Tournouër published a few papers on the geology and palaeontology of Patagonia, but, with the exception of two short general papers in a local natural history journal in 1914 and 1922, his palaeontological activities apparently came to an end sometime after 1905, possibly because of the death of his mentor Albert Gaudry in 1908 and also because, after getting married in 1906, he left Paris and moved to Le Havre, with fewer opportunities for research.



19 // Oral

Speaker

#### Museums and scientific exchanges in the global south. The fossil genus *Glossopteris* and some academics of the Continental Drift Theory, 1915-1940

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The general aim of this project consists in tracking back the exchanges conducted between 1915 and 1940 in different museums and between southern hemisphere geologists/palaeontologists that were interested in proving the ancient existence of an austral Pan-continent. The focus is to analyse how the specimens of the botanical genus *Glossopteris* have circulated and been incorporated in different collections, and how this traffic of specimens and drawings has determined or has been determined by the existent relations between certain individuals and institutions. Hence, this paper will present preliminary results of this doctoral project.

The project is oriented to the history of the collections, of the museums of natural history and the Earth sciences. Thus, it is aimed at the reevaluation of the documental heritage from the Italian geologist and Doctor Joaquín Frenguelli (1883-1958), whose manuscripts are conserved in the cited archive. Frenguelli was an important scientist of the Museum of La Plata in the first half of the 20th century. He had an invaluable role in the development of the sciences, in different fields, such as Geology, Geomorphology, Palaeontology, Zoology, Botany, Anthropology and Protistology. In his studies about Argentinian phytogeography, he presented the vegetation as an inseparable part of the geological structures. His observations and paleobotanical collections were essential to a synthesis of the stratigraphy of the continental Upper Paleozoic. The investigation of the Frenguelli archives, beyond their historical interest, will help to give visibility to collections with potential utility to the contemporaneous practice of paleobotany.

The collaboration between different regions of the world, each one with a particular access to the local evidence of the planet's history, allows the articulation of the local and global scales, a theme of particular interest in respect to the history of scientific cooperation. Therefore, these exchanges represent the material evidence of how the theories are 'thought' from objects and itineraries that are conditioned by the communication and the transportation of data and artefacts. In this way, the exchange of samples of *Glossopteris* represents a paradigmatic case to reconstruct not only an aspect of the theory of a Pancontinent, but also to analyse the influence that this exchange could have had in the development of the scientific relations between the involved countries in the countries in the 'Global South'.

IPC 5

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#### Marketing paleontology: Collections between knowledge production and communication

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Between 1909 and 1913, Berlin's Museum für Naturkunde (Berlin Museum of Natural History) unearthed more than 225 tons of fossils in former German East Africa and transported them to Berlin. Among them were the bones of Brachiosaurus brancai, which would eventually become the biggest mounted dinosaur in the world. By analyzing the social and communicative strategies that made this expedition possible, my talk aims to reveal several aspects of natural history knowledge production at the end of the long nineteenth century. Using rhetoric, the director of the Geological-Paleontological Museum in Berlin, Wilhelm von Branca, conducted a highly successful campaign to market the dinosaurs in Prussia and to convince public opinion and the Prussian central state of the value of paleontology. He fired the Prussian imagination and took advantage of the competitive urge to emulate American paleontology and industry. My talk examines how Branca's public relations strategies shaped the German biological "landscape" of the first decades of the twentieth century. It asks: When and under what conditions did paleontology successfully appeal to the public? How does communication dictate, shape, and constrain the development of a specific epistemic agenda? And what kind of power do the public and money have?



Speaker

#### The South American mammals collection at the Museo Geologico Giovanni Capellini (Bologna, Italy)

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Near the end of the 19th century, Professor Giovanni Capellini acquired a rich collection of fossil mammals remains from South America that today are part of the permanent exhibit in the Museum that bears his name. A restoration of the hall hosting the collection provided a unique opportunity to examine and further investigate their historic and taxonomic value. Furthermore, specimens had not been the subject of restoration and taxonomic revision since their arrival in Bologna more than a century ago.

In order to collect historic data, we investigated the private correspondence of G. Capellini, housed at the Archiginnasio Library in Bologna. Specimens were sent from Argentina by the German zoologist Carl Hermann Conrad Burmeister between 1863 and 1866. At the time, Burmeister was in charge of creating both the zoological and paleontological collections for the Museo Nacional of Buenos Aires. In Italy, Capellini was building the Geological Museum in Bologna and the two scientists agreed upon an exchange of specimens. Unfortunately, in the correspondence no data are provided on where South American specimens had been collected. Capellini's correspondence also included several letters with Florentino Ameghino. Son of Italian immigrants, his hometown (Lujàn, Argentina or Genova, Italy) is still the subject of debate. In one of his letter to Capellini, Ameghino himself wrote that he was born in Moneglia (Genova), Italy.

Detailed analyses on the South American material housed in Bologna revealed the presence of almost 500 specimens pertaining to glyptodont and giant ground sloths. Well preserved ornamentation of carapace fragment allowed for the identification of a minimum of five glyptodont genera in the Capellini collection. Furthermore, several skeletal elements referable to glyptodonts display cutmarks. Such cuts are distributed on skull, femur, ischium, astragalus, and calcaneus, and display a clear V-shape in section. As such, the specimens housed in Bologna do represent solid evidence, potentially the first, of human exploitation on this group of extinct mammals. This work emphasizes the importance of the study of paleontological collections and their history. A modern perspective may lead to collect new information about the methodologies applied in the past to study the specimens, about the relevance of taxa that can be found in the collection, and about what work is necessary to address nowadays in order to improve our knowledge.



S19 // Oral

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# When micropalaeontology meets history: natural history collecting by the French Navy in Indochina

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The micropalaeontology collections housed in the Muséum national d'Histoire naturelle (MNHN) of Paris have been gathered by various contributors: MNHN and external scientists, institutions, explorers and amateurs. These collections went through a difficult period from the end of the nineteen century to around 1960 when no micropalaeontology curator was appointed and their fate through this period stays unclear. For this reason, the acquisition history of some collections deposited during this time interval is almost undocumented. Of them, the "Lapérouse collection" was recently re-discovered: it is composed of negatives of photos of foraminifera on glass plates and Bristol boards bearing the name "Astrolabe", dates (from the 1st to the 4th of February 1926) and geographic coordinates or information. Thanks to a thorough archive and literature exploration, the history of this collection is traced back to the inter-war period when three vessels of the French Navy's Hydrographic Department, *Lapérouse* and its 2 annexes *Astrolabe* and *Octant*, were sailing back and forth along the Indochina coast to produce navigation maps. We describe the history of the *Lapérouse*, *Astrolabe* and *Octant*, from their involvement in WWI to their disappearance during WWII. With this contribution, we aim at illustrating the scientific and historic significance of such collections.



Speaker

#### Bolt's Farm Cave System (Cradle of Humankind-South Africa) from 1936 to 2018

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The Cradle of Humankind (declared a World Heritage Site by UNESCO in 1999) includes more than 30 fossiliferous Plio-Pleistocene sites. The first fossils were discovered at the end of the nineteenth century. The scientific research started early in 1936 with one of the most prominent pioneers in palaeontology, Robert Broom (1866-1951), discovering some fossil baboon remains at Sterkfontein in collaboration with G.W.H. Schepers and H. le Riche, and later in the same year (1936), also the first remains of australopithecines at Sterkfontein. During the 1936 expedition, Broom also discovered the first fossils at Bolt's Farm Cave System (BFCS). Until his death, he would return occasionally to BFCS and find a few fossils which he published as type specimens. When Broom wrote a catalogue for the fossils from BFCS, the information about the material was usually insufficient. During the 1947-1948 expedition, Camp (1948) established the first map of the fossiliferous area but exported most of the material to the USA. From 1980 to 2006, a few occasional collections were undertaken. In 2006 the research at BFCS, led by a French-South African team, obtained more results. New deposits have been discovered since the first excavation in 2011. This has led to Camp's map of 1948 being revised and now regularly updated. This new team practises a multidisciplinary approach as it studies not only fossils but also the geological deposits, geochronology and diagenesis. The method of preparation of fossils and of the breccia has developed since 1936, especially for the BFCS material. Acid preparation is preferred and a new laboratory was built and inaugurated at the Ditsong National Museum of Natural History (DNMNH) in 2010. This method is more appropriate to prepare very fragile fossils, particularly the microfauna, and this will help in shedding more light on the age of the deposit as well as on the palaeobiodiversity and palaeo-environment.



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## Digitizing the Fossil Insects of Los Angeles for an international research community

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The Invertebrate Paleontology Collection at the Natural History Museum of Los Angeles County (LACMIP) has received support to digitize the museum's collection of 28,000+ fossil insects (NSF DBI 1702342). "Fossil Insects of L.A." represents the final contribution to the Fossil Insect Collaborative, a consortium of 10 institutions working to digitally unite the largest paleoentomological collections in the United States in the context of understanding ecological and evolutionary response to past environmental changes (NSF DBI 1305066). Fossil Insects of L.A. will digitize four key collections to fill important taxonomic, temporal, and geographic gaps in the Collaborative's existing dataset.

Special emphasis will be placed on LACMIP's collection of latest Oligocene insects from the Rott Formation of Germany, known as the Georg Statz Collection. The Statz Collection is scientifically significant as the largest collection of insects from the Rott Formation in North America, and historically significant for narrowly escaping destruction during World War II. It includes over 4,200 specimens (899 types)-most of which have not been taxonomically reevaluated since the 1930s–40s-and abundant contextual information in the form of rare publications and ancillary documents. The entire collection will be databased and a selection will be imaged, including all types. This portion of the Fossil Insects of L.A. project will serve as a test case for the "enhancing Paleontological and Neontological Data Discovery API" (ePANDDA) project (NSF ICER 1821039), which will cross-reference these digitized resources with others available from iDigBio, iDigPaleo, and the Paleobiology Database.

A secondary focus of the Fossil Insects of L.A. project is digitization of the Barstow, Rancho La Brea, and McKittrick faunas. A relatively small proportion of these specimens will be imaged, but all will be databased and shared online. The Barstow arthropods represent a *Konservat-lagerstätte* that has received relatively little research attention since its discovery in 1954.

Likewise, insects of the Rancho La Brea and McKittrick asphalt seeps have been overshadowed by their more charismatic megafaunal counterparts until very recently. By making all resulting data and media publicly available via iDigBio and other online portals, we aim to stimulate novel studies on these collections for the benefit of the international research community.



Speaker

#### The paleontological advance and the search for mineral coal in the south of Brazil during the XIX<sup>th</sup> century and beginning of the XX<sup>th</sup> century

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The objective of this work is to carry out a historical survey on the paleontological works developed together with the exploration of mineral coal in the State of Santa Catarina, Brazil during the nineteenth and early twentieth centuries, through professionals and their expeditions. In 1827, the Prussian naturalist Friedrich Sellow (1789 - 1831) traveled to southern Brazil with the aim of collecting information on mineral coal. One of the results of this trip was the collection of several fossils of fish and plants present in the coal series in the city of Salto do Jacuí, in the State of Rio Grande do Sul. Sellow also sent samples of South Brazilian plants to the National Museum and Botanical Garden in Rio de Janeiro City, Brazil and to the Berlin Zoo Museum in Germany. In 1860, coal development in Santa Catarina prospered through Brazilian politician Felisberto Caldeira Brant Pontes (1802 - 1906) when he founded the company The Tubarão Coal Mining Company Limited. Even not working with fossils, Pontes expands mineral extraction to new areas, such as Imbutiba City and Araranguá City - Santa Catarina State, Brazil, until then little known. This contributed to new paleontological discoveries in the early twentieth century, carried out by the North American geologist Israel Charles White (1848-1927) hired to head the Commission for the Study of Stone Charcoal of Brazil (1904-1906) which aimed to study the deposits and the potential of Brazilian coal in view of the great need of the country's energy resources. In the final report (1908), White presents new data, suggests the application of new techniques (Briquetting), for a better use of coal. He reported the discovery of a new fossil vertebrate in the State of Paraná, which was sent to the Museum of Natural History of New York, and studied by Dr. John H. MacGregor, who defined it as Mesosaurus braziliensis. Species of fossil plants from all over southern Brazil were also sent to Dr. David White (1862-1935), who concluded that it was a mixture of ancient Gondwana and Permian, enumerating more than 40 species characterized in 4 groups: Plyellotheca, Glossopteris, Gangamopteris and Noeggerathiopsis. Thus, the abstract presents data from a research in development, presenting some notable researchers who, next to their work, contributed geological, geographical and paleontological data, elaborating maps, characterizing geological formations, discovering new fossils, and contributing to the development of coal research within the State of Santa Catarina and throughout southern Brazil.



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#### The fossil collections at the Geological Survey of Sweden, a part of the Swedish moveable geoheritage

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Geological collections at the Geological Survey of Sweden (SGU) date back to 1858, when the survey was founded. Only a few specimens are known to have been collected earlier, for instance those of the personal collection of Axel Erdmann, the founder of the Survey. Today the fossil collections at SGU comprise 100 000 fossils, from 1,8 Ga stromatolites to Quaternary subfossils. The most common fossils are Early Palaeozoic invertebrates. Between 1870 and 1983, the survey had its own geological museum and many fossils were put on display for the public. The type and figured collection comprises more than 9000 specimens.

Most fossil specimens were collected for biostratigraphical purposes during geological mapping, enabling recognition of the sedimentary rock succession in Sweden. The need of hydrocarbons in the early 20th century is but one example that initiated many detailed studies of the Cambrian Alum Shale Formation by A.H. Westergård, a palaeontologist at SGU, and resulted in pioneering work on Cambrian stratigraphy of Sweden.

Most of the specimens are from Sweden, however, there are exceptions. One example is the collections from Spitsbergen and eastern Greenland of Oskar Kulling. Kulling was a geologist at SGU and is maybe most famous for his work mapping the Swedish Caledonides. He had a wide area of interest and has also collected peculiar trace fossils and fossils from the Precambrian/Cambrian boundary in northern Sweden and described the most complete mammoth find in Sweden. All specimens are deposited at SGU.

Today new acquisition of fossils is rare, although SGU do get occasional donations and some collecting still occur within the survey, but not at all comparable to the rate of collecting during the 20th century.

Geological collections are a part of the moveable geoheritage, following the IUCN resolution of 2016. This new international resolution will show the importance of geological collections to the world of nature conservation, and hopefully it will also provide new opportunities.



Speaker

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Torsten Scheyer <i>et al.</i> // Trophic interactions between larger crocodylians and giant tortoises on Aldabra Atoll, Western Indian Ocean, during the Late Pleistocene



# The worm's turn: constraining the deep origin and evolution of parasitism with fossil evidence

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Helminths are large multicellular parasitic worms. Traditionally, they included parasitic flatworms (flukes, tapeworms), nematodes and acanthocephalans, although some authors even included tongue worms (pentastomids) and/or parasitic annelids (e.g., leeches). It is now clear that helminths are an artificial grouping of different clades with similarities in form and the convergent development of a parasitic mode of life. Both Acanthocephala and Pentastomida have been considered to be separately phyla, but are now firmly considered to be derived rotifers and crustaceans, respectively. We review the fossil record of helminths with the aim of providing suitable minimum and maximum constraints of their evolution as well as the degree of coevolution with their (vertebrate) hosts. Their body fossil record is usually considered poor, although in some phyla like nematoda and platyhelminthes it is better (less patchy) and older than that of their free-living relatives. Although parasitism is derived in metazoa, parasitism can be traced back to the Cambrian - Ordovician based on pentastomid arthropod fossils and ancient host associations in nematodes and platyhelminthes. In some groups (e.g., flatworms and nematodes), their fossil record is consistent with a long degree of association, in others (e.g., pentastomids) marked host switches are evident. There are no unambigious ancient fossils of acanthocephalan fossils. Fossil leeches seem to be more recent - known from fossil eggs since the Triassic. Nevertheless, more ancient parasitic annelids (e.g., myzostomids) or other helminths are known from characteristic traces or pathologies in their hosts earlier in the Paleozoic. Extant molecular studies focus often on derived parasites of societal importance, but ancient forms might be more crucial to reveal important aspects of parasite evolution and host co-evolution.



Speaker

#### Biotic interactions between platyceratid gastropods and crinoids: a review and new insights

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Crinoids and platyceratid gastropods represent one of the classic examples of biotic interactions in the fossil record. Crinoids served as hosts for platyceratid gastropods from the Ordovician until the latter's extinction in the Permian. Platyceratids typically attached firmly over the crinoid periproct where they remained during the lives of their host. Here we review various aspects of this association, including platyceratids' preference for certain crinoid morphotypes, the ecological impact platyceratids may have had on their hosts, and the evolutionary consequences of the interaction.

The traditional interpretation of the association between crinoids and platyceratids has been one of strict coprophagy: The snails fed on crinoid waste without negatively affecting their hosts. However, over the past three decades, new data have offered support for a parasitic relationship. These data show that the growth rates of platyceratid-infested crinoids were lower than the growth rates of uninfested individuals, suggesting that some snails were kleptoparasitic. In other words, they stole food from their hosts.

Consistent with the kleptoparasitic interpretation are results demonstrating that crinoids with the periproct positioned at the end of a long tube are rarely infested by platyceratids. The long tube made it more difficult for kleptoparasitic gastropods to access undigested nutrients. Moreover, long tubes, by increasing the length of the hindgut and thus nutrient absorption, would have made tubed crinoids less attractive to coprophagous gastropods as well. Interestingly, in the rare instances in which snails are found on tubed crinoids, they are never attached over the periproct but rather at the base of the tube, near the crinoid foregut. In order to access nutrients, infesting platyceratids breached the tube by drilling a circular hole through the plates of the tegmen. The development of long tubes in crinoids, which occurred multiple times, and the drilling abilities of platyceratids may represent a case of evolutionary escalation.



**S20 // Ora**l

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#### Symbioses between bryozoans and primary and secondary occupants of gastropod shells

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Bryozoans are sessile colonial invertebrates with a rich fossil record. The larvae of most species attach to firm substrates, such as shells or rocks, and colonies overgrow the substrate surface by budding zooids. Gastropods shells have been used as a substrate by bryozoans since Ordovician times. These fall into three categories: (1) empty shells of dead gastropods; (2) shells of living gastropods; and (3) shells of dead gastropods housing secondary occupants, termed 'conchicoles' by Vermeij. The three categories can generally be distinguished by differences in the pattern of bryozoan colony growth over the external shell surface, onto interior surfaces and outwards from the aperture. The categories are not exclusive: bryozoans encrusting the shells of living gastropods can continue to grow after the gastropod has died and the shell is empty or contains a conchicole. Categories (2) and (3) represent symbioses between the bryozoans and the primary or secondary shell occupants, respectively. The commonest conchicoles at the present- day are hermit crabs (pagurids). Numerous examples of inferred bryozoan-pagurid symbioses are known in the Cenozoic fossil record, with a few examples from the Mesozoic. Identities of Palaeozoic conchicoles are equivocal, but may include sipunculan worms and possibly non- pagurid arthropods. While the bryozoans benefit from their attachment to substrates that are less likely to be buried than inert substrates, the conchicoles can be provided with domiciles that increase in size as a result of bryozoan growth beyond the original shell aperture. Most individual bryozoan-conchicole symbioses are non-obligatory and have short geological durations, with little or no evidence for coevolution.

Speaker

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#### Polychelidan lobsters from La Voulte: first evidence of Eucarida brood care in the fossil record

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Polychelidan lobsters are the coelacanths of decapod crustaceans: for still unknown reasons, they are now far less diverse than during the Mesozoic and restricted to deep-water environments. They are relatively abundant in the Middle Jurassic Konservat-lagerstätte of La Voulte-sur- Rhône, a unique site given its relatively deep setting and probable hydrothermal activity. Among the exceptionally well-preserved specimens investigated by X-ray microtomography are a female polychelidan with mature ovaries and another lobster brooding hundreds of eggs under its pleon. The internal and external anatomical features of these fossils – masked inside 3D concretions – are also thoroughly described. This is the first evidence of brood care in the Eucarida fossil record. This discovery has its importance given the fact that this type of brood care is the name-giving autapomorphy of Pleocyemata Burkenroad, 1963, to which polychelidan lobsters are supposed to belong. This contrasts with the direct release of fertilised eggs in the water in Dendrobranchiata Spence Bate, 1888 and some group of Euphausiacea Dana, 1852. These examples of brooding and spawning fossil evidence also contribute to depict a rich deep-sea La Voulte palaeoecosystem, in which polychelidan lobsters lived and reproduced, alongside other crusteaceans, including probably large populations of Dendrobranchiate shrimps. Environmental conditions in La Voulte may have been particularly favourable for the reproduction of crustaceans, with probably warm temperatures and nutrient resources, linked to its hydrothermal activity.



Speaker

#### Silica phytoliths in angiosperms: phylogeny, early evolutionary history and a possible dinosaur connection

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The phenomenon silicon accumulation and phytolith formation by plants is one of nature's little mysteries. Despite some great advancement in the study of the physiology, ecology and evolution of this phenomenon, we are still puzzled by its distribution among plants, and moreover over the roles it probably plays in plant and global ecology and the drivers of its evolution. It appears that silica phytoliths play various roles in plants, and that these roles may also vary greatly among plant groups and habitats. Furthermore, phylogenetic analyses suggest that the genetic infrastructure for silicon uptake and accumulation is at least as old as land plants themselves, and that the emergence of silicon-rich clades does not coalesce with any clear environmental driver.

A detailed review of evidence for silicon and phytolith contents among angiosperms reveals that orders in which phytolith-rich taxa occur have emerged mostly during the Early/Late Cretaceous boundary, and account for much of order emergences at that time. When considering molecular and fossil evidence together, it appears that the main diversification stages of these orders took place mostly during the Late Cretaceous, possibly peaking around 85 million years BP.

At about the same time, we witness the evolution and diversification of two herbivorous dinosaur groups (hadrosaurs and ceratopsians) and some Gondwanatherians, which have all evolved characteristic mechanisms to cope with gritty food. The role of phytoliths as a quantitative antiherbivory defence, mostly because of their gritty and abrasive nature, has long been demonstrated in the literature. I suggest that these Late Cretaceous herbivores evolved this dentition as an adaptation to the common silicon-rich horsetails that constituted a significant portion of their diets.

It is possible, then, that early phytolith-rich angiosperms and herbivores coevolved. This coevolution can be direct, because phytoliths in early angiosperms evolved, at least in part, as an antiherbivory defence. This is corroborated by some phytolith assemblages recently discovered in titanosaur gut contents and hadrosaur dentition, suggesting that early phytolith-rich angiosperms were a part of herbivorous dinosaur diets at the time. It is also possible that through digestion of silicon-rich plants, herbivorous dinosaurs accelerated silicon cycling and made it more easily available for early silicon-rich angiosperms, from which they could gain greater benefits.



Speaker

### Evidence for early predation in Arctic Canada and implications for the evolution of Eukaryotes

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Predation is a common feeding behavior in modern eukaryotes. It enhances fitness in prey and is viewed as one of the probable drivers for biological transitions during the evolution of the Domain Eukaryota, namely, the major eukaryote diversification ca. 800 Ma. However, molecular clock estimates and earliest crown-group affiliated microfossils suggest that this diversification may have originated during the Mesoproterozoic. New assemblages of organic-walled microfossils are reported from the *ca*. 1151±13 Ma to 892±13 Ma lower Shaler Supergroup of Arctic Canada including a variety of eukaryotic forms. Specimens from various taxa display circular to ovoid perforations on their vesicle walls, which are interpreted as probable evidence of selective protist predation, between 100 to 300 Ma prior to their first reported appearance in the Neoproterozoic (in the 780-740 Ma Chuar Group, Arizona). This implies that eukaryotic diversification started earlier (ca 1100 Ma), and may have been associated with the evolution of selective eukaryovory, in parallel to the development of eukaryotic photosynthesis in marine environments.



20 // Oral

Speaker

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#### The earliest evidence of metazoan symbiosis

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The Cambrian Explosion represents a major metazoan radiation event, which is reflected in the dramatic increase of both taxonomic and ecological diversity. In light of recent fossil discoveries from exceptionally preserved Cambrian lagerstätten, the ecological complexity and trophic structures of these Cambrian marine communities have been further revealed. Here we will present the newly discovered worm species, *Inquicus fellatus* gen. et sp. nov, which infested the Cambrian scalidophoran worms *Cricocosmia* and *Mafangscolex*, representing the earliest examples of aggregate infestation, host specificity and host shift in metazoans. The exact taxonomic affinity of *I. fellatus* and the nature of its symbiotic relationship with *Cricocosmia* and *Mafangscolex* will be discussed. Other examples of metazoan symbiosis from Cambrian communities and their ecological and evolutionary implications will also be further explored.



Speaker

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#### Trends in drilling predation and parasitism on echinoids during the Mesozoic Marine Revolution

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The Mesozoic Marine Revolution (MMR), an 'evolutionary arms race' between predators and prey in marine ecosystems, is linked to escalating frequencies of biotic interactions, ecological complexity, and evolutionary adaptations. Substantial evidence for the MMR is derived from traces of predatory behavior on mollusks, such as drill holes and durophagous damage, while less attention has been paid to behaviors targeting another important marine invertebrate group, the echinoids. Predatory cassid and parasitic eulimid gastropods are known to produce drill hole traces on living echinoids, however, these biotic interactions are relatively understudied in the fossil record. The newly established and growing Echinoid-Associated Traces (EAT) Database aims to elucidate macroevolutionary and macroecological trends in traceproducing behaviors targeting echinoids, through the study of museum collections and primary literature surveys. Data on the frequency, morphology, size, location, selectivity, and ecology of drill holes and other trace occurrences on echinoid tests is currently being assembled in the database. Preliminary analyses focus on observing changes in drill hole frequencies during important evolutionary events in the history of tracemakers and their echinoid targets, such as the diversification of cassids and eulimids in the early Cenozoic, the radiation of infaunal echinoids in the Cretaceous, and the Cretaceous-Paleogene and Eocene-Oligocene extinctions. Preliminary observations show, as expected, near absence of drill hole occurrences in the Early Cretaceous. This is followed by a gradual increase in drill hole frequencies through the Late Cretaceous and Paleogene, coinciding with the appearance and diversification of the proposed tracemakers. Average drill hole frequencies drop significantly across the Eocene-Oligocene boundary, concurrent with an extinction of echinoid taxa (approximately 20% species loss). Predatory and parasitic drill hole average frequencies track each other, though predatory drill holes are generally more common in the fossil record. Modern drill hole frequencies, compiled from the primary literature, vary greatly between populations, but generally occur at much higher frequencies that those observed in the fossil record. Preliminary trends imply escalating intensity of these biotic interactions over the evolutionary history of the gastropod tracemakers.



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#### Spatio-temporal distribution of herbivory in the Permian flora from Gondwana

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The biodiversity is distributed heterogeneously across the Earth. One way to study the patterns of spatial distribution of biodiversity is along gradients across space and environmental conditions. Studies indicate that biodiversity respond to environmental gradients since the Paleozoic. During the Permian, the climate was differentiated, with latitudinal gradients, which appear to have been similar to Earth's modern interglacial. We analyzed the influence of geographical position and the floristic composition in the plantinsect interaction distribution from Early and Late Permian in Gondwana. Besides, we analyzed the variation of herbivory composition through the Permian. Plant megafossils were collected from 26 localities from Argentina, Australia and Brazil basins. The samples were classified for the presence of damage types based on the Damage Type Guide. To analyze the influence of latitude, longitude, and floristic composition in the plant-insect interaction distribution through the Gondwana, we performed a variation partitioning for Early and for Late Permian, separately. To analyze the variation of herbivory through Permian, we performed a MANOVA with permutation tests. In total, 5,402 samples were analyzed, and only 170 showed evidences of herbivory. The analyses showed that only floristic composition, explained the plant-insect distribution in Early and Late Permian. The analyses of variance indicated that herbivory differed between Early and Late Permian. Most herbivores are highly host-specific, So, the species composition from each floral site seem to be very important in the herbivores diets, and consequently in the distribution of damage types. The absence of association between plant-insect interactions and the geographical positions also could be a result of several factor, such as: the higher difference of the samples size among sites; the fossil record only represent wet environments, consisting in a biased record of the ancient habitats; the low latitudinal variation found among the localities; and the latitude/longitude did not play an important role in the distribution of herbivory throughout Gondwana during Permian.



S20 // Oral

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### Eocene isopods on electric rays: tracking ancient biological interactions in a complex fossil record

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Isopod crustaceans have developed a variety of feeding strategies impacting their various life habits over time. Apart from specific morphological adaptations and the typical secondary deformations that some parasitic isopods inflict on their hosts' exoskeleton, traces of feeding behaviours involving isopods on their victim/food are very uncommonly fossilized. Many of these rare occurrences consist of cases for which the degree of association between the isopods and their potential food source is fuzzy, or the interaction only very briefly interpreted (recent analysed cases excepted). These different studies show two limiting problems in trying to identify the biological nature of fossilized associations: 1) Direct associations of organisms preserved as "imprint" (as opposed to inclusions in cherts or amber) are shaped by several taphonomical events that are hard to identify (such as the organisms time of life, death, burial, and fossilization); 2) Even in modern nature, differences within syn-vivo interactions (like parasitism and micropredation) are poorly understood in marine systems. In this study we report the first occurrence of isopods associated to ancient chondrichthyans which is, at the same time, also a rare case of preservation of several fossil isopods on larger organisms. These organisms are articulated adult electric rays of the genus Titanonarke Carvalho, 2010 from the late Ypresian (Eocene) of the Monte Postale site, Bolca Lagerstätte, Italy. In examining (1) the involved lineages of rays and isopods, (2) the taphonomy of the association, (3) its environmental context and (4) biological/adaptive features, we identify this association as a selective case, either of ancient scavenging or of micropredation of specific electric rays by isopods.



Speaker

#### Trophic interactions between larger crocodylians and giant tortoises on Aldabra Atoll, Western Indian Ocean, during the Late Pleistocene

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The identification of species interactions in the form of predation is fundamental to understand ecosystem complexity and community structure, but evidence of predator-prey interactions is still rare in the vertebrate fossil record. Today, the UNESCO World Heritage Site of Aldabra Atoll is home to about 100,000 giant tortoises, Aldabrachelys gigantea, whereas large predators are absent. New Late Pleistocene fossils (age ca. 90–125,000 yrs.) from the atoll now revealed some appendicular bones and numerous shell fragments of giant tortoises, as well as cranial and postcranial elements of crocodylians. Several tortoise bones show circular holes, pits and scratch marks that are interpreted as bite marks of crocodylians. The presence of a Late Pleistocene crocodylian species, Aldabrachampsus dilophus, has been known for some time, but the recently found crocodylian remains presented herein are distinctly larger than those previously described. This indicates the presence of at least some larger crocodylians, either of the same or of a different species, on the atoll. The skull and dentary fragments indicate that a reconstructed dorsal cranial skull length of 40-50 cm is feasible which, using allometric regressions of for Crocodylus porosus, hints at snout vent lengths of 140-175 cm or total body lengths of ca. 290-370 cm. These larger crocodylians, likely the apex predators in the Aldabra ecosystem at the time, were well capable of inflicting damage on even very large giant tortoises. We thus propose an extinct predator-prey interaction between crocodylians and giant tortoises during the Late Pleistocene, when both groups were living sympatrically on Aldabra, and we discuss scenarios for the crocodylians directly attacking the tortoises or scavenging on recently deceased animals. Because Late Pleistocene fossil material is abundant on Aldabra, collections of additional material from the Cinq Cases region and elsewhere on the atoll could allow population-level morphological studies of the tortoises and crocodylians, which would shed further light on the details of the extinct trophic relationship (e.g., prey size selection).

S20 // Oral

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#### S21 - Konservat-Lagerstätten

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#### Taphonomic significance of the mineralogy of Burgess Shale fossils

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Burgess Shale fossils are often coated with clay minerals, yet their role in fossilization has been heavily debated. The clays may have precipitated on decaying carcasses or were bonded to them (and transformed millions of years later during greenschist alteration), or they formed de novo during metamorphism. The last scenario renders any role they might have performed in fossilization limited. Previous attempts to resolve when these minerals became associated with the fossils have relied on the investigation of the abundance of elements across fossil anatomy. This method only affords an imprecise guide to mineralogical variations. Our new results document mineralogy across fossil anatomy at the mmscale for the first time, based on an analysis of Canadia, Marrella, Opabinia, Ottoia, and Pikaia, all from the classic Burgess Shale Walcott Quarry. The tissues interpreted as most labile are often characterized by the presence of kaolinite, an aluminum-rich clay which is absent from the remainder of the fossil and the matrix. In combination with bulk rock composition and metamorphic history, these data imply that the premetamorphic assemblage included kaolinite which was quantitatively transformed to other phases, particularly in the matrix. The survival of kaolinite only in association with the more labile fossil tissues suggests that it originated as a result of clay-organic interactions early in diagenesis and persisted despite metamorphic conditions. Kaolinite is toxic to decay bacteria and would have aided the polymerization of organic remains, allowing it to play a critical role in the conservation of the most labile tissues in these iconic fossils.



Speaker

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### Anoxia can increase the rate of decay for cnidarian tissue: Using *Actnia equina* to understand the early fossil record

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An experimental methodology is developed on a cnidarian model organism to serve as a comparison to previous such studies on bilaterians. We examine whether there is inherent bias against the fossilization of cnidarian tissue and their diagnostic characters and under what conditions these occur and in what way. These experiments show that cnidarian decay begins with a primary rupturing of the epidermis, followed by rapid loss of recognizable internal morphological characters. It also suggests that unlike in bilaterian taxa, diploblastic tissue is not universally decayed more slowly under anoxic or reducing conditions and some cnidarian characters even decay more quickly under anoxic conditions than they do under oxic conditions. This suggests the decay pathways acting may be different to those affecting bilaterian tissue. Further, fossil Lagerstätten that rely on anoxia for soft tissue preservation such as the Burgess Shale Type deposits may be uniquely bad windows for diploblastic preservation. Such experiments are providing crucial insights in to how soft tissue is preserved in Konservat-lagerstätten and how we can best understand the exquisite fossils they contain.

Speaker

# The sea spiders from Solnhofen (Arthropoda: Pycnogonida)

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Sea spiders (Arthropoda: Pycnogonida) form a unique group of arthropods of which the oldest unambiguous fossil dates back to the Silurian (ca 425 million years). All extant species belong to the order Pantopoda characterized by cylindrical legs and an unsegmented, reduced abdomen, whereas the eight Paleozoic species exhibit a large panel of morphologies, including legs specialized for either paddling or walking, and various number of abdomen segments. Instead, the three Mesozoic fossils are assigned to Pantopoda. They all originate from the unique site of La Voulte-sur-Rhône, France (Callovian, ca 165 million years), remnant of a Middle Jurassic deep water environment. In the present study, we examined the morphology of nine undescribed fossil sea spiders from the Solnhofen-type outcrops of Germany, a remnant of the shallow lagoons of the European tropical archipelago of the Late Jurassic (ca 150 million years). We performed various macrophotographic techniques with image stacking, in order to reveal inconspicuous structures. All the fossils are pantopods, and two are even assigned to already described genera: the Middle Jurassic *Colossopantopodus*, and the extant *Eurycyde*. Other fossils are poorly preserved, however peculiar features indicate in some cases possible affinities to other extant genera. The existence of four extant families in Jurassic (Ammotheidae, Ascorhynchidae, Colossendeidae, Endeidae) suggests that the diversification of Pantopoda occurred prior to Middle Jurassic.



Speaker

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#### The Winneshiek biota, a Konservat-lagerstätte in an Ordovician impact crater

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The Middle Ordovician (Darriwilian) Winneshiek Konservat-lagerstätte occurs near the city of Decorah in northeast Iowa. The fossils are preserved within the laminated organic- rich sediments of the Winneshiek Shale. The biota represents an unusual marine assemblage including linguloid brachiopods, a eurypterid and a basal chelicerate, phyllocarid crustaceans, ostracods, conodonts, and jawless fish. The eurypterid is the oldest example described and the largest of Ordovician age; extrapolation indicates that it reached lengths of up to 1.7 metres. The largest conodont apparatuses (preserved as bedding plane assemblages) indicate animals more than half a metre in length. Associated with these taxa are a variety of three-dimensionally preserved coprolites and possible cololites, all of uncertain origin. The arthropods are preserved as remains of cuticles and carbonaceous films whereas the bromalites are phosphatized. Elements of arthropod feeding appendages (isolated setae and gnathobases), as well as acritarchs and filamentous green algae, have been extracted from the shale as small carbonaceous fossils. The Winneshiek Shale is exposed in a small section near Decorah that is mostly submerged by the Upper Iowa River. A combination of drilling and geophysical data, together with evidence from surface outcrops, shows that it was deposited within a shallow circular basin immediately around Decorah that is discordant with the surrounding geology. This circular structure, which is 5.6 km in diameter and ~200 m deep, is surrounded by Upper Cambrian to Lower-Ordovician platform strata. The basin fill includes the Winneshiek Shale, which overlies a poorly known sequence including breccias composed of fragments of the surrounding lithologies. Drill cuttings and core samples yield quartz grains with shock deformation features characteristic of a meteorite impact. The crater, which was probably close to land, was flooded by the sea but only a restricted fauna was established. Some similar fossils occur in the coeval Ames structure in Oklahoma suggesting that the Decorah crater may be the result of one of several related impacts. Impact structures represent an under recognized setting for exceptional preservation.



<sup>&</sup>lt;sup>'</sup> Speaker

#### The Herefordshire Konservat-lagerstätte, singular Silurian evidence for the history of invertebrate clades

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The Silurian (Wenlock Series, ~430 Myr BP) Herefordshire Konservat-lagerstätte in the Welsh Borderland, UK, is a critical source of unique three-dimensionally preserved fossil animals, most with soft tissues, from a key period of time following the Great Ordovician Biodiversification Event. It is the most important Silurian Konservat-lagerstätte known in terms of its taxonomic diversity and quality of preservation. Many of the animals have been documented in the last 20 years based on physical tomography and reconstruction as virtual fossils, and many more await detailed study. The taxa include an abundance of sponges, radiolarians, brachiopods, aplacophorans, a gastropod and other molluscs, a polychaete annelid, a lobopod, a diversity of arthropods including a stem-group arthropod, marrellomorph, trilobite, pycnogonid, horseshoe crab, stem-group mandibulates, ostracods, a pentastomid, barnacle and phyllocarid, graptolites, and echinoderms including an asteroid, edrioasteroid and ophiocystoid. The Herefordshire fossils are characterized by calcite replacement and an extraordinary level of detail within the concretions that preserve them. Thus, almost without exception, they have yielded morphological data that bear on the history and phylogeny of the group to which they belong, and a number represent unique stratigraphic records that provide age data to calibrate the chronology of animal evolution. The palaeoenvironmental setting of the fauna is outer shelf/upper slope within the Anglo-Welsh Basin. Ecological insights are based largely on functional morphology, but include evidence of arthropod brooding strategies and parasitism, and habitats vary from benthic to pelagic.



Speaker

#### Libeň and Letná formations Lagerstätten (Sandbian, Prague Basin, Barrandian area): state of art and perspectives

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Upper Ordovician (Sandbian) Letná and Libeň formations provide a unique insight into the poorly known part of Lower Palaezoic life. Several levels within both formations show exceptional preservation of non-mineralized and poorly mineralized fossils. Non-trilobite arthropods, including marrellomorph (Furca), cheloniellid (Duslia), aglaspidid-like arthropods (Zonozoe, Zonoscutum, Drabovaspis, Chacharejocaris ?, Triopus and Caryon), occur together with richly diverse trilobites. Soft parts have been documented in four trilobite genera, particularly in Birmanites, Dalmanitina, Deanaspis, and Selenopeltis. Some layers, characterized by massive occurrence of articulated trilobites, ophiuroids, asteroids and carpoids, represent cases of the Konzentrat-lagerstätten. The Drabovia -Aegiromena Fauna dominated by rich brachiopods includes also the aforementioned trilobites and non-trilobite arthropods; these associations are characteristic for the inshore quartzose sandstones. A poor atheloptic trilobite association is, on the contrary, typical for the offshore slope settings. Very rare graptolites, rare trilobites of the Cyclopygid Biofacies and especially the brachiopods of the Paterula Community are confined to the poorly oxygenated black shales in the central parts of the basin. Diverse ichnofossils (especially in Letná Formation) play an important role in the understanding and interpretation of the environment and faunal diversity. New data make possible a better assessment of stratigraphy and understanding of depositional environment. Investigation of the classical and newly discovered outcrops and their comparison provides important data for the re-definition of faunal communities. New concept of water-depth and substrate-related trilobite, bivalve, echinoderm, brachiopod, and ichnofossil assemblages and associations is in progress. The recent study is associated with systematic and functional evaluation of separate trilobite, non-trilobite arthropod, bivalve and echinoderm taxa and ichnotaxa, and by the palaeoecological and taphonomical interpretations. All these studies, however, should be related especially to the parallel investigation of the analogous Fezouata and Tafilalt biotas.

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<sup>°</sup> Speaker

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#### Fish assemblage from an upper Barremian Konservat Lagerstätte in the Sidi Aïch Formation of the Chotts basin (Southern Tunisia)

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The Sidi Aich Formation of the Chotts basin of southern Tunisia has yielded an upper Barremian fossil assemblage with coniferal plant remains, freshwater conchostracans, shrimps and fishes. The specimens are exquisitely well preserved in a fine grey claystone showing varved sequences interpreted as permanent inner foreshore ponds that received episodic influence of sea water. The fish assemblage comprises few specimens so far, but it is rather well diversified. Several uncomplete specimens show typical ichthyodectiform characters, in particular in the organisation of the vertebral column and fins, and may be included more specifically in the genus *Cladocyclus* thanks to the shape of its cleithrum. Two specimens show characters of osteoglossomorphs, and more specifically of osteoglossiforms. Interestingly, they also show characters of pantodontids, in particular very elongated pectoral fins. A tiny specimen, about 21 mm of standard length, is referred to the gonorynchiforms, probably a chanoid. Another small individual, 24 mm in standard length, is likely a stem otophysan with possible affinities with Clupavus and Lusitanichthys. Eventually, a few specimens, whose description is complete and almost published, represent a new genus and species of a paraclupeid ellimmichthyiform. The new taxon shows relationships with Early Cretaceous species from the incipient South Atlantic. From a palaeoenvironment point of view, the fish assemblage represents a mixture of taxa typical from freshwater, the osteoglossiform, with fishes that dwell in both marine and freshwater environments, such as Cladocyclus, the chanoid and the paracupeid, together with a taxon that lived mainly in marine environment, the otophysan (although paradoxically this clade represent today about two thirds of the diversity of freshwater ray-finned fishes).

The study of the assemblage, which constitutes a Konservat Lagerstätte, is still in its infancy, but it shows already a great potential for new discoveries and it fills geographical and temporal gaps for understanding the evolutionary history of Early Cretaceous ray-finned fish assemblages.



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### Palaeoenvironmental constraints of lithographic limestones: insights from the Upper Jurassic Wattendorf Plattenkalk Lagerstätte (Middle Kimmeridgian, Southern Germany)

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By combination of data from lithological, geochemical and taphonomic investigations, the palaeoenvironmental conditions and depositional history of the middle Kimmeridgian Wattendorf Plattenkalk of Southern Germany were reconstructed. The Wattendorf Plattenkalk, the stratigraphically oldest occurrence of lithographic limestone from Southern Germany, allows extensive taphonomic investigations because qualitative as well as quantitative data from a large number of fossils stemming from all bedding planes of a ca. 20 cm thick excavation level could be collected. Taphonomic data from 141 actinopterygian fish fossils was obtained because of their predisposition for biostratinomic modification. Successive grades of taphonomic features such as bending of the spinal column, grade of disarticulation and completeness were investigated and the combinations of these different biostratinomic features were grouped by layer. An Euclidean cluster analysis identifies four distinct taphofacies (Taphofacies WA to WD), representing four different water-energy regimes, with the transition from taphofacies WA to taphofacies WD marking a development from slight disturbance to higher disturbance having affected fish carcasses. The occurrence of soft-tissue permineralization in the Wattendorf Plattenkalk, such as phosphatization, pyritization and iron-oxide impregnation of cellular structures provides data on oxygen availability and pH level of the sediment. The size distribution of synsedimentary pyrite framboids indicates anoxic conditions in the water column and sediment of the Plattenkalk basin. Oxygen stable-isotope ratios from skeletal elements of belemnites, brachiopods and oysters show palaeo-water temperatures ranging from 9°C to 24 °C. The data obtained allowed to reconstruct the Wattendorf Plattenkalk basin as a restricted depositional environment exhibiting stable environmental conditions with widespread anoxia in a subtropical palaeoclimate. Periodically, palaeoenvironmental conditions fluctuated, possibly due to storm events. Strong perturbations in fossil fish preservation were induced by bottom-water currents and mixing of the water column which also introduced oxygenated waters to the bottom of the otherwise inhospitable basin.



<sup>.</sup> Speaker

#### The exceptionally preserved early fossil record of Euarthropoda and the Cambrian Explosion

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As the most abundant and diverse animal phylum, Euarthropoda have been major components of animal ecosystems for over 500 million years. Euarthropod fossils have also been key for examining the dynamics of the rapid early radiation of animals during the Cambrian Explosion. This event is documented by the Cambrian fossil record, however Precambrian ancestors to the Metazoa have long been sought. Here we use the early fossil record of euarthropods as a model to explore the quality of fossil data as it relates to the Cambrian Explosion. Numerous types of fossil preservation, including soft-bodied macrofossils from Burgess Shale Type (BST) localities, biomineralised exoskeletons, microfossils, and trace fossils are compared and contrasted across the Ediacaran-Cambrian boundary to constrain when euarthropods first evolved. BSTs provide the most complete metazoan example of phylum-level anatomical construction in the euarthropod stem lineage during the Cambrian from 518 million years ago (Ma). The stem lineage includes non-biomineralized groups such as Radiodonta (e.g. Anomalocaris) that provide insight into the step-by-step construction of euarthropod morphology, including the exoskeleton, biramous limbs, segmentation, and cephalic structures. Trilobites are crown group euarthropods that appear in the fossil record at 521 Ma, before the stem lineage fossils, implying a ghost lineage that needs to be constrained. These constraints come from the trace fossil record, which show the first evidence for total group Euarthropoda (Cruziana, Rusophycus, etc.) at around 537 Ma. A deep Precambrian root to the euarthropod evolutionary lineage is disproven by a comparison of Ediacaran and Cambrian lagerstätten. BSTs from the latest Ediacaran Period (e.g. Miaohe Biota, 550 Ma) are abundantly fossiliferous with algae but completely lack animals, which are also missing from other Ediacaran windows, such as phosphate deposits (e.g. Doushantuo, 560 Ma). This constrains the appearance of the euarthropod stem lineage to no older than 550 Ma. While each of the major types of fossil evidence (BSTs, trace fossils, and biomineralised preservation) have their limitations and are incomplete in different ways, when taken together they allow a coherent picture to emerge. In congruence with the most recent analyses from molecular paleobiology, our comprehensive fossil data set suggests an entirely Cambrian origin and subsequent radiation for total group Euarthropoda.



<sup>&</sup>lt;sup>°</sup> Speaker

### Phylogenetic affinities of erymid lobsters (Crustacea, Decapoda) using morphological characters and systematic implications

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Erymidae Van Straelen, 1925 are lobsters typical of the Mesozoic, representing almost 5% of the fossil decapod species. Despite the importance of these lobsters in crustacean fossil record, their phylogenetic affinities remain uncertain. Indeed, the "classic" idea consists in the integration of erymids with other clawed lobsters and crayfish into Astacidea, but some recent works suggest that Erymidae could be closely related to glypheid lobsters, within Glypheidea. Moreover, according to the different authors, some fossil taxa have been alternately considered to be erymids or not, but the most recent contributions restrict Erymidae to genera with an intercalated plate. The presence of this fusiform area located on the dorsal side of the cephalic region is considered to be unique among Decapoda. Recently, the presence of an intercalated plate was reported on the extant Enoplometopus Milne Edwards, 1862 and led some authors to assign Enoplometopus and Erymidae into the clade Erymida, questioning the extinct status of erymid lobsters. So, relying as far as possible on the recent review on erymid and glypheid lobsters, the purposes of our phylogenetic analysis were: 1) to clarify the phylogenetic affinities of erymid lobsters, 2) to delimit the group, and 3) to explore the internal relationships of the group. A cladistic analysis led us to recognize six genera to be erymids: Eryma Meyer, 1840, Enoploclytia M'Coy, 1849, Palaeastacus Bell, 1850, Pustulina Quenstedt, 1857, Stenodactylina Beurlen, 1928, and Tethysastacus Devillez et al., 2016. They are included within the clade Erymoidea, sister to that of other clawed lobsters. This supports the inclusion of erymids within Astacidea. Enoplometopus remains extern to Erymoidea, so its intercalated plate does not reflect close relationships with erymids. It is probably a convergence, so erymid lobsters have no extant representatives. The inclusion of the recently described post-orbital area in the dataset supports the split of Erymoidea in two clades that justifies a systematic rearrangement of erymid genera within two families: Enoploclytidae n. fam., lacking the post-orbital area (Enoploclytia, Pustulina), and Erymidae, showing the post-orbital area. Erymidae are also separated in two sub-families: the simplicity of the carapace groove pattern of Tethysastacus justifies its placement within Tethysastacinae n. s.-fam. while Eryma, Palaeastacus and Stenodactylina are assigned to Eryminae.



Speaker

#### Dysodiles: a new Konservat-Lagerstätte from the Lower Barremian of Lebanon

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Dysodiles were first described by Cordier in 1808. They are characterized by their fine laminations, organic content and richness in fossils. In Lebanon, these rocks croup out in different lacustrine geological formations. They were scarcely mentioned in the literature by the end of the 19th century-beginning of the 20th. Accordingly, old citations mentioned the presence of dysodiles in the Neocomian sandstones, in which Janensch described two fish species, while Fraas identified some fossil plants. Afterwards, Lebanese dysodiles were forgotten for a long time until recently, when we re-/discovered numerous outcrops in several Barremian and Albian localities across Lebanon. We present preliminary results of our study of five dysodile outcrops from the Lower Barremian of Lebanon. They belong to the "Grès du Liban" unit, represented by up to 300 meters of fluvio-deltaic sandy facies. The studied deposits correspond to small lakes of limited extension (of a few km2). They are mostly found nearby volcanic altered rocks, or associated to cinerites, suggesting a possible relation between the volcanism and their deposition and/or preservation. Our first investigations show a richness in microfossils such as pollens, spores and ostracods mainly belonging to Cypridea and that indicate a calm environment by the association of adults and juveniles, and the abundance of butterfly forms. Adding to that, a relatively high diversity of well-preserved macrofossils such as fishes of different sizes and shapes ('palaeonisciform' and teleosts including both pleuropholid-like fish and more derived taxa), fresh-water turtles and insects (Ephemeroptera larvae, Diptera and Hymenoptera), gastropods and plant debris. This fossil assemblage appears of interest to fill our lack of knowledge on the "Grès du Liban" diversity, and also more generally to complete the huge gaps in the knowledge about Early Cretaceous lacustrine fauna. Finally, a collaboration between geochemistry, sedimentology and paleontology is essential in order to understand the conditions that allowed these exceptional environments and the excellent preservation of the fossils, making from the dysodiles, really special and unique Konservat-lagerstätte.



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### Distribution and taphonomic characteristics of marine mammals in Cerro Hueco la Zorra, Miocene, Pisco Formation, Peru

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The sedimentary succession of Cerro Hueco la Zorra in southern Peru consists of very thick layers of fine sandstones and siltstones alternating with thin to very thin layers of pebble conglomerates. The finegrained sediments show hummocky and swalley cross-stratification, flaser bedding, and current structures indicative of a high-energy marine environment. Overlying this succession, very thick layers of diatomaceous mudstones alternate with very thin layers of carbonate-cemented, ripple cross-bedded fine sandstones. Scattered articulated Dosinia shells occur in lenses of fine sandstone and siltstone. The diatomaceous mudstones show lenticular bedding that transitions up section to massive beds with current structures. Marine mammal fossils are very abundant scattered in the sandstones and siltstones, and very abundant in the pebble conglomerates. Vertebrate fossils are less abundant in overlying mudstones. The skeletons are mostly complete and articulated or partially disarticulated, with few individuals fully disarticulated. A significant number of very small specimens that could be baby whales also occur, which have not been reported from any other locality in the Pisco Basin. Skulls are mostly dorsal-side up and include both mandibles. Cervical vertebrae are commonly articulated to the skull. Specimens show various degrees of articulation, with specimens that are fully articulated, and others with both articulated and disarticulated portions. Regardless the degree of articulation, all the skeletons are very well preserved, in both the upper and lower surfaces of the bones. There is no evidence of macro-bioerosion, scavenging, abrasion, or long residence on the seafloor prior to burial. The high degree of completeness, articulation and preservation precludes reworking or time-averaging of the skeletons; instead it suggests rapid sedimentation in a shallow marine environment. The diatomaceous mudstones were deposited in a deeper environment, but the occurrence of lenticular bedding and current structures indicate the influence of storms. In the pebble conglomerates, marine mammal fossils are predominantly fully disarticulated and scattered vertebrae, ribs, mandibles and skulls, with very few limb bones, although some clusters occur. In this layer, most specimens consist of disarticulated vertebrae, ribs, mandibles and skulls, with very few limb bones. All the bones show a similar degree of preservation with minimal abrasion, and there is no macrobioerosion marks. The pebble conglomerates suggest an intertidal marine environment. Preservation of bones in both fine sediments and pebble conglomerates suggest mass mortality events followed by rapid sedimentation instead of attritional death followed by slow burial.



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#### Arm hooks and statoliths of coleoid cephalopods from Jurassic lagerstatten in the Wessex Basin, Southern England

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The Jurassic succession of the Wessex Basin (especially that cropping out within the Dorset and East Devon World Heritage Site) contains important lagerstätten for many fossil groups, including coleoid cephalopods. The Blue Lias and Charmouth Mudstone formations of West Dorset, the Oxford Clay Formation of Wiltshire and the Kimmeridge Clay Formation of the Isle of Purbeck have provided large numbers of important, exceptionally preserved, body fossils that inform our knowledge of coleoid palaeobiology. This palaeontological heritage was begun by the collecting of Mary Anning (1799 - 1847), the species descriptions of William Buckland (1784 - 1856) and Richard Owen (1804 - 1892), and the early palaeoecological interpretations of Henry De La Beche (1796 - 1855). Many of these important specimens are housed in the collections of the Natural History Museum (London), Bristol Museum & Art Gallery and the new Museum of Jurassic Marine Life in Kimmeridge but fossils attributed to Lyme Regis are to be found in collections throughout the world. The exceptional preservation of belemnitids and teuthids, including phragmocones, ink sacks, permineralized muscle fibres and arm crowns (with hooks) has provided a wealth of valuable palaeobiological information. Associated with these fossil coleoids are mudstones and limestones that have been studied for microfossils (foraminifera, ostracods, etc.) and which are now known to contain exceptionally large numbers of dissociated arm hooks and statoliths (balancing organs). These microfossils can now be used, in some cases, to record the presence of key taxa (e.g., Belemnotheutis antiquus and Clarkeiteuthis montefiorei) in the absence of well - preserved body fossils. The present state of our knowledge of the Jurassic assemblages of arm hooks and statoliths in the Wessex Basin is presented and remaining issues identified.

One of the most important remaining questions is how such exceptional preservation, which often implies dysaerobic or even anoxic conditions on the sea floor can be associated with sediments containing abundant foraminifera and ostracods that are suggestive of oxygenated sea floor conditions. Understanding the complete depositional process, and subsequent taphonomy, remains elusive although locations such as the Christian Malford (Wiltshire) "squid bed" should allow description of the processes involved.



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## The diversity of feeding apparatuses of arthropods in the Rhynie Chert

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When we investigate modern-day ecosystems, the ecological roles of the different organisms living there can to be studied in detail, simply by observation. In fossil ecosystems, such direct observations of life styles are simply not possible. Instead they have to be inferred indirectly, for example, from morphological structures exhibited by the organisms. These structures can then be compared to similar structures in modern organisms of which the functional morphology is known. However, a requirement for such studies of fossil ecosystems is exceptional preservation of the organisms. One lagerstätte with especially exceptional preservation is the Lower Devonian Rhynie Chert from Scotland. The smallest structures preserved in these deposits are in the sub-micrometre range, such as minute setae, and can be visualised even three-dimensionally with certain micro-photographic methods. As the Rhynie Chert is the oldest known non-marine ecosystem with exceptional preservation, it provides important clues on early terrestrialisation events in deep time. While the Rhynie Chert is most famous for preserving the earliest terrestrial plants, also certain arthropods apparently made their first steps on land in the surroundings of the hot springs which formed the Rhynie Chert. Additionally, also several species of nonmarine aquatic arthropods are preserved here in great detail, even with different ontogenetic stages. The arthropods preserved in Rhynie Chert range from different spider-like chelicerates over different myriapod and insect species to several eucrustaceans, but also include possible representatives of now entirely extinct lineages. Of the preserved morphological structures, especially the appendages, which provide most information about the life habits of an arthropod, can be reconstructed down to their smallest sub-structures. One ecologically especially important structure formed by arthropod appendages is the feeding apparatus, which is responsible for gathering, processing, and intake of the food particles. By reinvestigating representatives the entire range of arthropods from the Rhynie Chert, I provide here an overview of the large diversity of feeding strategies in this non-marine ecosystem, which was previously unexpected.

Speaker

### A mineralogist's point of view on exceptional preservation: the case study of the La Voulte-sur-Rhône crustacean fossils

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*Konservat-lagerstätten* are geological deposits yielding "exceptionally" preserved fossils, which display fine morphological details (incl. soft tissues), usually not preserved in the fossil record. *Konservat-lagerstätten* constitute the most complete source of palaeobiological information (for a given location and time). Nevertheless, although it appears necessary to uncover any potential taphonomic biases and assess the robustness of paleontological reconstructions (anatomy, biology, and environment), the processes leading to such "exceptional preservation" remain poorly constrained.

To better constrain these processes, we investigated the geochemical and mineralogical compositions of a range of crustacean fossils from the Jurassic Konservat-lagerstätte of La Voulte- sur-Rhône (Ardèche, France). Chemical phase composition was investigated using SEM-EDS and synchrotronbased XRF elemental mapping (X-ray fluorescence). Mineralogical characterisation was performed using optical microscopy, powder X-ray diffraction (XRD) and mineral distribution inside the fossils was rendered using synchrotron-based XRD mapping.

Combining these techniques allowed identifying the mineralogical phases composing the fossils: a variety of minerals with complex structural relationships for the 3D-preserved fossils (Ca-phosphates, Fe-, Zn-, Pb-sulphides, Ca-sulphates, Fe-oxides and Ca-, Mg-carbonates) and Ca-phosphate with Fe-sulphides for the flattened fossils. The surrounding matrix for the two types of fossils (Mg, Ca-rich carbonates, clay and detrital silicates) was also documented. Phosphates and sulphides precipitated first, thereby allowing the preservation of delicate organic structures. Mg-calcite cement then consolidated the structures.

Different types of "exceptional" preservation exist in the Jurassic Konservat-lagerstätte of La Voulte-sur-Rhône. Fossils are preserved in 3D fossils within concretions or as compressions. These different styles of preservation may be explained with the same mineral phase chronology, with the sole difference being the lack of carbonate precipitation (and especially, Mg-calcite) in compressions, which would otherwise ensure cementation and nodule formation.



Speaker

### Geometric morphometrics and the evolution of wing colour patterns in fossil insects

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Wing colour patterns are the basis for diverse insect communication strategies and thus are critical to understanding aspects of the roles of innovation, homology, and convergence in driving insect evolution. Fossil insects often exhibit wing colour patterns, but with the exception of a single study on eyespot patterning in Kalligrammatidae (Neuroptera) there has been no systematic investigation of their evolution in fossil insects. We investigated colour patterns in Middle Jurassic neuropterans from the Daohugou Lagerstätte (Jurassic, China) using novel geometric morphometric methods. Digital wing images from 300 specimens were attributed to 11 descriptive morphogroups (e.g. vertical stripes, apex pattern, eyespots, spots). Eigenimage analysis tested whether these qualitative visual morphogroups represent mutually exclusive geometric pattern categories. Our results show that some pattern morphogroups are geometrically more diverse than others. Mapping taxonomic information onto the morphospace plots reveals how this geometric diversity relates to taxonomic diversity at the genus level. Our results confirm that quantitative, image-based analytical methods can be applied successfully to non-traditional morphometric data and can facilitate studies of evolutionary diversity through time.



Speaker

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# The middle Cambrian Spence Shale (Series 3: Stage 5) Lagerstätte: a key Cambrian ecosystem

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The middle Cambrian (Series 3: Stage 5) Spence Shale Member of the Langston Formation in northern Utah and southern Idaho (U.S.A.) is a relatively well-known Burgess Shale-type (BST) deposit preserving a diverse soft-bodied fauna including anomalocaridids, bivalved arthropods, priapulids, hyoliths, and lobopodians, as well as abundant trilobites, brachiopods, and echinoderms. Information from this deposit has provided important insights into middle Cambrian paleoecology, biodiversity, and phylogeny. Diversity in the Spence is well documented, although new taxa continue to be discovered. However, patterns of species co-occurrence and their environmental preferences are not well known due to lack of stratigraphic context for many previously collected specimens. Expanding knowledge in these areas will enhance our understanding of this BST deposit and aid in making comparisons between the Spence and other BST deposits.

To increase palaeoecological and palaeoenvironmental understanding of the Spence, we focused on the classic Miners Hollow exposure in the Wellsville Mountains of northern Utah. We re-measured the section and collected samples for lithological, geochemical, and paleontological study. Notably, the softbodied fauna is not restricted to one unit, with several fossil beds being identified. In conjunction with advances in mudstone sedimentology and understanding of shale depositional environments in general, these new data illuminate the depositional environments and diagenetic pathways in the Spence. They also highlight some of the differences between the Spence and other BST deposits in Utah, especially as the mudstones preserving the specimens are closer in composition to those in the Burgess Shale and the Rockslide Formation.

Data collected indicate that the preferred habitats of certain taxa can be characterized. For instance, the majority of the arthropod fauna occurs in the deeper water mudstones of the Wellsville Mountains. However, some species (e.g., *Gogia guntheri* and *Haplophrentis reesei*) also occur in varied environments across their different occurrences in the Spence. For subsequent field seasons, we will sample several outcrops to gain an understanding of the distal and proximal communities. Ultimately, better characterization of the Spence will help to decipher the multifarious nature of BST deposits in the Cambrian of western Laurentia.



Speaker

### Inside out exceptionally preserved Jurassic cephalopods

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The La-Voulte-sur-Rhône lagerstätte (Jurassic -Callovian) provides unique insights into cephalopod evolution for several reasons: the iron rich mineralisation preserved the soft tissues tridimensionally, some genera are only known from this site and it is one of the few records of a bathyal environment. Six coleoid species from this locality were described in a series of studies mostly done by Fischer and Riou. Nonetheless, the systematic position of La Voulte coleoids based on the external morphology is still debated and can now be reappraised using tomographic techniques. Indeed, CT and synchrotron CT provide new data on internal features and hidden morphological characters. Results from propagation based phase contrast synchrotron CT (proposal ESRF, ES-36) are here presented for several species such as *Vampyronassa rhodanica, Mastigophora* aff. *brevipennis* and undescribed specimens still embedded in the matrix. The preservation of internal structures is heterogeneous among the specimens. Some specimens preserve fine internal tissues such as gills, crop, ink sac and suckers. Such detailed preservation provides key information for comparisons with Recent Coleoidea systematics based on soft tissue and character evolution.



Speaker

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### The Ya Ha Tinda Lagerstätte: a newly documented Pliensbachian-Toarcian (Early Jurassic, ca. 183 Ma) fossil Konservat-lagerstätte from Alberta, Canada

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Konservat-lagerstätten - deposits of exceptionally preserved fossils - offer vital insights into evolutionary history. To date, only three Konservat-lagerstätten are known from Early Jurassic marine rocks (Osteno, Posidonia Shale, and Strawberry Bank), and these sites are all located in Europe. Recently, a new assemblage of exceptionally preserved fossils has been discovered at the Ya Ha Tinda Ranch in Alberta, Canada; this site is the first marine Konservat-lagerstätte described from the Jurassic of North America. The Ya Ha Tinda assemblage includes articulated vertebrates (fish, ichthyosaurs), crinoids, crustaceans, brachiopods, abundant mollusks (coleoids with soft tissues, ammonites, gastropods, and bivalves), wood, and microfossils. Paired bio- and chemostratigraphy show that Lagerstätte deposition occurred during the late Pliensbachian through early Toarcian, capturing the carbon isotope excursion (CIE) associated with the Toarcian Oceanic Anoxic Event. Therefore, the Ya Ha Tinda biota from the Panthalassa Ocean is coeval with Toarcian Lagerstätten from the Tethys Ocean, namely the Posidonia Shale and Strawberry Bank Lagerstätten. Comparisons among these deposits permit new insights into the diversity, ecology, and biogeography of Jurassic marine communities during a time of pronounced biological and environmental change (e.g., expanded subsurface anoxia, warming, and extinctions). They also highlight the possibility that Mesozoic anoxic events significantly enhance exceptional preservation in the fossil record. This presentation will outline the key characteristics of this new Konservat-lagerstätte (e.g., age, depositional environment, biota) as well as the recent discoveries made and the paleontological opportunities moving forward.



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### The morphology of *Spinolestes*, an Eutriconodont mammal from Las Hoyas (Lower Cretaceous, Spain)

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We present Spinolestes xenarthrosus, a Eutriconodont mammal that roamed a wetland in the Lower Cretaceous (Barremian) in what today is the Province of Cuenca (Spain). The specimen is yet another exquisitely preserved fossil from the Las Hoyas lagersttäten, and as such, its preservation is exceptional. However, this fossil not only is important because it is the first nearly complete skeleton of a Mesozoic mammal from the Iberian Penninsula, but also because it presents unprecedented-and unambiguousmorphological details of organs. In effect, it is possible to see the respiratory apparatus, including the lungs, the auditory system, including the primitive organization of ear bones and the typical mammalian outer pinnae (the cartilaginous ear), and the skin's epidermis and hair. Furthermore, the liver is interpretable as a marked red stain underneath the rib cage which, at the same time, allows to envisage the position of the characteristic mammalian diaphragm. Definitively more striking is the fact that it is possible to scrutinize structural features of the skin with unprecedented detail, such as the cell organization of the epidermis, features of follicle morphology and composition, and even cuticular and internal microstructure details of the hair. At this outstanding level of resolution, Spinolestes shows as series of previously unidentified tubular structures, presumably keratinous and microstructurally assembled as if they were spines, which were named protospines and give name to the species. Here, using high resolution imaging we will concentrate in reviewing such features of the morphology, most of them published but other more recently discovered, that allow understanding an animal of the Mesozoic almost as if we saw it in life.



Speaker

### Diverse 3D photonic crystal structures in fossil insect scales

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Beetles represent the most speciose order of modern insects, with many taxa displaying vibrant structural colours that result from the physical scattering of incident light by tissue structures with periodicities measuring from tens to hundreds of nanometres. These structures, which manipulate the flow of light by exploiting the periodic variation in the refractive index between their constituent materials, are termed photonic crystals (PCs). Across the animal kingdom, structural colours play a vital role in inter- and intraspecific visual communication strategies including sexual signalling, aposematism and crypsis. In beetles, as in most insects, structural colours are produced by 1D-PCs in the cuticle, i.e. thin-film and multilayer reflectors. Certain beetles (predominantly weevils and longhorns), however, have evolved more sophisti- cated 3D-PCs, housed within cuticular scales. These 3D-PCs are rarely fossilized, which may reflect, in part, the paucity of preserved scales. To date, 3D-PCs have been reported in only a single fossil weevil and therefore the evolutionary history of these tissue architectures, and the driving forces behind them, are unknown. Here, we report the discovery of diverse 3D-PCs in various Pleistocene beetle taxa from Canada and Switzerland. We used small-angle X-ray scattering (SAXS) in tandem with electron microscopy to characterize the ultrastructure of the fossil scales, identifying PCs akin to those reported in modern insects. These data will serve as a platform to deliver novel insights into the evolution, development and functionality of scales in coleopteran species.



Speaker

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# Exceptionally preserved skin structure reveals the coevolution of skin, feathers and metabolism in feathered dinosaurs and early birds

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Feathers are remarkable evolutionary innovations that are associated with complex adaptations of the skin in modern birds. Fossilized feathers in dinosaurs and basal birds provide insights into feather evolution, but how associated integumentary adaptations evolved is unclear. Here we report the discovery of fossil skin, preserved with remarkable nanoscale fidelity, in three non-avian maniraptoran dinosaurs and a basal bird from the Cretaceous Jehol biota (China). The skin comprises patches of desquamating epidermal corneocytes that preserve a cytoskeletal array of helically coiled  $\alpha$ -keratin tonofibrils. This structure confirms that basal birds and non-avian dinosaurs shed small epidermal flakes as in modern mammals and birds, but structural differences imply that these Cretaceous taxa had lower body heat production than modern birds. Feathered epidermis acquired many, but not all, anatomically modern attributes close to the base of the Maniraptora by the Middle Jurassic.

Speaker

#### Toward a documentation of the residual shell colour patterns for the Mesozoic times

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As stated by Williams (2016) almost nothing is known about the evolution of shell colour in Mollusca. Among the numerous questions about the shell colour and their related patterns, that of their evolution during the geological times is critical. In the geological record, two types of residual colour patterns can be distinguished: the colour patterns visible in natural light (= CPNL) and the colour patterns that we can only observe in UV light (= CPUV). Although CNPL are very ancient (Ordovician), they remain very rare and begin more numerous only in the Late Tertiary. Until very recently, CPUV, known on Cenozoic shells, were considered anecdotic and useless for evolutionary or taxonomic studies. However, based on European material, Caze et al. (2011) demonstrated that CPUV are potentially detectable continuously throughout the Cenozoic. Therefore, Cenozoic CPUV should be considered to be very common and now the last published works integrated CPUV for species characterization including intraspecific variabilities. If we can consider that Cenozoic CPUV are now better known than for 30 years ago, the Mesozoic era remains an unworked field. Caze et al. (2015) studied the diverse and exceptionally well-preserved molluscs from the Late Jurassic Cordebugle Konservat Lagerstätte (Calvados, France). They reveal CPUV of no less than 25 species of bivalves and gastropods. On the other hand, this Mesozoic experience of the Jurassic of Cordebugle took root in the idea that very well preserved fossil shells, as Cenozoic shells, can only provide numerous CPUV. Now, first we demonstrate that shells having already undergone a diagenetic alteration can also provide CPUV and second we enlarge the Mesozoic documentation by new CPUV from the late Cretaceous period (Maastrichtian, Campanian and Coniacian) and Triassic (Carnian). These last results suggest that Mesozoic CPUV are less rare than previously expected.



Speaker

#### Preliminary report on the first mid-Permian ecosystem from South Africa, as revealed by a new Lagerstätte near Sutherland, Northern Cape

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The fossil record of terrestrial invertebrates from the mid-Permian (Guadalupian) is very poor, especially in Gondwana; furthermore, the few known fossils generally do not preserve soft-tissue. Here we present preliminary details of a recently discovered and exceptionally well-preserved assemblage of freshwater and terrestrial invertebrates and plant fossils, from a Lagerstätte near Sutherland, South Africa. The locality represents a lacustrine environment, and includes a very high density of insect fossils and associated plants, in a very fine-grained mudrock. To date, the site has yielded impression fossils of insects (> 200 specimens), some potentially containing organic residues and evidence of soft-tissues, fine details such as setae, and even patterns of wing colouration. Many completely articulated insect bodies have been found, mostly aquatic nymphs, which are typically rare in the Permian fossil record. Specimens of arthropod groups such as the Hydrachnidia (water mites), Odonatoptera, Hemiptera, Coleoptera, Archaeorthoptera, Palaeodictyoptera, Dictyoptera, Grylloblattodea, and Plecoptera have been found so far. This assemblage shows some parallels with those from the Middle Permian of Russia and Brazil and has the potential to contribute significantly to our understanding of insect biodiversity and biogeography during the mid-Permian in Gondwana. Also recovered from the site are numerous, very well-preserved plant impressions (> 2000 specimens), including Glossopteris leaves and three new glossopterid fertile organs. Many of the leaves showed evidence of insect interactions (trace of predations and reproductive platforms). This highly diverse fossil biota shows a complex inter-relationships of organisms that once lived in and along the margins of a lacustrine environment during the mid-Permian. Along with input from regional studies of the coeval vertebrate fossils, these fossils capture an exceptional glimpse into the palaeodiversity of ecosystems at the time. Refined studies of the site will offer new insights into possible trophic connections, paleoenvironment and palaeoclimate of the southern Karoo Basin during the mid-Permian.

Speaker

#### A new specimen of azhdarchoid pterosaur (Pterodactyloidea, Thalassodromidae) from the Santana Formation of Brazil

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The specimen consists of an almost complete mandible and partial skull conserved in a nodule. The mandible has the two mandibular rami with a complete posterior region, including a complete articular region. Anteriorly, only part of the rostrum is preserved, while posteriorly only the posterior part of the ventral region is preserved. The distance between the dorsal margin of the orbit and the dorsal margin of the nasoantorbital fenestra appears relatively large, contrasting with the tapejarids, in which this difference is marginal. The straight, and non- downward projected rostrum is an additional character that separates it from the Tapejaridae. The relatively thin ventral side of the nasoantorbital fenestra and the shape of the mandible and maxilla further exclude it from Thalassodromeus, in which the mandible and maxilla were bent near the end of the nasoantorbital fenestra, interlocking with each other. The shape of the rostrum near the nasoantorbital fenestra is similar that of Tupuxuara and the angle between the maxilla and the premaxilla is about 30°. The crest consists of the premaxilla, frontals and parietals, of which only the frontal and parietal part of the crest is partially present in this specimen. Only the anterior most part of the premaxilla is present. A lateral suture between the premaxilla and the maxilla is visible. A palatal ridge is present. In the posterior region of the skull, the parietal, lacrimal and postorbital bones form a concave depression. The lacrimal region are not swollen, contrasting with other known specimens of Tupuxuara. No suture between the jugal and the lacrimal is visible. Posterior to the orbit the supratemporal fenestra is visible as a subtriangular fenestra. The orbit of this specimen is posteriorly inclined to the maxilla, resembling the orbit of Caupedactylus. The ventral border of the orbit is also more inclined than in Tupuxuara. A rounded occipital condyle is observed on the occiput. The two mandible fuse together at the mandibular symphysis, which contains a groove, probably corresponding to a palatal ridge. The cross section of the mandible is triangular, but it progressively becomes rectangular posteriorly. The retroarticular process of the mandible is triangular in lateral view. The new specimen represents a juvenile thalassodromid and the results from the CT scan and the phylogenetic analysis will reveal more about this group of Cretaceous pterosaurs.



S21 // Oral

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#### A new Lower Cretaceous Lagerstätte for Central Colombia: an overview of the Hauterivian-Aptian Paja Formation

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The Cretaceous greenhouse 'waterworld' was dominated by shallow epicontinental seas. Modernday Colombia, northern South America, had a Cretaceous palaeolatitude of 5-7 degrees north of the equator, and the current Alto Ricaurte region (Eastern Cordillera) preserves the Lower Cretaceous (Hauterivian-Aptian) deposits of the Paja Formation. The Paja Formation is dominated by black to variegated mudrocks, with lenses of gypsum and calcite, abundant pyrite, and an exceptional fossil fauna. Fossils include virtually complete and articulated marine reptiles, including both longand short-necked plesiosaurs, numerous ichthyosaurs, and marine turtles (some with eggs preserved inside the body cavity), diverse fish, numerous pelagic ammonites, and pseudo-planktonic wood-boring bivalves. However, the Paja Formation benthic fauna is depauperate, mainly thin-shelled bivalves with abundant evidence for bottomliving microbial mats. The exquisite preservation of the pelagic fauna permits the Paja Formation of the Alto Ricaurte to be recognised as a rare, Lower Cretaceous marine vertebrae Lagerstätte. The fossil fauna strongly suggests well-oxygenated surface waters, but dysoxic-anoxic bottom waters, separated by a temperature and/or density defined pycnocline. This interpretation argues against the previously proposed intertidal evaporitic (sabkha) environment for Paja Formation seas, and sedimentological, palaeobiological, taphonomic and diagenetic data is presented to argue for deeper water conditions for the Paja Formation Lagerstätte.

Speaker

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#### Lower Cretaceous marine boring bivalves, from the Paja Formation Lagerstätte of central Colombia, northern South America

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The Lower Cretaceous (Hauterivian-Aptian) Paja Formation Lagerstätte of the modern- day Alto Ricaurte region, Eastern Cordillera of Colombia (northern South America) resulted from flooding of an extensional back-arc basin close to the palaeo-equator. The Paja Formation fossil fauna is dominated by pelagic organisms (marine reptiles, fish, ammonites), with abundant evidence of continental influence, including a dinosaur and abundant terrestrial plant remains. Within the Arcillolitas Abigarradas (middle) Member of the Paja Formation, some horizons preserve abundant wood, which is frequently bored by pseudoplanktonic pholadoid bivalves, commonly referred to as 'shipworms' or 'piddocks'. The presence of wood boring bivalves in Paja Formation seas indicates the continued presence of xylic substrates, and long residence time of floating wood. The abundance of wood was a result of nearby landmasses with a well-lit, equatorial location 5-7 degrees north of the palaeoequator. These surrounding landmasses were under the ascending limb of the Hadley atmospheric cell, with high rainfall and high terrestrial nutrient production due to subaerial weathering, which taken with elevated Cretaceous partial pressures of atmospheric CO2, was conducive to high ('tropical rainforest') terrestrial plant primary productivity. Plentiful rainfall led to abundant runoff, and proximity to the northern 'hurricane belt' meant the area was frequently affected by tropical storms, leading to a constant supply of wood to the Paja Formation basin. However, not all Paja Formation fossil wood is bored, indicating some woods were not suitable for Cretaceous wood boring bivalve infestation. This may have been due to excessive wood hardness, rapid water logging and sinking, or chemical or other factors that prevented pholadoid larval attachment. However, that some wood floated for long periods is indicated by the presence of different size classes of wood boring bivalves in a single fossil log. Paja Formation bivalves are preserved in wood replaced by dark-coloured (organic-rich) sparry (coarsely crystalline) calcite, whereas rarer silicified wood does not preserve pholadoid borings. This suggests different taphonomic pathways for the two modes of Paja Formation wood preservation.



Speaker

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# Experimental degradation of circularly polarizing scarab beetles: testing the potential for fossilization of cuticular nanostructures

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Insect cuticles possess diverse structural colouration mechanisms that include helicoidal (Bouligand) structures formed by chitin fibrils in the exocuticle of some scarab beetles. With adequate spacing, these structures reflect light with a high degree of circular polarization, the biological function of which is unknown. While recent studies have illuminated the evolutionary history of other photonic structures in insects, the evolution of Bouligand structures in beetles remains enigmatic. To test the potential for Bouligand structures to be fossilized, we conducted decay and maturation experiments on cuticles from four taxa exhibiting optical activity and one that does not. Changes were assessed using lightand electron-microscopies, reflectance spectrophotometry and Mueller matrix analysis. Reflectance spectra of untreated cuticles illustrate variations within Bouligand structures and reveal striking taxonspecific differences in their taphonomy. Original colour and polarization survive decay in the cuticles of Ischiopsopha and Gymnopleurus, but not in Chrysina (in the optically inactive Torynorrhina, colour survives). This variation may reflect the presence of uric acid in unusual cusp-like arrangement of the exocuticule of Chrysina. Original colour and polarization are lost during maturation in all taxa, probably due to polymerization. These results reveal the potential for preservation of Bouligand structures in fossils not subjected to elevated temperatures and pressures burial during diagenesis and suggest subtle taxonspecific controls on preservation related to cuticle chemistry.



Speaker

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#### Early Cambrian fuxianhuiids from China reveal origin of the gnathobasic protopodite in euarthropods

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Euarthropods owe their evolutionary and ecological success to the morphological plasticity of their appendages. Although this variability is partly expressed in the specialization of the protopodite for a feeding function in the post-deutocerebral limbs, the origin of the former structure among Cambrian representatives remains uncertain. Here, we describe *Alacaris mirabilis* gen. et sp. nov. from the early Cambrian Xiaoshiba Lagerstätte in China, which reveals the proximal organization of fuxianhuiid appendages in exceptional detail. Proximally, the post- deutocerebral limbs possess an antero-posteriorly compressed protopodite with robust spines. The protopodite is attached to an endopod with more than a dozen podomeres, and an oval flap-shaped exopod. The gnathal edges of the protopodites form an axial food groove along the ventral side of the body, indicating a predatory/scavenging autecology. A cladistic analysis indicates that the fuxianhuiid protopodite represents the phylogenetically earliest occurrence of substantial proximal differentiation within stem-group Euarthropoda illuminating the origin of gnathobasic feeding.



Speaker

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#### Widespread pyritization at the Crato Formation (Upper Aptian), Brazil: patterns and possible explanations

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It is indisputable that pyritization is ubiquitous at the Crato Formation plattenkalk (including insects, fish, and feathers), one of the most remarkable Early Cretaceous terrestrial Konservat-lagerstätten. However, the mechanisms and factors are still undebated. Here we propose new explanations concerning the pyritization of insects and fish with light microscopy and SEM. According to our results, pyritization is widespread in the analysed facies, and occurred regardless of taxonomy and composition (e.g. polysaccharides and proteins). Nevertheless, regarding insects and fish, the fidelity degree of preservation varies within and between specimens, supporting the influence of different factors controlling pyritization. More specifically, only some insects have preserved muscles and genitalia, and some fish have muscles, tendons and eyes, while most specimens are devoid of pyritized delicate tissues-but still with iron oxyhydroxides (after pyrite) occurring at some regions. Regarding insects and fish, this preservational fidelity can vary over a single specimen. It also can be related to the size of the organisms: smaller fish, ~350 mm of maximum body length, more commonly present delicate features, than larger individuals. Regarding the widespread pyritization, extrinsic factors include: (a) low Corg-containing facies concentrating pyritization at carcasses; (b) episodic supply of weatheringderived Fe3+ oxyhydroxides; and -(c) stratification and low burial rates yielding shallow bacterial Fe/SO4reduction zones, fostering their sedimentary concentrations at shallow depths. On the other hand, variations in the preservational fidelity could have been controlled by such intrinsic factors: (a) distinct morphological structures decaying at different rates; (b) carcasses undergoing different exposure times in oxygenated environments; and (c) different fish sizes, with the pyritization of small carcasses requiring less Fe and SO4-, and H2S being more readily fixed by Fe, than the large ones, because the former had less volume of decay-prone organic matter. In conclusion, we create bases for formulating testable hypotheses that should address the role of extrinsic/intrinsic factors for pyritization and its preservational fidelity at the Crato Formation, and can possibly be extended to analogous deposits.

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#### Geometry and chemistry of eye melanosomes in cephalopods and vertebrates: implications for fossil identification

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Screening pigments regulate the exposure of photosensitive structures to light and are ubiquitous in the visual systems of animals. In vertebrates the screening pigment melanin is packaged within melanosomes, micron-sized sub-spherical to ellipsoidal organelles which are known to preserve in fossils. In the eyes of extant vertebrates, melanosomes are reported from the iris, choroid and retinal pigment epithelium (RPE). RPE melanosomes exhibit two distinct geometries, a feature currently understood to be unique to vertebrate eyes and thus an important character for identifying fossil vertebrates. We use a suite of analytical techniques (scanning electron microscopy, alkaline hydrogen peroxide oxidation high pressure liquid chromatography and Warthin-Starry histological staining) to show melanosomes also occur in the eyes of several extant cephalopod taxa. As in vertebrates, these cephalopod melanosomes can show partitioning into size-specific layers in the eye. Synchrotron X-ray fluorescence reveals that melanosome layers in cephalopods and basal vertebrates have distinct chemical signatures. Melanosome chemistry may thus allow more definitive interpretations of the phylogenetic affinities of enigmatic fossils in cases where melanosome geometry is equivocal.



Speaker

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#### Melanosome geometry and trace element chemistry reveal soft tissue anatomy in fossil vertebrates

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Melanosomes are important components of integumentary tissues in modern vertebrates and have been reported from various vertebrate and invertebrate fossils ranging in age from the upper Palaeozoic to the Cenozoic. Much previous work on vertebrate fossil melanin has focused on reconstructions of integumentary color. Modern vertebrates, however, also possess melanin pigmentation in internal tissues. The impact of these non-integumentary melanosomes on interpretations of fossil soft tissues has not been assessed and, critically, there is no known mechanism to discriminate between melanosomes from different tissue sources. Here we present the first systematic analysis of the anatomical distribution, morphology and chemistry of melanosomes in various tissues (lung, liver, heart, spleen, eye, skin, connective tissue) from extant amphibians, reptiles, birds and mammals, coupled with comparable data from fossils. Melanin extracts from 243 tissue samples were examined using scanning electron microscopy (SEM) and synchrotron X-ray fluorescence (XRF) to assess melanosome geometry and trace element chemistry, respectively; concentrations of melanin were assessed in a subset of samples with alkaline hydrogen peroxide oxidation (AHPO). Our results confirm the presence of melanin in all vertebrate tissues analyzed and reveal a pervasive tissue-specific signal for melanin geometry and trace element chemistry. Similar patterns also exist in fossils, confirming the ability of fossil melanin to constrain interpretations of the soft tissue anatomy of fossil vertebrates and providing unique insights into the evolution of trace metal metabolism in vertebrates.

Speaker

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#### Correlated patterns of anatomical decay and fossil preservation allow systematic analysis of exceptional preservation

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The exceptional preservation of soft-tissues in the fossil record provides unique and important insight into deep time evolutionary events. Attempts to constrain interpretations of these difficult and highly variable remains have focused on experimental decay data and reconstructions of preservation mode, but neither have empirical support nor mutual corroboration. Here we apply new methods to objectively reconstruct taphonomic variability from fossil data using the Palaeozoic vertebrates Euphanerops and Mayomyzon. Fossils represent a non-random spectrum of specimen completeness and character preservation which is significantly correlated with the order of character loss that occurs in modern experimental proxies. As such, the observed taphonomic incompleteness of fossils is consistent with patterns of empirical decay. Furthermore, the distribution of observed preservation modes is correlated with character occurence frequency and character decay: less frequent early decaying characters exhibit authigenic mineralization (phosphatization and pyritzation), whilst decay resistant characters, including melanosomes, are organically preserved. These analyses not only shed new light on the anatomy and affinity of fossil taxa, but also provide support for the applicability of experimental decay data to real world data. The outlined methods will be widely applicable to the many other important instances of exceptional preservation of soft-tissues requiring taphonomic constraints.



Speaker

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#### New oryctocephalid taxa from the Cambrian Balang Biota in NW Hunan with a review on the classification of oryctocephlids

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The Balang Formation (Cambrian Series 2, Stage 4), exposed mainly in NW Hunan and E Guizhou provinces, South China, is famous for yielding the Balang Biota, a Burgess Shale-type Lagerstätte with multiple fossil groups including trilobites, eocranoids, trilobitomorphs, bivalve arthropods, hyolithids, brachiopods, cnidarians, brachiopods, mollusks, sponges, chancelloriids, ichnofossils, and algae. In E Guizhou, the Balang Biota is dominated by both trilobites and eocranoids, whereas in NW Hunan by only trilobites with no eocranoids discovered yet. Trilobites are most abundant in the Balang Biota, but their diversity is relatively low, with only nine genera recorded up to now. In comparison, in the slightly younger Kaili Biota, they are highly diversified with as many as 62 trilobite genera (subgenra).

Oryctocephalid trilobites are particularly rich in the Balang Formation of NW Hunan, comprising socalled "A, B, C, D" taxa, i.e. *Arthricicephalus* (sensu lato), *Balangia, Changaspis,* and *Duyunaspis*. In addition, the Balang Formation yields also some non-oryctocephalid trilobites such as *Redlichia, Eosoptychoparia*, and *Dinesus*, although they are relatively rare.

A distinguish large-sized oryctocephalid trilobite with length more than 20 mm was found recently in NW Hunan. It represents a undescribed new species belonging to a new genus, and is characterized by having an elongated exoskeleton with broad axis region, a glabella that is parallel-sided in posterior half, evenly tapered in anterior half, and truncated anteriorly with all pitted glabellar furrows neither connected by transglabellar furrows nor extended outward to axial furrow, a non-fulcrate thorax with 17 or 18 segments in adult, and a tiny pygidium with a remarkable median indentation at posterior margin. All these features suffice to differ the new genus from all known non-spiny oryctocephalid genera. This finding further enriches the trilobite diversity of the Balang Biota. The classification of oryctocephalid trilobites are reviewed with regarding this group of trilobites as a family embracing three subfamilies and assigning the new taxa to the subfamily Oryctocarinae.



Speaker

### Experimental degradation of feathers: insights into the origins of mouldic melanosomes

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Melanosomes are micron-sized organelles rich in the pigment melanin and are responsible for the majority of pigmentation in integumentary structures such as feathers and hair. The preservation of melanosomes in many fossils has been attributed to the inherent resistance of melanin to microbial degradation and acid hydrolysis. Despite their recalcitrance, however, melanosomes are often preserved in fossils as external moulds, the origins of which have not been investigated. To resolve this issue, we carried out taphonomic experiments on black feathers from the zebra finch (*Taeniopygia guttata*) designed to investigated the respective roles of decay, maturation and oxidation (the latter under alkaline conditions) in isolation and in combination. Scanning- and transmission electron microscopy of experimentally degraded feather barbs reveal abundant melanosome-sized moulds within the keratin matrix of feathers treated with oxidation. This strongly suggests that oxidation under alkaline conditions is an important factor in the degradation of melanosomes during diagenesis. The preservation of mouldic melanosomes in fossil feathers thus constrains the diagenetic history of fossil birds and feathered dinosaurs and may serve as an indicator of which specimens are most appropriate for fossil biomarker studies.



Speaker

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#### The Konservat-lagerstätte Menat (Paleocene; France) – an overview and new insights

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The Paleocene is an important epoch in the development of the flora and fauna in the Cenozoic, but relatively few terrestrial fossil sites of this age are known in Europe. For many groups, like plants and mammals, the catastrophic events at the Cretaceous–Paleogene (K/Pg, formerly K/T) boundary had ushered in significant changes, and our understanding of western European flora and fauna during this period is still very incomplete. The Paleocene Konservat- Lagerstätte Menat (Puy-de-Dôme, France) is an archive of an ecosystem that can provide insights into this crucial epoch. The sediments of Menat were deposited in a former lake, probably a maar lake, and excavations during the last century have yielded an extensive flora and fauna. An overview of the current state of paleontological investigations is given and new results based on recent excavations are presented. We find that the preservation of organic matter strongly differs between different excavation sites, probably influenced by weathering processes. Recently our team collected many impression fossils, those in more bituminous layers being exceptionally well preserved, including three-dimensional plant remains. The occurrence of charcoal in many horizons at Menat signifies the occurrence of paleowildfires during the Paleocene in the vicinity of Paleolake Menat. These results demonstrate the high potential for further scientific studies at Menat.



Speaker

#### The Eocene Fossil-lagerstätte Geiseltal (Saxony-Anhalt, Germany) and its potential for future research

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The lignite open mine pits at Geiseltal, located ca. 20 km SW of Halle (Saale), Saxony- Anhalt, Germany, have produced abundant and excellently preserved fossils for more than 80 years. A Konzentratand Konservat-lagerstätte at the same time, the pits are flooded and inaccessible today. However, the Geiseltal Collection at the Center for Natural Science Collections of Martin-luther-University Halle-Wittenberg holds ca. 50,000 fossils, of which more than half are vertebrates. The collection, protected as national heritage, contains almost all fossil animals collected at Geiseltal. With an age of ~47.5–42.5 million years (MP 11–14), the deposits far exceed other German Eocene sites in range.

More than two dozen taxa were named from the site. Among invertebrates, insects constitute by far the largest group with 56 genera and 113 species. Fossil fish include "Amiidae", Lepisosteidae, Thaumaturidae, and Percidae. Amphibians include six frog taxa and at least two taxa of salamanders. The turtle fauna consists of testudinids, freshwater geomeydids, and softshell turtles. Squamates include several anguids, iguanians, gekkotans, stem-lacertids, platynotans, and boid snakes. Five crocodilian species reveal at least four sympatric taxa. Birds include the giant *Gastornis*, the ostrich-like *Palaeotis*, and a dozen additional genera. Among the 76 mammal taxa are the marsupial *Amphiperatherium*, primates (e.g. *Europolemur*), creodonts, early insectivores & bats, the pangolin *Eurotamandua*, rodents, a tillodontian, and many ungulates. Among the latter are early equids (*Eurohippus, Propalaeotherium, Hallensia*), the tapir-like *Lophiodon*, and *Hyrachyus*.

The palaeoenvironment has been reconstructed as a subtropical peat bog but with inputs of carbonate-rich waters. Vertebrate and invertebrate fossils are often articulated and near- complete; many preserve soft tissues as carbonaceous and mineralized remains that are reported to preserve cellular-level detail and evidence of colour. Following early studies in the 1930s, the biota remained largely unstudied for 80 years. Renewed access to the collections opens many research directions (e.g. taxonomic revisions, macroevolution over 5 ma, climate, geochemistry & fossilisation, palaeobiology). Enhanced technological capacity today will allow renewed and deeper investigation of the palaeobiology and diversity of the biota.



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#### Enigmatic mackenziids from the early Cambrian Chengjiang Biota, China

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Mackenzia is an enigmatic fossil genus described from Burgess Shale by Walcott in 1911, which has an elongate, cylindrical body with prominently longitudinal structures, a holdfast and an inconspicuous stalk. It was initially considered as a holothurian, but latterly being reinterpreted as a mud-living actinianlike animal that might be similar with extant Edwardsia. However, the affinity of Mackenzia still remains uncertain, primarily due to its simple morphology and the scarcity of available material. Here, we report two new enigmatic animals, Paramackenzia stelechos gen. et sp. nov. and Fissiflabellatum pygmeum gen. et sp. nov., from the early Cambrian Chengjiang biota, south-west China. A general body plan comprising a holdfast, a stalk and a body bearing longitudinal structures indicates that the two new taxa from Chengjiang are allied with Mackenzia in the Family Mackenziidae. The elongate, cylindrical body shape and the size of P. stelechos are all comparable with M. costalis, the only known species of mackenziids, but the new taxon from the Chengjiang has a more significant stalk and 12-14 longitudinal lineations, which occasionally show bifurcation and some distinguishable transverse folds. While the second new taxon, F. pygmeum, has a fanshaped body and is relatively smaller in size. Interestingly, the longitudinal lineations of F. pygmeum also show feature of bifurcation or branching near the stalk region. The new discovered fossils from early Cambrian extend the distribution of mackenziid and provide new information in understanding the morphology and phylogeny of this enigmatic fossil.



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Speaker

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#### S22 - Life in Palaeozoic seas and ocean

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### Paleoenvironmental investigations of early Paleozoic seas from the northern Canadian Atlantic Margin: results from core analyses of the southeastern Baffin Island Shelf and Hopedale Basin

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Preceding development of the Mesozoic, Labrador-Baffin Seaway rift succession, Paleozoic basins of the lapetus Ocean existed along what is now the northern Canadian Atlantic Margin. These Paleozoic basins are discontinuous and poorly understood in the offshore. Limited lower Paleozoic subsurface bedrock samples recovered from the margin offer unique glimpses into paleoenvironments that characterized the lapetus Ocean prior to its closing. Shallow seabed drill cores from the southeastern Baffin Island Shelf and conventional cores from industry wells in the Hopedale Basin, offshore Labrador, were described with a focus on lithology and biological components. Results from core and thin section analyses were used to interpret the paleoenvironments of the regions, with dissimilarities reflecting variations in local depositional conditions and burial history.

Lower Paleozoic seabed drill cores from the southeastern Baffin Island Shelf are primarily composed of fine-grained lime mudstone with rare dolomite observed in all but one core. A high diversity of fossil content reflects a range of normal marine depositional settings spanning shallow water environments within the photic zone, to deeper water domains. Seven exploration wells in Hopedale Basin intersect Paleozoic strata. Paleozoic cores recovered from the Labrador Margin are primarily fine-grained, lack macro-fossils, and typically represent deposition in deep water, foreslope environments. All carbonate cores contain fractures and stylolites but only one of the cores has been moderately to pervasively dolomitized. The higher degree of alteration observed in the Hopedale Basin carbonate cores can be attributed, in large part, to burial depths exceeding two kilometers.

The lower Paleozoic sediments located on the southeastern Baffin Island Shelf and in the Hopedale Basin are thought to be approximately syndepositional, but accumulated within independent depositional centers along the western margin of the Iapetus Ocean. The highly variable and fossiliferous Paleozoic limestone deposits on the southeastern Baffin Island Shelf differ from the dolomitized Paleozoic strata of the Hopedale Basin which are more diagentically altered and represent deposition in deeper water environments. Understanding depositional paleoenvironments in both regions provides valuable insights into the reconstruction of the Iapetus Ocean.



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#### Rates of evolution in actinistians (Osteichthyes: Sarcopterygii) and an exceptional new 3D coelacanth the Devonian of Australia

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Actinistians, or coelacanths, are a clade of lobe-finned fish that first appeared during the Devonian Period, close to 400 million years ago. Together with lungfish and tetrapods, they comprise the Sarcopterygii (lobe-fins) alive today. There are just two extant species of coelacanth (*Latimeria chalumnae* and *L. menadoensis*), but from the Carboniferous and throughout the Mesozoic Era, coelacanths increased in number and apparent morphological diversity. Two specimens of a new 3D-preserved coelacanth taxon from the Late Devonian (Frasnian) Gogo Formation of northern Western Australia are presented herein. The material is exceptionally- preserved and represents one partial braincase, and a second near-complete individual. Most early coelacanth fossils are compressed with little detail of their internal anatomy preserved. Micro-CT is used to elucidate internal cranial anatomy of the new taxon for comparison with the only other fossil coelacanth for which detailed internal anatomy is known, *Diplocercides*, from the Late Devonian of Germany. The new taxon is recovered as a basal member of the actinistian total group. Preliminary Bayesian tip-dated clock analyses elucidate the rates of evolution of coelacanths and reveal some surprising results for this enigmatic clade.

Speaker

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### Initial steps in ordering events of the Late Ordovician mass extinction: Chitinozoan contributions to Maquoketa Group holostratigraphy (upper Katian, Wisconsin, USA)

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The Maquoketa Group of the US Midcontinent records a series of carbonate carbon ( $\delta$ 13C) isotope excursions indicative of ocean-geochemical disturbances during the run-up to the Late Ordovician mass extinction and glacial maximum. To better understand the cause-and-effect relationship between the ocean, atmosphere and biosphere systems during these perturbations, ordering the regional stratigraphic succession to the global chronostratigraphic scheme is crucial. Preliminary chemostratigraphy and facies analyses demonstrate that significant regional changes within the Maquoketa Group occur along a continental interior to margin transect. We hypothesize that this variability reflects a diachronous succession that, when composited in total, captures one of the most complete and well-preserved records of the Upper Ordovician in the world. To test this hypothesis, we have developed a chitinozoan biostratigraphy for the Gardner Kiln drill core (Wisconsin, USA), which penetrates the entire Maquoketa Group. Forty samples yielded rich and well-preserved assemblages with 7.245 identified chitinozoan specimens assigned to 49 species. Ongoing analysis of another drill core, IGS-440 (Indiana, USA) also penetrates this interval and yields well-preserved chitinozoans, giving promising prospects for future correlation of these successions. The phenomenal palynomorph assemblage recovered from the Maquoketa Group illustrates the enormous potential for chitinozoans to become a key biostratigraphic tool in high-resolution integrated stratigraphic studies of the Upper Ordovician in the US Midcontinent region.



## Eifelien corals and reefs of S Belgium, new insights on a cold case

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The Eifelian is well exposed in S Belgium where it displays facies ranging from stromatoporoid biostromes to outershelf fine siliciclastics to proximal redbeds. The carbonate factory begun in the Late Emsian displays a vertical evolution from parabiostromes first with stromatoporoids and Heliolitids, then progressively enriched in solitary then colonial rugose corals. Eastwards the biostromes passe to bioherms dominated by colonial corals and stromatoporoids (Nismes). Their thickness decreases eastwards and in the Meuse valley, they are replaced by bioclastic siltstones. In the Beauraing area, a biohermal complex displays exceptionnal facies extremely rich in fauna. Eastwards silicilastics replace the carbonate. The position of the reefs, stratified carbonates and siliciclastics was seemingly driven by synsedimentary faults, witnessing that the structuration of the Basin started in the Early Devonian. This contribution focuses on the faunal assemblages of a yet undescribed early-middle Eifelian biohermal complex in the Beauraing area. Four successive faunal assemblage are encountered, witnessing the development of the reef. The base of the bioherm is made of thick lamellar stromatoporoids stabilizing with metre-thick beds of white crinoidal rudstone. The coral fauna is dominated by Alveolitids, the solitary Stringophyllum, and the colonial Fasciphyllum and Beugniastraea. This first phase correponds to the colonisation and stabilisation of the crinoidal deposits by stromatoporoids and generalists. The framework of the reef is constructed by large stromatoporoids, Thamnoporids, Heliolithids, Chaetetids and abundant and diverse rugose corals Fasciphyllum, Beugniesastraea, Spongophyllum, Xystriphyllum, Acanthophyllum, (Stringophyllum, Mesophyllum and Cyathophyllum. In non-constructed facies the same genera are joined by Cystiphyllum and Mesophyllum. This diversification phase is paralled with the development of micro-environment within the reef structure. The reef-crest facies are dominated by large bulbous stromatoporoids and massive Heliolithids with few Dendrostella and Fasciphyllum. When hydrodynamic conditions increased, only highenergy groups (stromatoporoids, Heliolithids) continued to develop. The reef is interrupted by an emersion surface (sequence boundary) and then covered by fine siliciclastics that yield abundant but poorly diverse association of Cystiphyllum-Mesophyllum-Acanthophyllum- Calceola, together with Alveolitids, Coenitids, and Favositids.

<sup>&</sup>lt;sup>°</sup> Speaker

#### Possible shell disease syndrome in late holaspid Ordovician trilobites

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Swellings in exoskeleton of Cambrian to Devonian trilobites are only rarely reported although they provide an important source of information on ecological interactions in early metazoan communities. This contribution documents numerous swellings occurring in five large asaphid trilobites, particularly in an articulated exoskeleton of *Asaphelus desideratus* (Barrande, 1872) earlier briefly described by Šnajdr (1978); in two isolated pygidia of *Nerudaspis aliena* (Barrande, 1872) and in two pygidia classified as Asaphidae indet. All studied specimens come from the Darriwilian (Middle Ordovician) Šárka Formation of the Barrandian area (Czech Republic). Swellings observed on exoskeletons of these late holaspid trilobites are tentatively explained as possible exoskeletal lesions comparable to "Shell Disease Syndrome (SDS)" in Recent crustaceans.

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#### Couscous ai frutti di mare – Early Devonian palaeoecology of the Moroccan mudmound locality Hamar Laghdad

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Hamar Laghdad is a world-renowned mudmound locality in the eastern Anti-Atlas. Following submarine volcanism during the Lochkovian, the submarine high was populated by crinoids. Subsequently, and until the Eifelian, tens of conical mudmounds formed on top of the crinoid limestones, presumably related to hydrothermalism. This locality is also called KessKess, referring to the numerous mudmound cones, which are reminiscent of heaps of couscous, the classical Moroccan dish. Together with the elements supplied from the hydrothermal vents, the highly differentiated new topography created a wealth of favourable habitats for marine organisms. We studied the local palaeoecology from the latest Lochkovian to the latest Emsian and found changes in the ratio of benthic to pelagic faunal elements and overall alpha diversity. The highest alpha diversity was recorded during the latest Emsian (dubbed 'Red Fauna' because of to its red colour due to high hematite-content), where the trophic nucleus comprises over 40 invertebrate species. The 'Red Fauna' is particularly rich in brachiopods, corals, trilobites, echinoderms and cephalopods. This shows how very localized abiotic events may create local biodiversity hotspots.



Speaker

#### Combining foraminifera identification, their extirpation and occurrence, $\delta^{18}O$ , $\delta^{13}C$ and % carbonate curves define global events in eutrophic environments and promote world-wide insights

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Proximal marginal marine environments during the Permian-Triassic transition that were attached to supercontinents were under constant terrestrial siliciclastic contribution (up to 90%) during global warming climate trend and less during cooling trend. Although these influxes developing stressed conditions to symbiotic organisms, oppressing the carbonate precipitation and creating correlation difficulties, the combined method however allowed to highlight several crisis and recovery attempts of the bio-system, C-cycle perturbations, and global climate changes, that are considered as a foreplay events to the P-T Earth-life transition. This research examined two successions from the SE Levan Basin facing northward the western tropical Tethyan seaway; the Guadalupian-lopingian boundary is defined below the FA of the species: Codonofusiella kwangsiana; C. erki; Geinitzina gloria; Nodosaria doraschamensis; Pseudomidiella labensis; Sichotenella sutchanica and Paraglobivalvulina mira, and instead of appearing at the peak of a global cooling trend, it appears at a major stage of its awakening and when the carbonate content level reached 55%. The outstanding global cooling trend was defined by the  $\delta^{18}$ O and  $\delta^{13}C_{carb}$ positive excursion in the upper part of the Guadalupian, increasing the carbonate content (up to 90%) and the diversity of foraminifera. The Wuchiapingian-Changhsingian boundary is defined after gradual decline of the Palaeofusulinidae, while the Ozawainellidae prevailed, and below the FA of Reichellina leveni; R. pulchra; R. media; Robuloides gibbus, Frondina permica, Colaniella minuta and C. minima, corresponds to a global warming and carbonate content reduced. Warming continued, along with siliciclastics content increase (80%) although few breaks in the global warming led to some amelioration within low diversity of Reichelling sp., but the immediate return to warming trend led to their diminishing at the Permian-Triassic boundary. In general, Milioloidae diversity tended to increase during global cooling periods while Nodosarioidae diversity increases during global warming trends. In times of Fusulinoida thrived, both noticeably decreased. The relatively high variety of the fusulinids kept through the Guadalupian – Lopingian boundary, gradually declined afterward similar to the Tethys and the peri-Gondwana provinces.



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#### Trilobite assemblages in Floian of Montagne Noire, France: focus on the upper part of the "Formation de Saint-Chinian"

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The Tremadocian and Floian of Montagne Noire have been studied for decades, resulting in the establishment of a biozonation using trilobites (FAD). Theses biozones have been defined in the South part of Montagne Noire, in the Saint Chinian area. The Saint-Chinian Formation is well known for its rich trilobite fauna found in nodules, collected at the surface of the vineyard fields in the Saint-Chinian vicinity.

In this wine area, a cliff of the Fourbidarias stream, near Saint-Cels hamlet, is a notable exception. This fossiliferous dark shale exposure was discovered a century ago by Jean Miquel, a famous Barroubio wine grower and fossil collector. This site was the first to show the *Asaphellina barroisi* and *Taihungshania miqueli* coexistence, yielding to the definition of the trilobite 'faunizone' G, at the topmost of the Saint-Chinian Formation.

This cliff has been recently re-sampled in detail, in order to propose a detailed succession of the trilobite associations. More than 30 species of trilobites have been identified, in addition to the coeval fauna, such as gastropods, bivalves, orthoconic cephalopods, graptolites and echinoderms. Even most of the assemblages can be referred to a raphiophoridbiofacies, the trilobite distribution across the samples shows abundance variations of some species that might be used to refine assemblages within the *Asaphellina barroisi* and *Taihungshania miqueli* Biozones. *Ampyx* and *Paramegalaspis* are the most common genera in the lower two-thirds of the section. *Paramegalaspis* becomes rare after being probably ecologically replaced by *Asaphellus*. A new raphioporid species, only present at the first third of the section, exceeds *Ampyx* frequency before a complete disappearance. The genera *Parabathycheilus, Symphysurus, Platycalymene* are restricted to few specific layers. *Euloma* occurs at the base of the section, disappears suddenly and spottily reoccurs in a particular level full of *Agerina* and in a distinctive protaspis bed. Theses trilobite associations can reach one meter thick but some might be thinner (less 30 cm or millimetric for the protaspis bed). The turnover of those trilobite associations might have been driven by quick environmental changes in the Lower Floian of Montagne Noire.



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Speaker

### Evolutionary modifications of early developmental stages in Cambrian trilobites

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Early developmental stages of Cambrian trilobites show a wide variety of morphologies, but it is generally believed these morphologies are quite conservative among closely related taxa or within a particular clade. However, it has been repeatedly reported for various metazoans that the early developmental stages of close related taxa can display quite different morphologies, presumably the result of differing selective pressures. Here I report morphological modifications of early stages in three trilobite clades from the Cambrian Series 2 and 3: Olenelloidea, Ellipsocephaloidea and Paradoxidoidea.

In Olenelloidea, early developmental stages of *Nephrolenellus* and *Olenellus* display modification of the plesiomorphic cephalic morphology of the clade. This is mainly related to the different direction of intergenal spines and the shorter preglabellar field in former two taxa. The intergenal spine modification could have allowed for an increase in buoyancy, or helped to avoid predation. Similar modifications are observed in early developmental stages of *Estaingia*, a taxon belonging to Ellipsocephaloidea. *Estaingia* shows elongated pleural spines and accelerated development of the cranidium when compared with other taxa of the same clade. As in Olenelloidea, such modifications might have facilitated a planktonic mode of life and/or predation avoidance. Finally, morphological modifications in the early stages of *Eccaparadoxides* and *Hydrocephalus* (Paradoxidoidea) consist of a larger body size, acceleration of the development and inflation of the glabella. These modifications are related to lecithotrophic development.

Evolutionary modifications during the development of closely related taxa highlight the morphological plasticity of Cambrian trilobites. These modifications also show that even early trilobite lineages were effectively reacting to various selective pressures by exploring new habitats or avoiding predation pressure. Our understanding of such evolutionary modifications might bring new insights into explaining trilobite biogeography or their reactions to changes of global ecosystems.



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#### Phosphatisation and bacterial – hyolithid association in the Middle Cambrian of Western Canada

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An unusual biotic assemblage, recovered from a horizon within the Middle Cambrian Stephen Formation (~505-Ma) in western Canada, is preserved via phosphatisation. This horizon occurs at the top of the carbonate lower member (Narao Member) of the formation and is sharply overlain by black shale of the upper member (Waputik Member). The observed taphonomic preservational style, is often attributed to organic-rich suboxic to anoxic environments, which facilitate anaerobic microbial metabolic activity, supersaturating pore water with  $P_2O_5$ , allowing apatite precipitation. Abundant phosphatic fecal pellets of roughly uniform oblong shape and size (~200–300  $\mu$ m long) co-occur with the phosphatised remains. Regions lacking these pellets do not contain phosphatised fossils, but do contain similar fauna with original or recrystallised remains. The phosphatised remains have been preserved in extremely fine detail, and the biota includes abundant hyolithid conchs, edrioasteroid plates, and microbial and bacterial filaments. Some hyolithid specimens also contain prominent fecal pellet linings. The pellet packing arrangement is so tight and regular that an abiotic depositional mechanism is considered unlikely. These pelletal-linings harbour well preserved non-branching filaments that retain a great degree of detail. The filaments average 2-3  $\mu$ m in width and some have a 'sausage-link' cellular appearance. Energy dispersive x-ray spectroscopy (EDS) indicates that the filaments are mainly preserved of carbon. The association of these filaments to pelletlined conchs may be entirely coincidental, possibly an example of bacterial infestation. Alternatively, we hypothesise that the association may be intentional and could represent an early form of symbiosis between these hyoliths and the bacteria, or represent a commensal relationship between some later occupier of the conchs in association with bacteria. It is postulated that the hyoliths during life, or an organism simply using or inhabiting abandoned conchs, may have engaged in a form of bacterial farming using fecal pellets as a growth medium. This may have provided a trophic energy transfer during intervals of reduced nutrient availability or may have allowed these organisms to inhabit marginal environments. This potential symbiotic relationship, if correct, would be one of the earliest representations of this type of behaviour in the fossil record.



<sup>&</sup>lt;sup>°</sup> Speaker

### Global biogeography and biostratigraphy of Silurian myodocope ostracods

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Ostracods have proven utility in Silurian biostratigraphy and biogeography in well-studied Laurentian and European regions but wider afield and in general they have been under-utilised. Benthic palaeocopids and podocopids currently provide the best means of interregional correlation using Silurian ostracods.

Because of their relatively scarce geological occurrence, Silurian myodocopes can easily be overlooked, being normally associated with lithofacies (characteristically mud-silt laminites) that at first sight appear unpromising as possible ostracod-yielding deposits. Such drawbacks should not, however, hinder the realisation of the biostratigraphical and palaeobiogeographical utility and palaeoecological importance of such faunas. They demonstrate, from their wide, transoceanic geographical distribution that pelagic Ostracoda were present by the Silurian, and that there is the prospect of establishing (especially in the upper Silurian) a myodocope ostracod biostratigraphy of similar resolution to coeval graptolite/chitinozoan/conodont biozones.

Our studies establish seven myodocope biozones for the upper Wenlock (Homerian Stage) and Ludlow series, affording a time-resolution for each zone of *circa* 1 million years: the *Nudator angiportatus* Biozone (equivalent to the *C. lundgreni* and *G. nassa* graptolite biozones); the *Seminova depressa* Biozone (equivalent to the *C. ludensis* graptolite biozone); the *Silurocypridina calva* Biozone (equivalent to the *N. nilssoni* graptolite biozone); the *Silurocypridina retroreticulata* Biozone (equivalent to the *L. scanicus* graptolite biozone); the *Silurocypridina retroreticulata* Biozone (equivalent to the *L. scanicus* graptolite biozone); the *Parabolbozoe armoricana* Biozone (equivalent to the *S. incipiens* graptolite Biozone); the *Richteria migrans* Biozone (equivalent to the *S. leintwardinensis* graptolite biozone); and the *Bolbozoe acuta* Biozone (equivalent to the *Bohemograptus* proliferation interval of the UK), which may extend to the top of the Ludfordian Stage.

These biozones provide a means of high-resolution correlation across Europe and into Arctic Russia and central Asia. They also provide a biostratigraphical tool for examining the timing and duration of biodiversity loss and recovery during the Homerian 'Big Crisis'.



Speaker

# Mississippian foraminifers from South China: their chronostratigraphic significance and implications for glacioeustasy

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Mississippian is a critical period in the geological history, when some major geological events happened such as the formation of the Pangaea and the beginning of the large-scale Gondwana glaciation. Due to their rapid evolution and wide distribution, foraminifers are significantly useful in high-precision biostratigraphic correlations for Mississippian strata. During Mississippian, South China was located at a subequatorial-equatorial position in the east Paleotethys, with relatively continuous sedimentary sequences and abundant marine fossils. According to samples from sections located in different depositional environment in South China, this study conducts the following researches: 1) After obtaining an understanding of the systematics, evolution, and the spatial and temporal distribution of Mississippian foraminifers from South China, a refined high-resolution Mississippian zonal scheme of foraminifers is preliminarily established, instead of the traditional one broadly defined by genera, long-ranging species or local species. New zones named for cosmopolitan species allow better international correlations, and show the evolution of important groups such as the Archaediscacean foraminifers. 2) By investigating the foraminiferal succession of the Visean/Serpukhovian boundary interval in south China and its accurate correlation with conodonts from the Visean/Serpukhovian boundary GSSP candidate section-the Naging section and other auxiliary sections, the problem of basal Serpukhovian foraminiferal indices in shallowwater sections is solved. The appearances of Plectomillerella tortula, Janischewskina delicate, Asteroarchaediscus postrugosus, and Eolasiodiscus donbassicus are valuable indices to the base of the Serpukhovian which is defined by the FAD of the conodont Lochriea ziegleri. 3) Based on correlations of transgressive-regressive sequences and foraminiferal zonations, chronostratigraphical framework of cyclothems from South China can be established and it could contribute to resolutions of debates on the timing of the onset, and the average cycle period of the Late Paleozoic Ice Age.



<sup>\*</sup> Speaker

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### Ecosystem dynamics and the consequences of invasive species

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Although a leading cause of extinction in modern ecosystems, the effects of biotic invasions on ecosystem structure and functioning remain poorly understood. Food web data before invasion are rare, and without direct comparisons before and after invasion, differences in overall network structure are difficult to identify. The fossil record contains intervals of dramatic ecosystem changes, and can thus provide insights into persistent ecosystem conditions over evolutionary timescales, particularly before and after invasions.

Shallow marine food webs from the Late Ordovician (Cincinnati Arch, USA) were compared before and after the Richmondian Invasion, a well-documented influx of invasive species. Invasions may trigger significant ecosystem restructuring and major changes in energy transfer pathways, such as patterns of interactions and the distribution of taxa among trophic levels. Network structure and functioning was therefore examined using descriptive metrics and Cascading Extinction on Graphs models. We observed a loss of richness which corresponded with a decrease in the number of functional groups, but few differences in link density, average path length, modularity, and trophic levels. Despite the similarity in overall structure, the post-invasion community was less stable and resistant suggesting that functional richness may play a more critical role in ecosystem stability than biodiversity.

These results, therefore, are consistent with functional homogenization, and thus have important implications for conservation and management efforts, which typically focus on preservation of biodiversity. A better understanding of biotic invasions on multiple spatiotemporal scales will prove useful in ecosystem management, for preventing invasions and predicting their long-term effects.



Speaker

### Silurian vertebrates from northern Mongolia: diversity, ecology and environment

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The present day territory of northwestern Mongolia was a part of Siberian palaeocontinent, an independent landmass, which persisted during the whole Palaeozoic era as the only large palaeoterrane in the Northern Hemisphere. Early Silurian (Llandovery) vertebrates from the northwestern Mongolia are known for their diversity and a great number of endemic taxa, and represents the earliest known Silurian vertebrate ecosystem of the Siberian palaeobiogeographical province. The foreshore and lagoonal facies rich in vertebrate microremains comprise acanthodians, chondrichthyans, galeaspids, heterostracans, mongolepids, tesakoviaspids, thelodonts, and possible eriptychiids. In this work we present new data on palaeobiodiversity and palaeoenvironment, including oxygen isotope and REE data, in attempt to reconstruct this ancient ecosystem and conditions favouring diverse vertebrate fauna in relatively high northern palaeolatitudes.



Speaker

#### Improving Echinoderm biodiversity estimates and interpretations of paleoecology through analysis of disarticulated columnals: A Silurian example

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The fossil record of pelmatozoan echinoderms is dominated by portions of the column; however, this material, with a few exceptions, has not been fully utilized in studies of paleoecology and calculations of alpha diversity. The present study represents a case study of the value of portions of disarticulated stems in improving interpretations of morphological (and potentially taxonomic) diversity, relative abundance patterns, environmental distribution, and preferences of infesting parasites using middle Silurian crinoid and stalked blastozoan stem material. Samples of argillaceous limestone, weathered clastic mudstone, and microbioherm-flank sediment were collected from the Wenlock (Sheinwoodian) Massie Formation as exposed at the Napoleon guarry of southeastern Indiana, USA. These samples yielded fewer than 15 crinoid calyx plates, diploporitan thecal fragments and coronoid thecae, but produced more than 3000 columnals, pluricolumnals, and attachment structures representing at least 20 species. The most abundant taxa known from thecal material (Eucalyptocrinites and Caryocrinites) also produced the largest amount of stem material, though the relative abundance of stem material attributable to Caryocrinites varies significantly, with a larger number of specimens in carbonate rocks. Dimerocrinitids and Periechocrinus are strongly under-represented by crown material relative to pluricolumnals and attachment structures. Frequencies of encrustation and parasitic embedment structures indicated host-specificity among stalked pelmatozoans. Notably, small pentameric stems attributable to dendrocrinid cladids are disproportionally afflicted with parasitic pits (Tremichnus ispp.). Future paleocommunity studies will benefit from continued and increased attention to disarticulated pelmatozoans, particularly when columnals, pluricolumnals, and attachment structures are incorporated into diversity calculations.

Speaker

#### Early Devonian organic-walled microfossils from outcrop samples of the Cordobés Formation, Durazno Group, Norte Basin, Uruguay

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The Durazno Group documented an Early Devonian transgressive-regressive cycle of sedimentation in the southernmost portion of the intracratonic Paraná Basin, in Uruguay known as the Norte Basin. The group comprises from base to top the Cerrezuelo, Cordobés and La Paloma Formations. The Cordobés Formation was deposited during the maximum flooding of the transgressive event, and contains Malvinokaffric marine invertebrates that inhabited Gondwanan cold marine waters, acanthodian fishes and trace fossils. The first palynological studies of the Cordobés Formation date from the 60's and 70's, from one outcrop, which reports the presence of phytoplankton and miospores but they only described a few acritarchs. In recent years, works referred to this unit have notably increased due to hydrocarbons exploration, but the results come from samples obtained mainly from boreholes. In order to expand the knowledge regarding Devonian palynofloras of Uruguay, in this contribution, we document the palynological assemblages collected from outcrop samples of the Cordobés Formation, near Blanquillo town in the Durazno Department. Some identified species allowed constraining the age of the unit and its correlation with other Early Devonian assemblages from South America. The studied samples contain acritarchs, prasinophytes, chlorophytes, chitinozoans, scolecodonts and miospores. The most representative phytoplankton species are Cordobesia urguayensis, Dictyotidium dictyotum, Estiastra uruguaia, Exochoderma arca, E. triangularis, Palacanthus ledanoisii, Polyedrixium fragosulum, Triangulina alargada, Quadrisporites horridus, Veryhachium trispinosum and V. woodii. The miospores include the following species: Apiculiretusispora brandtii, Cymbohilates sp., Emphanisporites rotatus, Dibolisporites echinaceus, Dictyotriletes emsiensis and Knoxisporites riondae. The presence of the acritarch Veryachium woodii, recently described from borehole samples of the Cordobés Formation, allows to constrain the age at the proximity of the Pragian-Emsian boundary, where also Knoxisporites riondae becomes a common taxa. Cordobesia species and Dictyotriletes emsiensis are forms restricted to Gondwana. Besides this, Dictyotriletes emsiensis allows the correlation with Furnas and Ponta Grossa Formations (Brazil) and Talacasto Formation (Argentina). The Early Devonian age is also supported by fossil invertebrates as well as U-Pb ages of detrital zircons obtained from the Duranzo Group.



<sup>&</sup>lt;sup>°</sup> Speaker

#### Conodonts from the boundary interval of the Sandaogou and Pingliang formations (Middle and Upper Ordovician) in Pingliang, Gansu Province, China

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The Guanzhuang section (also known as the Pingliang section) located in Pingliang City of Gansu Province, is well-known for being the type locality of the Pingliang Formation and being previously selected as one of the stratotype candidates for the base of the Upper Series of the Ordovician System. Conodonts of the Pingliang Formation in this classic section have been extensively researched for decades. However, the lowermost few meters of this formation and the underlying Sandaogou Formation were not included in these researches because of not being well exposed in the study section. It results in poor knowledge of the biostratigraphy of the Pingliang-Sandaogou interval . Fortunately, a fresh outcrop of this interval has been studied recently in a disused quarry, about 200m west of the classic location of the Guanzhuang section. At this new locality, the bottom of the Pingliang Formation consists of shale with intercalated limestone beds, and the top of the Sandaogou Formation is characterized by medium to thick bedded limestones. Conodonts from this interval are sampled and examined. Fossils are not recovered from the bottom of the Pingliang Formation, but this assemblage is quite rich in samples collected from the top of the Sandaogou Formation. The fauna comprises 17 species and 14 genera, mainly including Pygodus anserinus, Erismodus typus, Microcoelodus asymmetricus, Periodon aculeatus, Spinodus spinatus, Protopanderodus varicostatus, P. robustus and Panderodus gracilis. The Pygodus anserinus conodont biozone is recognized. This biozone occurs in the lower part of the Pingliang Formation as well according to previous studies at the classic locality. Therefore, it is evident that the Pingliang Formation conformably overlies the Sandaogou Formation in the study area.



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#### Conodont fauna and biostratigraphy of the Valentin Törl Section, Carnic Alps, Austria

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The Paleozoic of the Carnic Alps is represented by almost complete sequences (Middle Ordovician– Upper Permian in age) which crop out along the Italian-Austrian border with an east-west orientation. The Silurian is differentiated here within the Peri-Gondwanan paleogeographic sector for the variety of facies and for the rich fossil content which has allowed a detailed dating of the successions with conodonts, graptolites, cephalopods, trilobites, brachiopods, bivalves and other groups of nannofossils. In the Lake Wolayer area, several Silurian sections are exposed (e.g., Seekopf Sockel/Costone Lambertenghi, Base of Seewarte, Rauchkofel Boden, Seewarte, Rifugio Lambertenghi Fontana I and III, and Valentin Törl). Detailed conodont data are available from most of those sections, whereas information for Valentin Törl are limited to an approximate dating carried out during the geological mapping of the area during the 1970's. A recent detailed conodont sampling of 26 levels from the Valentin Törl section in four main subsections (for a total of 110 kg of rock material) has allowed the documentation of several Silurian conodont biozones from the *Kockelella crassa* Zone to the *Oulodus elegans detortus* Zone, thus assigning a biostratigraphic range from the base of the Ludlow (Gorstian) to the Pridoli, with several sedimentary gaps documented in between. At the top of the succession, 4 m of light grey limestones are assigned to the Lower Devonian (*Icriodus hesperius* Zone).

Speaker

#### Global scale diversity of phytoplankton in the Palaeozoic: progress report

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Phytoplanktonic organisms play a major role in Earth's ecosystems. They constitute a major part of the base of marine food chains and represent the starting point for nearly all biological activity in the marine realm. Furthermore, phytoplankton is the biggest producer of oxygen and responsible for most the carbon dioxide transfer from the atmosphere to the oceans. It can, therefore, be inferred that changes in ancient phytoplankton populations had considerable effects on both, the palaeoclimates and palaeoecosystems. The study of ancient phytoplankton diversity on a regional and global scale is therefore of great interest as it can provide valuable insights into the evolution of marine ecosystems and on climate history.

Using a database of more than 6,000 species, a comprehensive investigation of the diversity of Palaeozoic phytoplankton is conducted. This database was initiated in the phytoPal Project (Mullins et al. 2006, Palynology 30: 224) and comprises data from all published literature, including taxonomic, geographic and stratigraphic information. The main goal of this study is the creation of unbiased diversity trajectories for marine phytoplankton throughout the Palaeozoic. By highlighting the evolutionary consequences of diversification and extinction events the results allow not only to assess the phytoplankton evolutionary dynamics, but also, on a larger scale, its influence on marine ecosystems. Moreover, correlating the diversity fluctuations with palaeoecological and palaeoclimatological data allows a better understanding of the climate history of the Earth.

The first diversity curves show clear trends with several diversification and extinction events. The early Palaeozoic is generally characterized by high diversity values, punctuated by few extinctions. Major diversification events can be observed in the middle Cambrian to Early Ordovician and in the Middle to Late Devonian. Distinct diversity declines are shown in the Late Ordovician, from the Sheinwoodian to the Eifelian and from the Late Devonian to the Carboniferous.



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#### Late Mississippian (Carboniferous) rugose corals from the Jianshanzi Section, Inner Mongolia

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The Jianshanzi Section is located near the boundary between Innner Mongolia and the Gansu province. It mainly consists in siliclastic and muddy deposits, with several beds of bioclastic limestone in the middle part. The limestone beds contain abundant rugose corals, including 12 species belonging to nine genera (with one new genus left in open nomenclature). The coral assemblage dates the beds latest Visean to Serpukhovian. Systematically, they resembles the assemblages from the coeval beds in South China, but also contains endemic members, such as *Qinghaiphyllum*, which are often found in adjacent regions (Qinghai and Gansu). In the aspect of palaeoecology, the assemblage is dominated by massive compound corals, namely *Aulina, Lithostrotion* and the new genus. The coral colonies are mostly flat-domed. The lithostrotionids often show a semi-fasciculate growth form, and the branching corallites were heavily eroded in dissepimentarium, indicating frequent surges of strong, muddy water currents. The new massive coral genus morphologically resembles some species from the tabulate coral genus *Michelinia*. However, the presence of columella and septa in some corallites, and the absence of pores suggest an affiliation to rugose coral. This genus is highly abundant in our collection. It is temporarily left in open nomenclature because of its astogeny unknown and the need of further study.



Speaker

#### Cleidophoridae new family (Nuculoida, Bivalvia): systematics, paleogeography and paleoenvironment

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This paper represents the culimation of research started in 1999 by the author, who recognized that species then included in Nuculites Conrad, 1842 represent more than one genus, and that Cleidophorus Hall, 1847 should be recognized as valid, instead of synonymized with Nuculites. Paleozoic nuculanoid genera with an anterior, internal plate studies had showed that these Paleozoic genera merit one or more separate families, and that the Malletiidae as defined by Sanders and Allen in 1985 should be restricted to Mesozoic and Cenozoic forms. Based on the literature and described specimens deposited at collections of the American Museum of Natural History (NY), New York State Museum (NY), National Museum of Natural History (Smithsonian Institution) (Washington D.C.) and Yale Pebody Museum (CT), the genus Cleidophorus is revalidated and the new family Cleidophoridae is proposed, also containing the new genus Lamelliodonta. Considering conchiological characters used in recent and fossils classifications of bivalves, it used mainly the follow ones: hinge type; hinge structure; shell microstructure; ligament; adductor and accessory muscles; pallial line and internal and external surfaces. Cleidophoridae is characterized as Paleozoic nuculanoids with narrow hinge-plates, and with taxodont hinge dentition arranged in two series, the anterior series much shorter tooth row than the posterior series, and both series with elongated teeth parallel or obliquely parallel teeth to the hinge axis. It contains two genera: Cleidophorus Hall, 1847 and Lamelliodonta, gen. nov. Cleidophorus is an Cleidophorid with sub-rhomboidal shell shape and a rectilinear, thin, anterior interior septum, represented by the species Cleidophorus planulatus (Conrad, 1841), occurring in the Late Ordovician Pulaski (USA) and Nicolet River (Canada) Formations. Lamelliodonta, represented by its type specie L. pomeroyensis, is an Cleidophorid with a modiomorphoid shell shape and without a rectilinear, thin, anterior interior septum. The latter species was described in 1982 by Tunncliff as an unusual and enigmatic bivalve from the Tirnaskea Formation (Ashgill-Hirnantian), Pomeroy, Tyrone County, Ireland, and related it to the extant genus Silicula. These taxa are the oldest record of anteriorplate nuculoids (Late Ordovician). They seemed to be restricted to Laurentia, where they occurred in both warm-shallow-water siliciclastic and carbonatic pellitic sediments, showing preference for low latitudes.

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Speaker

#### Orthotetida Waagen, 1884 (Brachiopoda) in the Devonian of Brazil

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The Devonian seas are represented by thick sedimentary packages in the Amazon, Parnaiba and Parana basins, Brazil. Among the brachiopods, the order Orthotedida Waagen, 1884 is represented by the species "Schuchertella" agassizi (Rathbun, 1874) in the Amazon (Mesodevonian Maecuru and Erere Formations) and Parana (Eodevonian Ponta Grossa Formation) basins. Up to now, it is absent in the Parnaiba Basin. This species was originally described from the Erere Formation, being later attributed to the Maecuru Formation specimens and, finally, of the Ponta Grossa Formation shales. John Clarke, in 1913, also identified in the Ponta Grossa Formation S. sullivani (Morris & Sharpe, 1846) (currently Schellwienella sullivani), known from the Devonian of the Falkland Islands, but herein it was not confirmed. Studying the specimens of this species deposited in the scientific collections "Paleozoic Fossils" of the Federal University of Rio de Janeiro (UNIRIO) and the Institute of Geosciences of the University of Sao Paulo (USP), made it possible to elucidate some of the taxonomic problems of this group in Brazil. The few studies of Orthotetida Wagen, 1884 in the Paleozoic fossiliferous associations of Brazil, especially in the Devonian, the problematic that involves the classification of the genus Schuchertella Girty, 1904 and its supposed cosmopolitanism have made it difficult to get a more precise identification of this group. Until now, it was possible to confirm the existence of the species "Schuchertella" agassizi in the Erere Formation, however, not belonging to the genus Schuchertella. This conclusion was based on the original description of the species and the description of specimens collected in the same fossiliferous horizon, which characters diverge from those that define Schuchertella. However, taphonomic issues made it difficult to get an accurate taxonomic identification. It was found that the specimens from the Ponta Grossa Formation belonged to a new species of the genus Schellwienella Thomas, 1910, named S. clarkei. Concerning the Maecuru Formation specimens, it was possible to identify a new species, possibly belonging to the genus Iridistrophia Havlicek, 1965. Based on the literature and the analysis of the fossil specimens, more taxonomic studies about this group, as well as the redefinition of its diagnostic characters.



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## Turnover between crinoids and blastozoans in a Devonian mudmound seeting of Morocco

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Mudmounds are carbonated build-ups composed predominantly of mudstones and wackestones with a large amount of lime mud, suggesting a formation in relatively deep and/or quiet water settings. Hamar Laghdad (south-eastern Morocco) is word-renowned among geoscientists for its perfectly exhumed and highly fossiliferous mudmounds. During the Devonian, this region was covered by epicontinental sea in the northwestern Gondwana. The build-ups history starts with the accumulation of crinoid skeletal elements on a submarine topographic high during the Pragian, serving as basis for the development, during the Emsian, of the mounds and their diversified bottom dweller communities, mainly composed of tabulate and small solitary rugose corals, trilobites, cystoids and crinoids. Most of these organisms are suspension feeders, which likely profited from the wealth of micro-organisms benefiting from the minerals and nutrients provided from the hydrothermal wells. Echinoderms represent a large part of the bottom-dweller community. The new material has been collected in the past few years by the team conducted by Christian Klug (University of Zurich), who nicely provided the study material. It is composed of more than 60 crinoid cups, 15 complete thecas of blastozoan diploporitans, in addition to one partial peduncle of edrioasteroid. The rest of the material corresponds to various fragments of crinoid stems, and five fragments of diploporitan thecas. Preliminary taxonomic results suggest a relatively low diversity among crinoids (less than four species identified with a restricted disparity), one peduncle of rhenopyrgid, and a surprising high diversity of three species identified among the 15 diploporitan specimens. The diploporitan material offers the opportunity to challenge the controversial synonymization of four genera among the sphaeronitids and to propose a new phylogenetic frame for this family.



Speaker

### Conodonts of the genus *Lochriea* near the Visean– Serpukhovian boundary (Mississippian) at the Naqing section, Guizhou Province, South China

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The First Appearance Datum (FAD) of the conodont *Lochriea ziegleri* in the lineage *Lochriea nodosa* –*L. ziegleri* has been considered as the most suitable definition and global correlation-level for the revised base of the Serpukhovian Stage. Abundant specimens of *Lochriea* are recorded throughout the Late Visean–early Serpukhovian interval in the Naqing section. Among them, the P1 elements, with wide morphological variability, enables confirmation and refinement of known lineages within the genus. *L. nodosa* is recognized as a species with nodes or ridges on both the right and left sides of the upper platform. With this definition, *L. costata* and *L. monocostata* in their distribution charts and perhaps a possible paleoenvironmental importance should be attributed to the distinction between weakly noded and ridged species of *Lochriea* as Nemirovskaya et al. (1994) did with specimens that possessed strongly ornamented platforms. Two lineages are proposed: 1) noded *Lochriea* species, such as *L. monocostata* –*L. cruciformis*.



Speaker

### An attempt for finding the root causes of climate cooling tendency through Ordovician until glaciations and influence of rise of atmospheric oxygen

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The climate during Ordovician evolved from a relative greenhouse state toward a glaciation, located on the Gondwana paleocontinent. This study aims to present an analysis to evaluate the suggested primary drivers' variations contributing to the climate evolution: the solar irradiance, the surface albedo and the global sea level changes, the variations of atmospheric CO<sub>2</sub> and O<sub>2</sub>. The studied period for the drivers' variations is from Early Ordovician (480 Ma) to Late Ordovician-Early Silurian (440 Ma). For each driver's variation, the radiative forcing is evaluated (positive or negative), then a global radiative forcing is done by addition of the radiative forcings for the primary drivers. Determined through a proxy defined by paired bulk carbonate and organic isotope records, the increase of atmospheric O<sub>2</sub> is estimated in the range of + 9,5% to +16,5% and associated radiative forcing between -7,25 to -12,6 W/m<sup>2</sup>. For pCO<sub>2</sub> a radiative forcing range between -1,7 to -3,2 W/m<sup>2</sup> is evaluated, due to a decrease of atmospheric CO<sub>2</sub> of – 300 ppmv. So the drivers involving negative forcing lead to a range of -8,95 to -15,8 W/m<sup>2</sup>. The positive increase of the solar total irradiance is estimated to +3,6 W/m<sup>2</sup>. The variation of surface albedo linked with the estimated sea level rise of 100-150 meters is valued to around - 0,008 +0,002 and the radiative forcing is estimated to the range +8 to +10, 6 W/m<sup>2</sup>. The drivers involving positive forcing lead to a range of +11,6 to +14,2 W/m<sup>2</sup>. There is a domain where negative forcing exceeds positive forcing. And cooling climate trend can be so explained until glaciations. Increase of oxygen production should come from the photosynthetic marine life and appearance of terrestrial plants and should favorish the GOBE (Great Ordovician Biodiversification Event). The role of ozone variation is not considered here but could be added for reinforcing the climate cooling. The role of methane and nitrogen variation should also be studied but probably with minor impacts.



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### Occurrence of two *Lingulida* genera (Brachiopoda) at the Late Ordovician-Early Silurian interval of the Paraná Basin northern border, Brazil

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The samples were collected from shales with dropstones of the Vila Maria Formation (Hirnantian to Llandovery) from Mato Grosso State, Central Brazil. The studied stratigraphic interval is the sedimentary record of processes associated with the Late Ordovician glaciation, when most of the Gondwana was covered by widespread ice caps. The studied sedimentary rocks represent a lowstand system tract (LST) followed by a transgressive system tract (TST); the depositional environment is a glacially influenced shallow epicontinental sea. The brachiopod specimens belongs to the Lingulida Order, such as the Obolid Paleoglossa Cockerell, 1911 and the Discinid Kosoidea Havlicek and Mergl, 1988. Although only one adult valve of each genera was found, hundreds of disarticulated juvenile valves pertaining to both genera were recovered from the same interval. The juveniles from both genera are almost identical and techniques for their identification are being studied and will be published elsewere. Moreover, few specimens of calcitic brachiopods were found, but they are very poorly preserved. As preserved mainly at the TST beds, the fossils prevail among other similar sized particles, in a muddy matrix. The typical taphonomic signature of the TST is usually interpreted as specimens with bad preservation, due to transport. The fossils are small (2-3 mm in diameter, in general) and size-selected in these beds, and the preservation state is good although the transport by bottom currents is evident. Both genera have already been described for the Hirnantian (Upper Ordovician) of South Africa (the lagerstätte deposit of the Soom Shale Member, Cedarberg Formation). The presence of Kosoidea sp. and Paleoglossa sp. described for the first time in the Paraná Basin in South America pinpoints regional correlation and possible paleogeographic connection with South African Basins.

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Speaker

#### The palynological studies from the Cambrian of China: an overview

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The present study constitutes a summary of all palynological investigations conducted from the Cambrian of China. Cambrian palynological evidence was first documented in China in 1982 with first acritarch studies. Since then, Chinese palynology has experienced remarkable advances. To date, about 30 scientific studies have been published on the Chinese Cambrian palynological fossil record. Many of the published studies are written in Chinese language and are generally poorly known by a larger public. Most studies concern acritarch diversity, and they concern in majority South China. Importantly, key evidence from the most basal Phanerozoic is included. A few chitinozoan and cryptospore investigations are also documented. A compilation of palynological evidence reveals over 180Cambrian fossil species belonging to about 80 genera. Complete lists of these taxa are produced, and the palaeogeographical distribution is analyzed. The stratigraphic distribution of the documented diversity is also illustrated. The data present from the Chinese Cambrian highlight both the relevance and the limitations of the published palynological evidence. Upper Cambrian data are sparse, and documentation of Cambrian cryptospores from China are so far very limited. The Chinese Cambrian bears a great potential for further research and additional studies are urgently needed.



Speaker

# S23 - Life in the time of Pangaea: volcanism, warming, anoxia, acidification and extinction

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## Brobdingnagian bivalves: body size increase within various Lower Jurassic bivalve molluscs

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Within the upper Lilstock and Blue Lias Formations (upper Rhaetian to Lower Jurassic) of Britain several bivalve molluscs undergo an increase in body size. These trends are not only recorded at the generic level, but more crucially within individual species, therefore they are not an example of Cope's Rule (phylogenetic size increase) in action. Body size increases are not confined to ecological guilds and occur in tandem with biotic recovery from the end-Triassic mass extinction event (ca. 201 Ma). The most striking example of body size increase is seen in the epibyssate bivalve *Plagiostoma giganteum* (Sowerby), which undergoes a 170% mean body size increase from its first common occurrence. Environmental parameters are assessed to test for possible causes of body size change. Pyrite framboid size distributions are generated spanning the recovery interval and beyond in order to test for the effects of marine oxygenation. Temperature, sea level and substrate are also considered.

For this study Rhaetian and Lower Jurassic exposures were sampled in South West Britain, Northern Ireland and North Yorkshire and supplemented with measurements of specimens housed in museum collections. This study now comprises size data of over 5000 bivalve specimens belonging to over 100 species and provides an understanding of how Lower Jurassic ecosystems responded during the recovery from the End-Triassic mass extinction event. The trend to large size within a species is proposed to be a Brobdingnagian one – named after Swift's giants, the counterpoise to the tiny Lilliputians in his novel *Gulliver's Travels*.



Speaker

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#### The role of ocean acidification during the latest Permian mass extinction event

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The latest Permian mass extinction event was the most catastrophic biodiversity crisis in Earth's history, with the extinctions in the oceans thought to have been caused by the combined role of deoxygenation, high temperatures, and ocean acidification. The role of ocean acidification in the extinctions is, however, controversial, and there are several inconsistencies: geochemical evidence for ocean acidification does not correlate with the main extinction pulse; and sedimentological proxies for ocean acidification have been associated with other formation processes. Currently, the only robust evidence for ocean acidification is the observed selective extinction of heavily-calcified organisms. The categorization of marine invertebrates as heavy-calcifiers in previous studies is, however, both coarse (i.e. at the phylum and class-level) and subjective, leading to questionable interpretations. The timing of this selectivity is also equivocal, and it is unknown if the selective extinction occurred during the mass extinction event or during a hypothesized subsequent extinction event in the Early Triassic. To better understand the selectivity of the latest Permian mass extinction we, therefore, compiled a high-resolution dataset spanning the Permian-Triassic transition from the well-studied South China region. The dataset includes marine invertebrates, foraminifera, calcareous algae, problematica and conodonts, with each taxon quantitatively assigned to ecological attributes (skeletal mineralogy, carbonate load, tiering, motility, and respiratory protein) that reflect each organism's physiology. Here we show that using the subjective classification of previous studies heavily-calcified organisms were selected against during the latest Permian mass extinction. On the other hand, analysis of the quantitative assignments of ecological variables to each taxon shows that taxa with low-Mg calcite shells, and the respiratory protein hemerythrin were selected against, which is not consistent with an ocean acidification hypothesis. In addition, the mass extinction event was not selective against organisms with higher carbonate loads. These new results suggest that ocean acidification was either not a significant factor in the Late Permian mass extinction, or that the acidification was so catastrophic that it did not only select against the animals that were the most susceptible.



Speaker

#### The impact of Large Igneous Province volcanism on Pangaean life

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The supercontinent of Pangaea existed during the Late Permian to Middle Jurassic Period. This time period was marked by unusually low marine faunal diversity, punctuated by two of the so called 'Big Five' mass extinctions of the Phanerozoic Aeon (the end-Permian and end- Triassic extinctions), and numerous other extinction events and episodes of palaeoceanographic and palaeoclimatic upheaval (e.g. the Toarcian Oceanic Anoxic Event – T-OAE). Many of these events have been causally linked with the formation of Large Igneous Provinces (LIPs), which represent the geologically abrupt emplacement of millions of cubic kilometres of (chiefly) basaltic material. Evidence for such a relationship comes from the coincidence in the apparent ages of many of these events with the determined ages of LIP volcanism, and from the sedimentary record, where stratigraphic horizons recording extinction events commonly show perturbations in sedimentary proxies for volcanism.

In this context, Hg/TOC (mercury/total organic carbon) excursions in sedimentary archives have been used to indicate large-scale volcanic activity related to LIP formation, as volcanic outgassing is one of the main natural sources of mercury to the modern environment. Here, the Hg/TOC records of multiple events from the time of Pangaea are reviewed, with particular focus on those of the end-Triassic mass extinction (201.5 Ma) and the T-OAE (183 Ma). These trends are also compared with other established geochemical proxies for carbon-cycle perturbations (carbon isotopes and leaf stomatal data) and weathering rates (osmium isotopes).

These comparisons indicate a strong correlation in increased atmospheric mercury and  $CO_2$  at the onset of both events, likely resulting from volcanogenic processes. For the Toarcian, these perturbations also broadly correlate with evidence of increased weathering rates. Taken together, these observations strongly support a model of increased atmospheric  $CO_2$  resulting from volcanogenic processes, subsequently causing enhanced global weathering rates and nutrient influx to the marine realm. Whilst such processes would have initially encouraged widespread marine anoxia, they would ultimately have caused the drawn-down of excess  $CO_2$  through one or both of enhanced silicate weathering and organic-matter burial. With such a mechanism supported for the end-Triassic and Toarcian events, future work should compare these events with others from both during and before/after the time of Pangaea.



Speaker

### The Carnian Pluvial Episode linked to the diversification of dinosaurs and the origin of modern terrestrial vertebrate faunas

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In this contribution, we present evidence for a major inflection point in the history of tetrapods on land, a jump in the diversification of archosauromorphs at 232–230 Ma. This corresponds to a long-noted changeover in Triassic terrestrial tetrapod faunas, from those dominated by synapsids, many of them holdovers from the Permian, to those dominated by dinosaurs. We provide evidence that dinosaurs rapidly rose in diversity and ecological importance during this time, corresponding to a phase of increased rainfall and perturbation of oceans and atmospheres, the Carnian Pluvial Episode (CPE), which was followed by substantial aridification.

The rock record through the CPE confirms that this event shared many characteristics with other mass extinctions driven by the eruption of large igneous provinces, in this case the Wrangellia flood basalts of the west coast of North America. If this was a catastrophic extinction event, then the environmental perturbations of the CPE explain the sharp disappearance of various terrestrial tetrapods, and the subsequent sharp rise of dinosaurs and perhaps other clades too, especially those that constitute much of the modern terrestrial fauna, such as lissamphibians, turtles, crocodiles, lizards, and mammals.

We conclude that, in this view, a new model emerges whereby (non-avian) dinosaur evolution was shaped by three deep global ecosystem perturbations: they originated just after the Permian-Triassic mass extinction, rapidly diversified during the CPE, and went extinct at the end-Cretaceous extinction.



Speaker

#### A little walk between Liassic sponges and corals

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Distinguishing corals from sponges is an easy task in modern specimens when soft tissues are available, but the distinction is not so easy in fossil skeletons. Over the last few decades a number of extinct taxa have been re-classified as corals or sponges (originally identified as other taxa). The classification issue has been a matter of debate for archaeocyaths, tabulates, stromatoporoids, and among them chaetetids. In the last few decades, the study of chaetetids has highlighted significant differences between scleractinian and chaetetid skeletal microstructures. Nevertheless, without well-preserved specimens, the distinction between coral and chaetetids remains difficult.

During a study of Hettangian-Pliensbachian-aged fossils in the region of Amellago (the High Atlas Mountains of Morocco), we were challenged with a similar issue. We discovered several Early Jurassic specimens for which the taxonomic classification is unclear; in the literature, similar specimens have been assigned to both sponges and corals. Turnsek et al. (1975) interpreted these forms as a colonial Amphiastreid coral of the genus *Hispaniastraea*; however, Fischer (1970) and Beauvais (1980) asssigned these forms to *Chaetetes* (*Pseudoseptifer*), a Chaetetid sponge. Our study, based on all available diagnostic macrostructural characters of the material allows us to establish two groups of specimens, one with characters specific to scleractinian corals and the other with characteristics of chaetetids. Thus, we have tested the hypothesis of an evolutionary convergence between *Hispaniastraea* and *Chaetetes* (*Pseudoseptifer*).

Considering the new specimens discovered in the High and Middle Atlas Mountains (Morocco) and Languedoc (south of France), it appears necessary to revise the systematics of both genera and outline clear criteria to distinguish one from the other. The study of this fauna has been supported by biometrical and morphometrical approaches. Furthermore, computerized tomography (CT-scan) is used to provide a better resolution of morphological and ontogenetic differences CT scans provide critical information about the internal structures of the specimens, for example the fissiparous division mode characteristic of the *Chaetetes (Pseudoseptifer)* sub-genera.

This contribution is part of the long-term research project on reef and carbonate build-up development (REEFCADE to R.M.), started in 2007 and supported by the Swiss National Science Foundation.

\* Speaker

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#### The shallow-water Permian-Triassic extinction record in western Tethys (Hungary and Turkey): evidence for ocean acidification or marine anoxia?

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The Permian-Triassic (PT) extinction is Earth's greatest ever crisis. Extensive damage was done to both terrestrial and marine ecosystems in a brief interval around the boundary. Proposed kill mechanisms include volcanic winter, hypercapnia, global warming, increased sediment flux to the oceans, ozone destruction and increased harmful ultraviolet-B radiation, acid rain, atmospheric oxygen depletion and toxic trace metals poisoning, with origins in Siberian Traps volcanism.

We examine evidence from shallow-water sections in western Tethys for two volcanically-induced stresses: anoxia and ocean acidification. The development of anoxia is linked to global warming of the oceans and recent studies point to a marked increase in sea surface temperatures between the Late Permian and Early Triassic. However, the timing and duration of anoxic events in boundary sections is complex and many shallow-water settings lack typically anoxic facies, inferring that anoxia cannot have been the oceanic killer. CO<sub>2</sub>-driven ocean acidification features in PT extinction models with extinction selectivity, isotope proxies, and a purported carbonate dissolution surface in China, Japan, and Turkey being cited as evidence. The origin of such surfaces is controversial: sea-level fall and karstification generate the same features.

Our facies, fossil, petrographic and geochemical ( $\delta^{13}C_{carb}$  and trace metals) study of PT boundary sections from Tethys (Çürük Dag in Turkey and Bálvány in Hungary) indicates that the geological record through the extinction event is near-complete in each.  $\delta^{13}C_{carb}$  curves from both show close correspondence with global records and feature a prominent negative excursion of 5-6 ‰. The duration of any hiatus recorded by a prominent sequence boundary (the purported "acidification surface") at Çürük Dag was therefore likely brief (no such surface is recorded by the deeper facies at Bálvány). An abrupt extinction of foraminifera occurs immediately above this sequence boundary at Çürük Dag, within the negative carbon isotope shift, whereas at Bálvány the foraminifera disappear within the "Boundary Shale" bed prior to the isotope shift. In both sections a decline in benthic oxygen levels at the extinction level is supported by pyrite framboid distributions (Bálvány) and trace metal concentrations (Çürük Dag).

We conclude that the "acidification surface" in our shallowest-water section, Çürük Dag, has its origins in karstification during a brief sea-level fall prior to the main extinction level. The extinction in both locations coincides with a deterioration in benthic oxygen levels. Marine anoxia (or dysoxia) during an interval of rapid global warming is the most likely extinction driver in this region - evidence for ocean acidification is unsubstantiated.



<sup>&</sup>lt;sup>°</sup> Speaker

#### Rapid biotic rebound during the late Griesbachian indicates heterogeneous recovery patterns after the Permian-Triassic mass extinction

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Spatiotemporal recovery patterns following the Permian-Triassic mass extinction (PTME) are debated. Depauperate faunas were prevailed throughout the Early Triassic, and not until the Middle Triassic did diversity rebound. Contrary to the prolonged recovery scenario, recent studies on conodonts, ammonoids and foraminifers reveal a rapid recovery pattern that shows diversification was not underway until the Smithian, less than ~1.5 million years after the PTME. New fossil data of two Early Triassic (Griesbachian to Dienerian) sections (Gujiao and Jianzishan) from South China show unusually high levels of both benthic and nektonic taxonomic richness, occurring in the late Griesbachian. A total of 68 species (including 26 species of Triassic-type species) among mollusks, brachiopods, foraminifers, conodonts, ostracods, and echinoderms occur in the late Griesbachian, indicating well-established and relatively complex marine communities. Furthermore, the nektons show higher origination rates than the benthos, e.g. ammonoid (proptychitids). This difference between nektonic and benthic taxa may result from the relatively stronger mobility of nektonic organisms such as cephalopods, which makes them better able to avoid spatially variable hostile environments. It could also reflect the intrinsically evolutionary rate of ammonoids that tends to be high, compared to other mollusk groups, at all times during the clades' history.

Analyses of sedimentary facies, ichnofossils and size distribution of pyrite framboids show that this high-diversity interval is associated with well-oxygenated environments. In contrast to the previously suggested scenario that persistently harsh environmental conditions impeded the biotic recovery during the Early Triassic, our new findings, combined with recent works, indicate a fitful regional recovery pattern after the Permian-Triassic crisis resulting in three main diversity highs: late Griesbachian-early Dienerian, early-middle Smithian and Spathian. The transient rebound episodes are therefore influenced by both extrinsic local (e.g. redox condition, temperature) and intrinsic (e.g. biological tolerances, origination rate) parameters.



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### A warming and aridification event in terrestrial ecosystem of North China during the early Jurassic, possibly linked to the Toarcian Oceanic Anoxic Event

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The Lower and Middle Jurassic in North China consist chiefly of coal-bearing formations and are extremely rich in plant fossils. A consensus amongst the Chinese palaeobotanists is that the Early-Middle Jurassic flora in this area is dominated by ferns and ginkgoes. It is regarded as typical flora in temperate zone, indicating warm-humid climates. However, further studies show that this flora can be subdivided into several assemblages presenting variation of climate. Recently, a series of macroand micro-floral assemblages have been established from the Upper Triassic and Lower-Middle Jurassic at the Haojiagou section of the Junggar basin, Northwest China. A striking feature is that the macrofloral assemblage from the upper of the Lower Jurassic (the Sangonghe Formation) is greatly different from both the older (from the Badaowan Formation of middle Early Jurassic) and the younger (from the Xishanyao Formation of early Middle Jurassic) ones in composition. It contains a dramatic high ratio (up to 40%) of the thermophilous or desiccation tolerant elements, such as Dictyophyllum, Marattiopsis and Phlebopteris of ferns, Otozamites, Zamites and Dictyozamites of bennettitales, Brachyphyllum (Hirmeriella) of scale-leaf conifer and ephedrales-like plant Cadmisega. In contrast, these elements are almost totally absent from both the older and the younger assemblages. These indicate that the climate in the Junggar Basin was semi-arid in tropicsubtropic zone during late Early Jurassic, but warm-humid in temperate zone during the middle of Early Jurassic and Middle Jurassic, showing a temperature rising and aridification event in the late Early Jurassic. Additionally, a coeval content spike (over 50%) of the hot-arid climate indicative pollen Classopollis and absence of coal bed and coal seem in the Sangonghe Formation provide further positive evidences for this palaeoclimatic event. Further investigations in several basins through North China confirm that it is an extensive palaeoclimatic event in all North China, and it is most likely occurred in the Toarcian, comparable well with the Toarcian temperature rising event in the Mid-Asia and Siberia suggested by Russian palaeobotanist Vachrameev in 1991. Moreover, this palaeoclimatic event is inferred to be coincided with the Toarcian Oceanic Anoxic Event (T-OAE) and is the response of the terrestrial ecosystem to the environmental change event in marine ecosystem.



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#### Modelling extinction during Mesozoic hyperthermal events

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The Late Triassic and early Toarcian extinction events are both associated with greenhouse warming events triggered by massive volcanism. These Mesozoic hyperthermals were responsible for the extinction of 50% and 25% of marine genera, respectively, and resulted in significant ecological upheaval. It has, however, been suggested that these extinction events merely represented intensifications of background extinction rates rather than significant shifts in macroevolutionary regime and extinction selectivity. For the first time, we apply a multivariate modelling approach to a vast global database of marine organisms to test whether extinction selectivity varied through the Late Triassic and Early Jurassic. We show that these Mesozoic hyperthermals do represent significant shifts in macroevolutionary regime and record very different extinction selectivity compared to periods of Triassic and Jurassic background extinction. The Late Triassic hyperthermal selected against tropical organisms with photosymbiotic and suspension feeding habits, whereas the early Toarcian hyperthermal selected against photosymbiotic organisms and those residing at higher latitudes in the restricted basins of the Tethys Ocean.



Speaker

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### Late Cisuralian and Late Guadalupian ecological events: biotic and sedimentological evidence from different climatic zones in the Urals, Timan and South Primorye (Russia)

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Large scale photozoan and heterozoan turnovers are described from sections that record different climatic zones in the Urals, Timan and South Primorye (Russia). The Sakmarian-Kungurian transition saw the replacement of highly diverse fusulinid foraminifera and colonial rugose corals (a photozoan assemblage) with small foraminifera and solitary corals (heterozoans). The greatest diversity of massive colonial Rugosa is known from the Sakmarian reef facies whereas in contemporaneous slope deposits diversity is low. Even in non-reef carbonates in the inner part of carbonate platform diversity is high and comparable with reef facies. A major ecological event occurred in the Uralian-Timan basin during the mid Artinskian and manifest as sequential but asynchronous losses amongst different groups of photozoans. Diversity loss in the colonial rugose corals began in the Early Artinskian, when fusulinids were still rather diverse. The main losses of fusulinids in the southern Urals took place at the Artinskian-Kungurian boundary. In our sections, and in the Timan-Pechora region, fusulinids are unknown above the Artinskian. Associated facies shifts saw shallow inner shelf deposits replaced by deep open shelf facies, and the event level also records a negative  $\delta$ 13Ccarb excursion. We consider these changes to be linked to the P2 global interglacial. A younger photozoan to heterozoan shift is documented from Capitanian?Wuchiapingian strata in South Primorye (Russian Far East), where it is correlated with the global "Kamura Event". Here, the disappearance of fusulinids and their replacement by small foraminifera occurred in slope deposits of the carbonate platform, whilst photozoans were much more diverse in contemporaneous reef environments. An assemblage dominated by sphinctozoans and small foraminifera developed in Capitanian strata and is considered characteristic of stressed environments. According to stable isotope data ( $\delta \delta^{13}C_{carb}$ ) and facies analyses, the Capitanian "Kamura Event" saw the gradual destruction of the carbonate platform, at a time that might have experienced external stresses such as ocean acidification and probable warming, as a result of large igneous province volcanism.



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### Volcanism, C-cycle perturbations and Earth-life transition reciprocity; the Triassic-Jurassic boundary as a case study in the Levant region

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Global earth life transition, C-cycle perturbations and extensive volcanism tend to appear together but the causes of their mutual relationship are under debate, mainly due to correlation problems between volcanic and marine settings; the Triassic- Jurassic transition is one example for this relationship. Three adjacent successions that include the Triassic-Jurassic transition, where two of them include volcanic series and one is volcanic-free are an exemplary opportunity to highlight many important aspects regarding this relationship in the Levant region. Applying limited biostratigraphy and <sup>87</sup>Sr/<sup>86</sup>Sr chronostratigraphy allowed age constraining the TJ transition. The C & O stable isotopes systematics indicated events of  $\delta^{13}C_{carb}$ negative excursions: late Norian - early Rhaetian (203 Ma); the Hettangian (198 Ma) and during the Sinemurian (195 and 191 Ma). Linking between different stages of the regional volcanism and the  $\delta^{13}C_{carb}$ negative excursions, leads to an understanding of the patterns of environmental impact. Phases of magma penetration and submarine activity caused a warming trend which lasted during the Norian and the early Rhaetian. This warming event led to extreme monsoonal storm and extensive land erosion. A change into subaerial eruption type during the Rhaetian (between 203 to 199 Ma), included thermal uplift and subaerial extrusive aerosols causing an abrupt decline of temperatures. This global cooling ceased the monsoonal pattern in the subtropics. The negative excursions in the carbon cycle found in this study well correlated with other studies. In this work are correlated with high siliciclastic content, hence indicating terrestrial organic matter influxes as probable source of excess <sup>12</sup>C<sub>carb</sub>. Finally, the regional volcanism (203 to 199 Ma) synchronous with the CAMP (201.6 Ma) and other volcanism, may reflect global volcanism as a crucial factor for the climate change, but an indirect factor for the occurrence of  $\delta \delta^{13}C_{carb}$  negative events.



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#### Paleoenvironmental and paleoecological trends leading up to the end-Triassic mass extinction event at Ferguson Hill, Nevada

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High-resolution petrographic (119 thin-sections) and carbon isotope (68 samples) analyses at the Ferguson Hill section, Nevada give new insights into the pre-extinction conditions present in western Panthalassa during the late Rhaetian. The stratigraphic section encompasses 5.5 m of the uppermost Mount Hyatt Member (MHM) overlain by 3.2 m of the lowermost Muller Canyon Member (MCM) of the Gabbs Formation. The depositional environment is interpreted to represent mid- to outer-shelf based on lithology, faunal distribution and sedimentary features. The extinction interval is defined by the last occurrence of the last Triassic ammonite Choristoceras crickmayi. For the first time the highest occurrence of C. crickmayi is found at the base of the N3 bed at this locality which records the primary negative carbon isotope excursion (NIE) occurring worldwide in association with the end-Triassic mass extinction (ETE) and generally is interpreted as evidence for a primary productivity collapse. Organic carbon isotope data reveals the presence of an initial NIE of 1.6 at -4.5 m, 7 m below the extinction interval. An identical NIE is documented in Levanto, Peru suggesting that observed shifts in the carbon cycle occurred globally preceding the major biotic collapse. An elevated amount of sulphide pseudomorphs (goethite framboids after pyrite) coincides with the initial NIE and reoccurs at 0.9 m and above in the section. The presence of sulphide pseudomorphs suggests anoxic conditions within the sediment and potentially within the water column, supported by the depauperate benthic community and absence of bioturbation. Microfacies analysis of bioclasts documents the vanishing of benthic macrofauna at 2.5 m, right below the extinction interval and the primary NIE. Petrographic analysis of early cemented beds records the longest interval of an unusual carbonate system from 1.2 m to 2.4 m, ~30 cm below the extinction interval. In the upper part of the section,  $\delta^{13}C_{carb}$  values vary between -0.5 and 0.5 while in the lower part of the section  $\delta^{13}C_{carb}$  values vary between -1.5 and 1.5. Relatively enriched  $\delta^{13}C_{carb}$  values of pore-filling cement imply cementation very close to the sediment water interface. This first high-resolution study of the pre-extinction interval at Ferguson Hill, Nevada suggests that stressed conditions began before the global environmental and biotic collapse as indicated by multiple lines of evidence.



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#### The record of Early Jurassic (Pliensbachian-Toarcian) lithiotid bivalve and coral reef collapse, survival, and recovery from the Central High Atlas of Morocco

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Extinction events and carbon cycle perturbations have profoundly affected the history of life on Earth. To date, there remains a significant gap in our knowledge about the shallow- water record of Early Jurassic events at the Pliensbachian-Toarcian boundary and the Toarcian Oceanic Anoxic Event (T-OAE). Specifically, there is no detailed analysis of how these events influenced the fate of reef ecosystems and their associated marine communities. This research discusses the record of shallow-water marine extinction and reef collapse in Morocco during these Early Jurassic events.

The Central High Atlas Mountains provide an excellent record of the Pliensbachian-Toarcian stage boundary and the T-OAE in both ramp and platform settings. In the late Pliensbachian, reef communities are abundant in shallow-water environments and during this time, a group of large, reef-building bivalves called lithiotids proliferated. In proximal, shallow marine environments, lithiotid bivalves formed small mounds and extensive biostromes, while corals and thick, encrusting microbes formed patch reefs. Notably, colonial and solitary corals have been observed in the lithiotid biostromes and the occasional lithiotid bivalve can be observed in the coral and coral-microbial reefs. This ecological association seems to be unique to Morocco.

At the Pliensbachian-Toarcian stage boundary the carbonate factory collapsed and corals experienced a taxonomic turnover. Nevertheless, lithiotid biostromes (with subordinate corals) persisted into the Early Toarcian forming extensive biostromes once the carbonate factory recovered in the late Tenuicostatum chronozone. Unlike the coral reefs, lithiotid biostromes do not appear to have been significantly affected by the extinction at the stage boundary. There is notable heterogeneity of lithiotid associations (both taxonomically and by growth form) within biostromes. During the T-OAE, the carbonate factory shut down once again, causing another coral turnover, and spelling the demise of the lithiotid biostromes as an ecosystem. Despite the collapse of the lithiotid communities, coral reefs were quick to recover from the T-OAE, with post-OAE Toarcian patch reefs occurring in deeper environments than the Pliensbachian coral reefs.

In sum, the unique, high-resolution paleoecological data from Morocco will allow us to build a more nuanced understanding of Early Jurassic reef ecosystems, as well as their collapse, survival, and recovery during this interval.

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## Searching for mass extinction drivers: common cause or lost cause?

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Mass extinctions have shaped the course of evolution but it is still debated whether these events share a set common causes or if they are a response to a more unpredictable set of drivers. Periodicity of mass extinction would be indicative a potential common mass extinction driver, but there has not been conclusive evidence of mass extinctions occurring at regular intervals. Some extinction drivers may be more unique, such as the bolide impact at the Cretaceous-Palaeogene boundary. However, many mass extinction events correlate with periods of warming: the Permo-Triassic mass extinction, the Cretaceous-Palaeogene, and others occurred alongside Large Igneous Province (LIP) activity. Furthermore, many events correlate with continent aggregation. We hypothesise that extinction risk resulted from climate warming due to LIP activity increasing levels of atmospheric carbon dioxide, and continent aggregation reducing carbon dioxide release through factors such as low silicate weathering rates. Here we take a statistical approach by analysing rates of extinction through time alongside these potential drivers of mass extinctions. We analyse a large-scale metazoan invertebrate database spanning the Phanerozoic and simultaneous account for vagaries in fossil record preservation. This approach can highlight if mass extinctions events are predictable, and thus understand if macroevolution is predictable in response to climactic changes.



Speaker

### The effect of the Pliensbachian-Toarcian crisis on body size: the case of Peniche section belemnites (Lusitanian Basin, Portugal)

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Body size is a determinant key of how organisms interact with their environment as it constrains in important ways ecological and physiological traits and it can be modulated by environmental stressors. Body size reduction has been seen as an important response to climate warming and it has been suggested for multiple mass extinction events including the Pliensbachian – Toarcian (Pli-Toa) crisis. This interval is characterized by palaeoenvironmental perturbations, namely rapid warming, anoxia, and perturbations of the carbon cycle, and their impact on marine biota. These perturbations have been associated with volcanic activity in the Karoo-Ferrar igneous province.

For this study, we focused on the Peniche section (Lusitanian Basin, Portugal), where the effects the T-OAE, namely anoxia, were not so dramatically felted, in contrast with NW European sections (e.g. Cleveland Basin). Mercury concentration peaks are recorded across the studied interval, alongside with increasing seawater temperatures, and interpreted as an effect of distal volcanic activity pulses. From the Emaciatum Zone (uppermost Pliensbachian) – Levisoni Zone (uppermost lower Toarcian), 930 belemnites rostra were collected. Post-phragmocone length was used as a proxy for belemnites body size.

As a working hypothesis, we aim to assess the existence of a belemnite body size reduction across the Pli-Toa boundary at different levels of organization (individuals, populations and communities). The ultimate hypothesis to test is the link between belemnites body size dynamics and temperature related stressors.

A statistically significant reduction in belemnites body size was recognized across the PliensbachianToarcian boundary at the assemblage level (i.e. community level of organization). From the analysis of the different taxa recorded, it seems that adult specimens of *Pseudohastites longiformis* are driving the body size pattern observed. Multiple regression analyses, taking into account paleotemperature ( $\delta^{18}$ O as a proxy), volcanic activity peaks (mercury concentration as a proxy) and/or perturbations of the carbon cycle ( $\delta^{13}$ C as a proxy), indicate that seawater temperature best explains the pattern in body size changes. However, the synergy with other related stressors cannot always be discarded.



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#### Differences in body size distributions between Toarcian belemnite battlefields

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Body size changes have been reported across multiple extinction events. Belemnites – now considered extant relatives of squid – have rarely been investigated for this purpose, and the few results have been ambiguous. Here we investigate two Toarcian belemnite battlefields from a morphometric point of view. The aim of this study is to test whether a difference in body size can be observed between the rostra in these two accumulations, from individual lineage to community, and which proxy provides more reliable data. A significant decrease in median size from the Early Toarcian (Tenuicostatum Zone) to the Middle Toarcian (Variabilis Zone) is recognized. This is observed on the community level of organization, considering the whole assemblage, but also within *Passaloteuthis-Acrocoelites* lineage. It is also demonstrated that diameter-based measurements are not reliable, and therefore, three-dimensional approximations, which take into account all dimensions (such as the geometric mean or the volume of the post-phragmocone rostrum) are more advisable. This is especially important when comparing specimens with markedly different shapes. Further studies are, however, still necessary to corroborate the mechanisms behind the reduction in rostrum size within the Toarcian and their possible environmental causes.



Speaker

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## Limuloid trackways from the Permian – Triassic continental successions of North China

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Dozens of *Kouphichnium* specimens, a typical limuloid (horseshoe crab) trackway, are reported and systematically studied for the first time from continental Upper Permian to Lower Triassic successions in North China. A new ichnotaxa system of *Kouphichnium* is proposed according to the ichnotaxobase of limuloid trackways, including simple foot tracks, pusher imprints, median impressions and genal spine impressions. In total, one ichnogenus and six ichnospecies are recognised, one of which is new: *Kouphichnium liulinensis* sp. nov. The ichnogenus *Paramphibius* is regarded as a synonym of *Kouphichnium* and the diagnoses of ichnogenus *Kouphichnium* and two early ichnospecies, i. e. type ichnospecies *Kouphichnium lithographicus* Oppel, and *Kouphichnium (Paramphibius) didactylus* Willard, are revised. An ideal model of these six ichnospecies from continental Upper Permian to Lower Triassic successions in North China is established with varied palaeoethological interpretations of each type. The sizes of trackmakers are estimated from the external width of trackways, and it shows a drastical decrease from the Late Permian to Early Triassic, followed by a gradual increase in the Early Triassic. This variation of trackmaker (limuloid) sizes during the Permian-Triassic transition, especially the drastic drop, indicates environmental stress during the critical time. In addition, analysis of the sizes of pusher imprints from certain well-preserved trackways suggests potential sexual dimorphism of limuloids.



Speaker

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#### Abrupt ecosystem changes during an Early Jurassic (Toarcian) global warming episode

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The Early Jurassic Toarcian Ocean Anoxic Event (T-OAE; ~183 million years ago) is as- sociated with rapid global warming, mass extinction in the marine realm and widespread ocean oxygen deficiency. The event is marked by a major negative carbon isotope excursion (CIE), signifying a massive release of isotopically light carbon into the atmosphere. Proposed causal mechanisms for the event include elevated CO2 concentrations as a result of the emplacement of the Karoo-Ferrar large igneous province in the Southern Hemisphere, and the release of ther- mogenic and/or biogenic methane. Efforts to understand the biological consequences of the Toarcian event have primarily focussed on marine ecosystems; responses include the temporary and/or complete disappearance of marine plankton groups (e.g. dinoflagellates), and widespread extinction among macroinvertebrates. Comparatively few studies have investigated the effects of the Toarcian event on terrestrial environments. Here we examine the palynological record across the Pliensbachian/Toarcian boundary and the T-OAE sequences found globally. We aim to track how this episode impacted terrestrial and marine ecosystems and examine links between continental and marine environments. We record abrupt changes across the event and reveal how shifts in floral and marine communities are intimately linked with climatic changes.



Speaker

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#### Oceanic anoxia during the Carnian Humid Episode

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The mid-Carnian (Late Triassic, ~233 Ma) represents an interval of major climatic changes. However, oceanic redox conditions during this critical interval remain least understood. We investigated sections in the Austrian Alps, India Himalaya, Oman and South China to document the redox history during the Carnian Humid Episode. Anoxic facies in the Scheiblingsgraben section, (Austrian Alps) is evidenced by mid-Carnian black shales developed above platform carbonates. However, in the condensed basinal Hallstatt facies (Feuerkogel section), red ammonoid-bearing limestones are developed, showing no evidence of anoxic depositional conditions. In the Spiti Valley (Indian Himalaya), carbonate deposition was replaced by dark grey shales and black paper shales, indicating a transition from dysoxic to anoxic conditions. In the Nanpanjiang Basin (South China), basin-wide intense anoxia/euxinia was long-lasting and coincided with the final termination of the Yangtze Platform. Thus, oceanic anoxia were widespread in the mid-Carnian, but with large regional variations in duration and intensity and occurred contemporaneously with global warming, a negative carbon isotope excursion as well as flood basalt volcanism.

Speaker

#### Variations in coral faunas across the Pliensbachian-Toarcian crisis: a diachronous event?

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The boundary between the Pliensbachian and Toarcian stages of Lower Jurassic (Upper Lias) is an important interval for the understanding of worldwide ecological turnovers. This interval records evidence of important biological extinction events concerning different taxonomic groups as well as markers of major paleoenvironmental modifications. At the Pliensbachian/Toarcian boundary, groups such as ammonites, brachiopods, and bivalves suffered huge faunal turnovers at different taxonomic scales; which have been temporally linked with the Karoo-Ferrar large igneous province in Southern Pangea. In addition, large-scale negative excursions of the  $\delta^{13}$ C record and significant variations of  ${}^{87}$ Sr/ ${}^{86}$ Sr ratio at both the Pliensbachian/Toarcian boundary and within the Toarcian Oceanic Anoxic Event (T-OAE) indicate that there are global perturbations to the carbon cycle and other geochemical cycles in this interval. At the T-OAE, these perturbations correspond to significant organic matter-rich strata (black shales) in Europe, North America, and South America. Associated to these events, global reef collapses have been documented; there is a 99% loss of reef carbonate production recorded worldwide. Bibliographic studies of Lathuilière and Marchal (2009) about populations of corals (cnidarians) fossils suggest a significant extinction in this group for the same period. C are particularly sensitive indicators of major ecological perturbations, as evidenced by their significant turnovers during the "Big 5" biological crisis. This presentation reports on a work in progress, which aims to characterize and quantify the faunal turnovers suffered by corals across the Pliensbachian/Toarcian boundary as well as across the T-OAE. The distinction of the ecological turnover and impacts of each of these two events will open new perspectives in the interpretation of the data and results in terms of paleoecology and taxonomic turnovers. We are addressing this question in the southern Atlas of Morocco, where Pliensbachian and Toarcian deposits are exceptionally expanded in comparison to other localities worldwide.



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#### Tetrapod spatial biodiversity patterns across the end-Permian mass extinction and recovery interval

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The latitudinal diversity gradient (LDG), which describes the general trend of increasing species richness that occurs from the poles to the tropics, is one of the most widely recognized large-scale biological patterns of the modern day. However, our understanding of the processes that drive the LDG is limited, and whether the pattern we see today has been consistent throughout geological time remains unclear. One approach to answering both of these questions is to examine spatial biodiversity patterns in the geological past when global climate and continental configuration contrasted with those of the modern.

An ideal candidate time period is the latest Palaeozoic to earliest Mesozoic. During the Late Permian-late Triassic, global temperatures were generally high, with average seawater temperatures reaching as much as 38°C in the Early Triassic. This coincided with a number of mass extinctions and biotic turnover events associated with significant environmental perturbations. In addition to the emplacement and eruption of a number of large igneous provinces, the major landmasses had coalesced into the supercontinent Pangaea, both of which are likely to have played a major role in altering global climate feedback systems at this time.

The latest Palaeozoic-earliest Mesozoic is also a significant time in the evolution of the Tetrapoda, with the previously dominant Synapsida suffering severe losses during the end-Permian mass extinction, facilitating the diversification of the Archosauromorpha in the Triassic. Following this, the Triassic-Jurassic mass extinction also resulted in many extinctions in the group, including the loss of the Aetosauria, Phytosauria and Rauisuchia, however subsequent recovery eventually led to the Dinosauria becoming the dominant terrestrial animals of the Mesozoic. Examining the spatial distributions of tetrapods during the Late Permian-late Triassic may shed light on the evolutionary mechanisms behind some these biotic turnovers.

Here, we set out to characterise large-scale spatial biodiversity patterns in the Tetrapoda during the Late Permian-late Triassic by applying a number of established quantitative techniques to a global data set of tetrapod fossil occurrences.



Speaker

#### New insights in the Lower to Middle Triassic floras of Argentina (Southwestern Gondwana)

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Argentinean Triassic floras are known since more than a century, and evolution models, biostratigraphic schemes and biogeographic provinces were proposed by several authors in the last three decades. Nevertheless, in most recent years, new methodologies in the stratigraphy and radiometric techniques offering more accurate ages have been quivered the previous palaeofloristic models. Here we revised the biostratigraphy and the palaeoflora evolution of the Lower to Middle Triassic from Argentina under the light of the recent stratigraphic and chronologic advances. We focus on Sorocayense Group (San Juan province), Puesto Viejo Group (Mendoza province) and Los Menucos Group (Río Negro province). In previous schemes, the appearance of the Dicroidium Flora was regarded to the upper part of the Barrealian Stage (Anisian) which would have succeeded the "Pleuromeia Flora" recorded in the Quebrada de los Fósiles Formation (Puesto Viejo Group), the last being considered as Lower Triassic. The diverse plant assemblage (interpreted as forests with various species of Zuberia, cycads and voltzialeans) from Los Menucos Group was first correlated to the Early to Middle Triassic Dicroidium zuberi Oppel Zone from Australia, but afterwards a radiometric age pointed it as early Late Triassic. Then again, recent radiometric analyses indicate that the Vera Formation of Los Menucos Group was deposited during the earliest Triassic. On the other hand, new fossil findings in Quebrada de los Fósiles Formation led to interpret it as early Middle Triassic, and to infer that its sedimentation environment comprised lowlands with pleuromeid accompanied with other lycopodiopsids and sphenopsids, and uplands with corystosperms and other gymnosperms. Finally, the Barreal Formation (Anisian, Sorocayense Group) contains a preserved forest dominated by Zuberia, with a remarkably diverse Dipteridaceae fern assemblage in its understory. The evolution of Argentinian floras is now more compatible with the Australian biostratigraphic scheme, with Zuberia in the Early Triassic and Dicroidium odontopteroides since the early Middle Triassic. Both lycopodiopsids and ferns are known as pioneer species in the ecosystem succession; their presence as lowland-dominants in the Anisian is coeval with the last stages of the Gondwanic magmatism which affected this zone. Ladinian and Late Triassic deposits show the best development of the Dicroidium flora in the lowlands. The case of the earliest Triassic Los Menucos flora poses new questions. This is a Zuberia flora in the lowlands suffering a nearby and active volcanic system, hardly interpretable as a refugium like those recorded during stress events. One explanation is that this Zuberia flora colonized the lowlands under stress, but also, we could be in front of the remnants of a Permian flora, resisting the strikes of the volcanic stress, preparing to take refuge in the uplands to grow stronger and go back to the lowlands in the Middle Triassic.



<sup>&</sup>lt;sup>\*</sup> Speaker

## Carbon cycle perturbations and ocean acidification at the onset of the end-Permian mass extinction

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The Permian-Triassic boundary-interval (PTB) witnessed the most severe environmental crisis in Earth history, which dictated the course for evolution of life until today. Current lines of evidence on causation point towards massive flood-basalt volcanism from Siberian traps, involving a combination of global warming by ~6°C, substantial input of relatively light carbon to the atmosphere, sporadic to widespread anoxia or euxinia, and ocean acidification, however the trigger mechanism is yet to be fully understood. In order to reconstruct potential changes in seawater chemistry during this time interval, we examined the boron isotope composition ( $\delta^{11}$ B) of pristine brachiopod shells. Although to-date hardly applied in Paleozoic settings, the  $\delta^{11}$ B of marine biogenic carbonates is considered to be one of the most reliable paleo-pH proxy. Brachiopods present an advantageous and largely underutilised archive for Phanerozoic reconstructions considering their high abundance in the geological record and its origin dating back to the early Cambrian. Moreover, their low-magnesium calcite shell renders them more resilient to post-depositional diagenetic alteration of primary chemical signals. Using carefully chosen pristine specimens (class Rhynchonellata and Strophomenata), selected  $\delta^{11}$ B to pH relationships, and bulk seawater  $\delta^{11}$ B scenarios we present a high-resolution seawater pH record for the Tethys Ocean. This interval covers the negative carbon isotope excursion in excess of 4 and is associated with major climate and environmental changes that led to the mass extinction event. Our results show a significant decline in  $\delta^{11}$ B succeeding the  $\delta^{13}$ C excursion, suggesting a substantial drop in seawater pH at the onset of the extinction event in the Late Permian related to carbon cycle perturbations. Combining our pH record with paired  $\delta^{13}$ C data and a quantitative modelling approach, we delineate the unfolding carbon cycle dynamic and budget that may have been responsible for initiating the catastrophic extinction event.



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### Research group poster: Temperature-Related Stresses as a Unifying Principle in Ancient Extinctions (TERSANE)

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Combined with local and regional anthropogenic factors, current human-induced climate warming is thought to be a major threat to biodiversity. The ecological imprint of climate change is already visible on land and in the oceans. The imprint is largely manifested in demographic/abundance changes and phenological and distribution shifts, whereas only local extinctions are yet attributable to climate change with some confidence. This is expected to change in the near future owing to direct heat stress, shortage of food, mismatches in the timing of seasonal activities, geographic barriers to migration, and new biological interactions. Additional stressors are associated with climate warming in marine systems, namely acidification and deoxygenation. Ocean acidification is caused by the ocean's absorption of  $CO_2$  and deoxygenation is a result of warmer water, increased ocean stratification and upwelling of hypoxic waters. The combination of warming, acidification and deoxygenation is known as the deadly trio". Temperature is the most pervasive environmental factor shaping the functional characteristics and limits to life and is central to the generation and biological effects of hypoxic waters and to modulating the effects of ocean acidification, with and without concomitant hypoxia. Due to the key role of temperature in the interaction of the three drivers we termed these temperature-related stressors (TRS). This Postersindexes IPC5 contributions from the research group, TERSANE, on topics from current ecophysiology, body size dynamics, current and past biogeography, to extinction pattern studies, from databases at Phanerozoic scales and from stratigraphic studies of specific intervals.



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#### Marine invertebrate responses to temperaturerelated stressors and their interactions

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As the global climate adjusts to anthropogenic high levels of CO<sub>2</sub>, marine organisms have to cope with multiple changing environmental stressors that influence their performance. Marine metazoan hard limits to temperature and chronic anoxia have long been known. However, interactions between stressors, such as synergies between temperature and both low oxygen levels and acidification, have emerged relatively recently as concordant across many experiments and organisms. Understanding interactions is critical because stressors rarely occur singly. Multiple temperature related stressors (TRS) have been implicated at most, if not all, past extinction crises, although their geographical distributions may be relevant to their impact. We present a meta-analysis of experiments involving multiple TRS and their interactions. Results have implications to be wider than previously reported within TRS, and to vary by response type and organism ontogenetic stage. Forecasting the effects of TRS on marine organisms by modelling single stressors, such as temperature, is unlikely to reveal more than a low estimate of the severity of response. Geographical context is also likely to be important, although general trends are evident. Cross-checking biological responses between fossil and current evidence is recommended as best practice.



Speaker

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#### A phylogenetic and stratigraphic approach to analysing diversification dynamics in deep time

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The fossilised birth-death (FBD) process is a phylogenetic model that incorporates the species diversification and fossil sampling processes explicitly. The model can be applied to the analysis of stratigraphic ranges, defined as the interval between first and last appearance times in the fossil record, and used to estimate speciation and extinction rates during different geological intervals. In this model, fossils are distributed over time according to a uniform Poisson sampling process, and sampling rate may vary across intervals in a piecewise manner. In the initial application of this model, reliable estimates of diversification and sampling rates were demonstrated to depend on the exact number of sampled specimens and the age of first and last appearances times being specified accurately. This is problematic since (i) the number of fossil specimens sampled during different geological intervals may be challenging to constrain and (ii) the uncertainty associated with the age of first and last appearances is often large. We introduce a novel FBD model that relaxes these requirements. Here, we allow for the possibility that we may only know whether a given taxon was sampled or not during each geological interval, but not the frequency or at which precise time points the taxon was sampled (referred to as presence/absence sampling). We assess the performance of our modelling framework using simulations and demonstrate that although precision decreases given presence/absence data, we can still obtain reliable estimates of diversification and sampling parameters. Finally, we apply our new model to the analysis of the Triassic-Jurassic extinction interval, for which presence/absence data only is available at the sub-stage level, and we re-examine the diversification dynamics across this important and turbulent episode in earth's history. Together, our findings demonstrate the importance of explicitly accommodating the diversification and sampling processes in combination. Our new model should be of broad application in palaeodiversity studies, given that many fossil datasets are comprised of presence/absence data only, making it challenging to analyse such datasets using existing phylogenetic models. Future development of phylogenetic models in palaeobiology should continue to consider seriously the nature of the incompleteness of fossil occurrence databases.



Speaker

#### Anoxia events and conodonts occurrence in Campáleo outcrop, Itaraté Group, Lontras Shale, Cisuralian of the Paraná Basin, Brazil

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The Campáleo outcrop is situated in Mafra City, State of Santa Catarina, Brazil. It presents a sedimentary succession, characteristic of thaw deposits, related to the top of the Campo Mourão Formation, Itararé Group. The sedimentation is composed, at the base, by layers of varvites with approximately 10 m and, at the top, by a fossiliferous silty shale of 1,1 m; this succession is called Lontras Shale. The fossiliferous content of the Lontras, at Campáleo, is concentrated in the shale and presents exceptional taphonomic preservation, being considered as a Lagerstätte. It mainly comprises fossils of: paleoniscids osteichthys fish, chondrichthyes, fragments of feeding apparatus of conodonts, sponge, insects, crustaceans, scolecodonts, brachiopods, vegetal fragments, among other microfossils. It is a recurrent shale layer along the eastern border of the Paraná Basin, since it occurs in great regional amplitude and its depositional thickness varies sharply throughout the basin. Based on the observation of stratigraphic oriented profiles, carried out in this sedimentary package, as well as chemical analyzes and detailed observation in stereomicroscope of the fossils and of the lithologies, it is possible to suggest the occurrence of three outstanding anoxic events that coincide with the maximum flood observable in the sedimentary section of Campáleo and that reflect in isochrone in the basin. The occurrence, just above the anoxic levels, of conodonts of the Mesogondolella genus, typical of deep cool waters in other paleogeographic provinces worldwide, as well as they had been pelagic animals that tolerated living in marine environments with low oxygenation, help to corroborate these anoxic events and also suggest detritivorous habits for the conodonts animals, seen that in the section its fossil distribution is constant and of the other taxa vary according to the maximum of flood.



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#### Reconstructing trophic networks across the early Toarcian Ocean Anoxic Event (Lower Jurassic)

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Trophic guild diversity, connectivity, and robustness of trophic networks decreases across the Early Toarcian Ocean Anoxic Event. We focus on the reconstruction of trophic network dynamics across the early Toarcian extinction event; which is thought to have been driven by an Ocean Anoxic Event. The analysis is based on a field database collected from the Pliensbachian- Toarcian of the Yorkshire Coast, with 162 macrofossil species assigned to trophic guilds using the Bambach ecospace model. Although there is limited evidence for the decoupling of pelagic and benthic ecosystems, there is a major loss of motile, metabolically demanding benthic fauna. Network connectivity is greater in the late post-extinction recovery than in pre-extinction, although the number of guilds remain equal. This is likely due to the appearance of new predatory guilds that display a high degree of centrality, i.e. well connected to other nodes, in the networks. The results suggest that the early Toarcian extinction event was likely a top-down extinction with metabolically demanding benthic guilds, such as motile predators, disappearing during the Ocean Anoxic Event, as they were more sensitive to dysoxic and anoxic conditions than stationary benthic faunas with lower metabolic demands.



Speaker

#### S24 - Macroecology and the Fossil Record

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#### Geographic distributions of benthic invertebrate species are diversity-dependent across the Phanerozoic

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Geographic distribution is a fundamental property of species and is thought to respond to and control processes such as biotic competition, extinction, and speciation. Adaptive radiation, ecological saturation, diversity-dependent diversification, and other fundamental evolutionary theories assume that biotic pressures largely control species' distributions. Species in sympatry with many other species may be limited in distribution (competitive exclusion), but can spread when competitors are removed (competitive release). Few studies, however, have tested conclusively the degree to which competition structures geographic ranges over large spatio-temporal scales. We investigated the link between geographic distributions and changes in biotic pressure over the Phanerozoic using the Paleobiology Database marine record of brachiopod and bivalve species. We devised a subsampling approach to control for heterogeneous spatial preservation of species' distributions through time, while standardizing species counts with coverage-based rarefaction. We then constructed time series of species' geographic distribution metrics, regional species counts, and instantaneous extinction and origination rates. We implemented two approaches to test for potential effects of competition on range sizes. First, we assessed the relationships between range size and total species count and origination and extinction rate. Hypotheses of competitive exclusion and release predict range size to respond inversely to changes in taxic diversity. This pattern, however, may also reflect the dynamics of speciation and extinction, which we also consider. In a second approach, we compared changes in species count to mean changes in distribution of species that survived stage boundaries. We found a negative and significant correlation between the number of species in a regional assemblage and the geographic distributions of constituent species. The correlation of average range size with extinction rate was also strongly negative. Moreover, species that survived biodiversity crises expanded their geographic ranges significantly. In comparison, ranges of survivors remained constant across background boundaries. Taken together, our results suggest that competitive release has occurred and that geographic distribution mediates a negative feedback between diversity and extinction rate, thus supporting a fundamental assumption of key evolutionary theories.



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#### Move out or die: climate change driven metacommunity dynamics during the late Miocene

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The study of how long-term changes affect metacommunities is a relevant topic, which involves the evaluation of connections among biological assemblages across different spatio- temporal scales, in order to fully understand links between global changes and macroevolutionary patterns. We applied multivariate statistical analyses and diversity tests using a large data matrix of rodent fossil sites in order to analyse long-term faunal changes. Late Miocene rodent faunas from southwestern Europe were classified into metacommunities, presumably sharing ecological affinities, which followed temporal and environmental non-random assembly and disassembly patterns. Metacommunity dynamics of these faunas were driven by environmental changes associated with temperature variability, but there was also some influence from the aridity shifts described for this region during the late Miocene. Additionally, while variations in the structure of rodent assemblages were directly influenced by global climatic changes in the southern province, the northern sites showed a pattern of climatic influence mediated by diversity-dependent processes.



Speaker

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# Exploring macroevolutionary and macroecological patterns using early Pliensbachian ammonites from the western Tethys

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The early Pliensbachian (Early Jurassic, 190.8 Ma to 187.6 Ma) was a time of marked provincialism in the marine realm, notably between the Mediterranean Tethys (MED) and North–West Europe (NWE). Using a large dataset based on the comprehensive revision of early Pliensbachian ammonites from the Western Tethys (214 species, 104 localities, 1765 occurrences) and a species- level phylogenetic hypothesis, we explore various macroecological and biogeographical patterns at the scale of the chronozone and sub-chronozone. Our main results are as follows: **Biogeography and richness:** Both NWE and MED ammonite provinces record similar trends in richness and endemism despite their sharp contrast in taxonomic composition and richness. The low richness in the Davoei chronozone may be related to a coeval warming of seawaters, but the latter was insufficient to affect biotic interchanges between the two provinces.

**Phylogenetic distribution of extinctions:** Ammonite extinctions were significantly clustered phylogenetically and this pattern prevailed throughout the studied interval. We show that phylogenetic conservatism is scale-dependent and that the intensity of the signal is sensitive to temporal resolution. We suggest that a combined use of Moran's *I*, Pearson's *phi* and Fritz and Purvis' *D* statistics is an appropriate approach because it can highlight different facets of the phylogenetic pattern of extinctions and/or survivals in fossil organisms.

**Similarity distance decay:** The similarity distance decay (SDD) relationship (the decrease in compositional similarity among communities with geographical distance) is a pattern widely investigated in biogeography. Using a multi-scale approach, we showed that sampling scale may influence SDD rates in an unpredictable way and that the phylogenetic level has a major impact on SDD patterns. In addition, SDD relationship can be inappropriate for detecting a biogeographical structuring. The long-distance dispersal of early Pliensbachian ammonites does not seem to be related to shell size and shape, but rather to the environmental characteristics of the province to which they belong.

**Heritability of species range size:** Although species range size may be partly heritable phylogenetically, we found that this conservatism can be strongly affected by spatio-temporal environmental stability. The phylogenetic signal of range size heritability can be labile through time within the same lineage and it may differ among contemporaneous species of the same group.

\* Speaker



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#### Macroecological analysis of Cenozoic terrestrial mammals in North America

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Local and regional species assemblages can be viewed as a combination of strictly deterministic processes resulting from primary principles of ecosystem functioning (energy and space availability, interactions among individuals and populations through mutualism and/or competition, etc.) and a purely stochastic ecological drift resulting from random dispersal and local extinction. Determining the primary process (niche- vs. dispersal-assembly) driving the construction of such assemblages is an old, central and ongoing question in ecology. In this context we introduce a new methodology based on Clarke's SIMPER analysis, an initially descriptive method aiming at identifying which taxa are primarily responsible for an observed compositional difference between two or more groups of species assemblages. By adding a random permutation- based step (PER-SIMPER) we are able to identify the underlying first-order process of assembly for the analysed sample groups. The accuracy and efficiency of the procedure is demonstrated through cellular automaton-like simulations generating niche- and/or dispersal-based patterns of occurrence. The PER-SIMPER method is used to analyse the assembly dynamics of the well-known Cenozoic mammal fossil record of North America. Extending from the Cretaceous- Paleogene limit up to the early Pleistocene, this dataset covers eight major biogeographic regions from the west coast to the Great Plains and from Mexico to the western part of Canada. Treating these biogeographic regions as sample groups within the NALMA biochronological framework, we evidence contrasted first-order assembly dynamics that are discussed in the context of the already well-known evolutionary and biotope history of Cenozoic North-American mammals. Results highlight consistent and meaningful relationships between large scale assembly dynamics and global biogeographic and climatic conditions, showing how the PER-SIMPER method sheds light into the deep-time macroecological history underlying the analysed dataset.



S24 // Ora

Speaker

#### The biogeographic imprint of mass extinctions

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The consequences of mass extinctions have been studied from multiple perspectives, but a rigorous assessment of their biogeographic impact is still lacking. The geographic patterns of extinctions, subsequent originations, and the redistribution of survivor species should lead to massive changes in the global biogeographic structure. In order to assess the impact of mass extinctions quantitatively, we revealed the global biogeographic structure of the marine fossil record with a composition network approach. By treating space and time equally in this framework, we outlined time-traceable bioregions for macrobenthic marine species across the post-Cambrian Phanerozoic. The "Big Five" mass extinction events and some minor episodes stand out in the geographic rendering of bioregions. The end-Permian mass extinction figures prominently with a severely homogenized biogeographic structure of marine life in its aftermath. The temporal dynamics in bioregion emergence and disintegration can be visualized in a similar fashion as species-turnover rates. Biogeographic turnover shows no distinct trend over time, but supports the hypothesis that biogeographic upheaval is concentrated at mass extinction episodes.

Speaker

# The Signor-lipps effect in macroecology and evolution

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In 1982, Signor and Lipps noted that gradual extinction patterns preceded all mass extinctions; David Raup later named this the Signor-lipps Effect. The Signor-lipps publication became a "landmark paper" in the mass extinction debates, a topic of debate itself, an item of classroom instruction, and included in text-books. When plots of taxa ranges approach an extinction event, the gradual S-I Effect appears. The S-I Effect was found at many places and at many times in the fossil record and is a general pattern. Most workers assumed that if they did better and more intensive sampling in the field and laboratory, a true sudden pattern would emerge. This assumes that the species occur in every sample over their biogeographic limits and evolutionary lifetimes. To test this, ranges of various organisms occurring up to every sampling site in several stratigraphic successions showed a gradual range truncation at every sample, even though all species occurred in subsequent younger samples. Thus, inadequate sampling at the outcrop or inadequate sample processing and examination do not explain the Signor- Lipps Effect. Instead other geological and biological processes create such patterns, including taphonomic changes, diagenesis, missing strata, solution or breakage, removal of specimens by predation or competition during life, or emigration of populations during life from the sampling site to another area. Numerical processing of data considering this problem assumes that the fossils occur in all samples but this is clearly not the case. Until these other factors are clearly defined, the statistical methods will produce incorrect results. In macroecology, the Signor-lipps Effect is thus important for the evaluation of the complete biodiversity and macroecology of an evolving sequence of organisms. For example, biotas that occur for some time before and after the event and that are sufficiently different demonstrate a mass extinction.



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<sup>&</sup>lt;sup>•</sup> Speaker

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#### The role of functional traits in mammalian community structure across the Pleistocene-Holocene transition

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The study of communities over time allows us to evaluate the degree to which ecological processes are affected by climate change and human activity. Such knowledge is critical to predicting how species will assemble into communities in response to future climate change. Recent work documenting the co-occurrence structure of communities over the past 300,000,000 years attributed a shift from aggregated (species that occur together more frequently than expected by chance) to segregated (species that occur together more frequently than expected by chance) to segregated (species that occur together less frequently than expected by chance) species pairs in the mid-Holocene to human impacts. Here, we investigate the complex role of climate and species traits in the co-occurrence structure of mammals across the late Pleistocene to the modern. We find that the climate change and biodiversity loss at the terminal Pleistocene fundamentally changed species. Moreover, the interaction strength of pairs that contained an extinct species was stronger for aggregations, but not segregations suggesting that the loss of the megafauna had differential effects on the co- occurrence of surviving species. Specific species traits, such as body mass or trophic interaction, declined in their importance or switched from promoting aggregations to promoting segregations amongst surviving species. We conclude that future climate change and extinction are likely to exacerbate these trends.



Speaker

## Combining macroecology and palaeoecology in understanding biodiversity: microfossils as a model

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There is growing interest in the integration of macroecology and palaeoecology towards a better understanding of past, present, and anticipated future biodiversity dynamics. However, the empirical basis for this integration has thus far been limited. Here we review prospects for a macroecology-palaeoecology integration in biodiversity analyses with a focus on marine microfossils [i.e. small (or small parts of) organisms with high fossilization potential, such as foraminifera, ostracodes, diatoms, radiolaria, coccolithophores, dinoflagellates, and ichthyoliths]. Marine microfossils represent a useful model system for such integrative research because of their high abundance, large spatiotemporal coverage, and good taxonomic and temporal resolution. The microfossil record allows for quantitative cross-scale research designs, which help in answering fundamental questions about marine biodiversity, including the causes behind similarities in patterns of latitudinal and longitudinal variation across taxa, the degree of constancy of observed gradients over time, and the relative importance of hypothesized drivers that may explain past or present biodiversity patterns. The inclusion of a deep-time perspective based on high-resolution microfossil records may be an important step for the further maturation of macroecology. An improved integration of macroecology and palaeoecology would aid in our understanding of the balance of ecological and evolutionary mechanisms that have shaped the biosphere we inhabit today and affect how it may change in the future.



Speaker

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#### Where are Australia's bears and America's antechinus? Ecomorphology and convergence in past and present predator guilds

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Predators have well-documented, disproportionate impacts on their communities, but the factors that determine the structure of predator guilds are not as well understood. Comparing morphospace occupancy of geographically and phylogenetically distinct predator guilds can be an effective means of testing hypotheses of community dynamics. An especially informative comparison can be made between Australian marsupial predators and Northern Hemisphere carnivorans, which have long been interpreted as being convergent. Such convergence could indicate that drivers of predator guild structure are similar for all mammal communities. However, the modern Australian predator fauna provides an incomplete sample of marsupial morphological disparity. As recently as the Pleistocene, the diversity of dasyuromorphs was much greater, as was the diversity of non-dasyuromorphs predators with no obvious Northern Hemisphere analogs (thylacoleonids and hypsiprymnodontid kangaroos). Likewise, most analyses of convergence between Australian mammalian predators and those of other continents have been limited to large-bodied taxa, despite the enormous diversity of small-bodied dasyurids and mustelids. I calculated cranial, dental, and postcranial functional indices for Pleistocene and modern Australian marsupial faunivores and carnivorans from the continental United States and used a principal components analysis to visualize the ecomorphospace occupied by mammalian predators on both continents. While there was substantial overlap between North American and Australian taxa, each guild occupied an area of morphospace not occupied by the other. The bulk of dasyuromorph diversity is composed of small, insectivorous taxa. While there are few carnivoran analogs for this body plan in North America, small dasyurids may be convergent on North American soricids. Large-bodied omnivores such as ursids and procyonids are well- represented in North America, but except for the kangaroo Propleopus are absent from the Australian record. This paucity of omnivores may be due to ecosystem variables such as the low levels of primary productivity in Australia, to biotic interactions with prey or large reptilian predators, or to phylogenetic or developmental constraints. In any case, the convergence between predator guilds in Australia and on other continents may be weaker than other studies have indicated, suggesting that the factors determining guild structure can vary widely between communities.



S24 // Oral

<sup>&</sup>lt;sup>'</sup> Speaker

#### **Macroevolution through mass extinctions**

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Mass extinctions have periodically devastated life's history and altered the course of macroevolution. There are a number of controversies in how we expect macroevolution to be affected by and respond to mass extinction events. For example it would be expected that mass extinctions are still selective in regard to traits, but many studies have indicated survival is through these perturbations is a random 'field of bullets' with little selective pressure. Additionally, mass extinctions are believed to clear morphospace to allow for rapid radiation in their aftermath, and to facilitate the replacement of previously dominant taxa that have diminished or gone extinct. Here we test these theories and others by using a novel simulation approach in which trees and traits evolve in a single framework, and go through 'mass extinction' events. In the simulation framework, trees evolve via a birth-death process and along each branch continuous traits evolve in a null Brownian motion framework with varying amounts of trait covariation. The mass extinctions are either selective or non-selective with regards to the evolving traits, and have different amounts of intensity in terms of lineage loss. These simulations provide a simple framework to guide expectations of trait evolution through a mass extinction boundaries, and in particular indicate what patterns we should expect in terms of trait disparity and lineage diversity in the fossil record.

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## Climate change and the latitudinal selectivity of ancient marine extinctions

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Geologically rapid climate change is anticipated to increase extinction risk non-uniformly across the Earth's surface. Tropical marine species loss is expected to follow low seawater oxygen levels and high climate velocities, alongside temperatures already at or around species' thermal maxima. Such temperature related stressors (TRS), including ocean acidification, should be traceable in the past by extinction patterns that vary by latitude. We combine a statistical assessment of latitudinal extinction selectivity with the current consensus on TRS occurring at extinction crises and million year scale environmental data. Our initial findings reveal idiosyncratic links between the inferred direction of climate change and extinction selectivity and selectivity is not restricted to extinction crises. Among the classical Big Five mass extinction episodes, the end-Permian mass extinction stands out in showing a temperate preference of extinctions, whereas the Late Devonian and end-Triassic selectively hit tropical genera. Latitudinal patterns of extinction selectivity in the fossil record do not straight-forwardly evidence climate change. Instead, inclusion of sampling patterns and continental shelf area changes in the model recovers an association between elevated temperatures and tropical selectivity. Global warmth and habitat area loss, including via widespread ocean anoxia or other conditions inimical to marine life, figure prominently in generating geographical patterns in extinction.



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# Metabolic rates, climate and macroevolution: a case study using Neogene molluscs

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Basal metabolic rate is posited to be a fundamental control on the structure and dynamics of ecological networks, influencing organism resource use and rates of senescence. Differences in the maintenance energy requirements of individual species therefore potentially predict extinction likelihood. If validated, this would comprise an important link between organismic ecology and macroevolutionary dynamics. To test this hypothesis, the basal metabolic rates of organisms within fossil species were determined using body size and temperature data and considered in light of species' survival and extinction through time. Our analysis focused on the high-resolution record of Pliocene to recent molluscs (bivalves and gastropods) from the western Atlantic. Species-specific basal metabolic rates were calculated by measuring the size range of specimens from museum collections, determining ocean temperature using the HadCM3 global climate model, and deriving values based on relevant equations. Intriguingly, a statistically significant difference in metabolic rate exists between those bivalve and gastropod species that went extinct and those that survived throughout the course of the Neogene. This indicates that there is a scaling up from organismic properties to species survival for these taxa. Metabolic rate therefore may represent an important metric for predicting future extinction patterns, with changes in global climate potentially affecting the lifespan of individuals, ultimately leading to the extinction of the species they are contained within. We also find that, at the assemblage level, there is no significant difference in metabolic rates for different time intervals throughout the entire study period. This suggests that Neogene mollusc communities have remained energetically stable, despite many extinctions. Together, these findings demonstrate that an understanding of metabolic rates for fossil communities can provide crucial insight into extinction as an ecological and genealogical phenomenon.

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<sup>&</sup>lt;sup>•</sup> Speaker

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# Testing the efficiency of isotherm tracking by marine bivalves and brachiopods

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Rapid climate changes can force range retreats and expansions along latitudinal or bathymetric (or altitudinal) gradients in marine (or terrestrial) environments. Although poleward shifts in response to temperature changes are well-documented in marine environments, bathymetric expansions or retreats remain poorly documented at regional and broad geographic scales. Marine species tracking isothermal bands along latitudinal gradients should effectively occur at any depth within the bounds of their thermal niches. In such case, the slope of intraspecific relationship between latitude and minimum annual temperature (inhabited by a given species) should be about zero (maximum annual temperature cannot remain constant towards higher latitudes, but minimum temperature is not affected by this constraint) and the intraspecific relation between depth and latitude should be positive. Here, to test these two hypotheses that underlie most macroecological and biogeographic concepts predicting changes in species geographic limits along latitudinal gradients, we quantify relation between latitude, temperature, and depth in brachiopod species at global scales and in bivalve species in the Eastern Atlantic. We find that, first, the slopes of the intraspecific relation between depth and latitude are rather close to zero, and second, within the same species, poleward populations experience significantly colder temperatures than equatorward populations. Therefore, isotherm tracking seems to be weak and is probably significantly constrained by depth factors unrelated to temperature. Brachiopod and bivalve species at low latitudes do not seem to fully realize they full thermal range especially at large water depths.



Speaker

# Rapoport effect and the climatic variability hypothesis in Early Jurassic ammonites

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The increase of species range sizes towards high latitudes, known as the "Rapoport's rule", remains one of the most debated and poorly understood macroecological patterns. Numerous studies have challenged its universality, which led to rename it the "Rapoport effect", as well as the main mechanism originally proposed to explain this pattern, *i.e.* the climatic variability hypothesis. In addition, studies of the Rapoport effect have been essentially conducted on extant terrestrial organisms in the northern hemisphere. Here we study this macroecological pattern on a group of fossil marine organisms: the early Pliensbachian (Early Jurassic) ammonites of the western Tethys. Using a dataset including 214 species distributed among 104 localities, we test for the existence of a Rapoport effect for the three chronozones of the early Pliensbachian. We further take into account the influence of the marked provincialism prevailing at that time, with a Mediterranean province (MED) and a Northwest European province (NWE) located on each side of a latitudinally-oriented palaeobiogeographic barrier. We find that only species from the NWE province display a Rapoport effect, whereas species from the more tropical MED province show a boundary effect and have larger range sizes in average. This dual pattern can be explained by an alternative climatic variability hypothesis that better captures latitudinal seasonal variations and outlines the influence of the intertropical zone. The latter is indeed characterized by stable and homogeneous climate that allows species to disperse over very large areas regardless of their thermal tolerance. Accordingly, the NWE province probably displayed a gradient of seasonal climatic variations which caused the emergence of a Rapoport effect, whereas the MED province was probably located in the intertropical zone where no gradient in species range size is expected. Our multi-scale approach further shows that the Rapoport effect is scale dependent and may be labile through time. This probably explains the conflicting results of previous studies carried out at various spatio-temporal scales. Our results also support the hypothesis that temperature was an important factor controlling ammonite spatial distribution and that the Rapoport effect is probably a phenomenon occurring mainly out of the tropics.



S24 // Oral

Speaker

#### Biomic specialization and the influence on diversification rates of squirrels (Sciuridae, Mammalia) during the Cenozoic

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With a current diversity approaching 300 species, squirrels have conquered all the world's biomes and almost all the continents (except Antarctica and Australia) since their origin in the Eocene, which makes them an exceptional group for studying ecological preference evolution. Therefore, we obtained a multifossil-calibrated phylogenetic tree including 229 species of Sciuridae (Rodentia, Mammalia) and we calculated the diversification rates. Then, we tested one of the predictions of the resource-use hypothesis proposed by E.S. Vrba, which foretells that generalist species have lower diversification rates than specialist species due to a better adaptive capacity during an environmental change episode. We compared speciation rates between biome specialists (stenobiomic species) and biome generalists (eurybiomic species) using a Multiple State 'Speciation' and Extinction model ("MuSSE") in R. We considered three groups relying on the biomic specialization index (BSI), which is based on the number of biomes occupied by each species: specialists (BSI = 1), generalists (BSI between 1 and 5) and extreme generalists (BSI $\geq$ 5). Furthermore, we performed an ancestral reconstruction of biomic specialization in the phylogenetic tree. Our results are consistent with the predictions of the resource-use hypothesis, which predicts a higher speciation rate of lineages restricted to a single biome (specialists) than lineages which occupied several biomes (generalists). Additionally, we found that the biomes with higher proportions of specialist species are the tropical rainforest (I) with around 36% of species restricted to this biome and the steppes and cold deserts (VII), which comprise 24 stenobiomic species (32.4%). This is also congruent with the resource-use hypothesis, which predicts higher specialization of species inhabiting biomes that underwent a high degree of fragmentation and contraction associated to global climatic changes; while rainforest distribution is very fragmented during glacial maxima, steppes are more affected by interglacial maxima.



<sup>\*</sup> Speaker

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#### The old and the new plankton: ecological replacement of associations of cephalopod plankton by holoplanktonic gastropods after the Cretaceous?

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Ammonites and belemnites are cephalopods that played essential roles in Mesozoic oceans. The respective roles of juveniles and adults in the food web are rarely analysed separately. Ammonites and belemnites show a size increase by two to three orders of magnitude, which suggests fundamental changes in their respective ecological roles. To estimate the ecological role of ammonoid juveniles (including eggs and hatchlings), we calculated the fecundity of ammonoids by calculating gonad volume (as a proxy of the number of eggs they could produce) of the largest ammonite Parapuzosia seppenradensis using an equation introduced by Raup & Chamberlain (1967). Based on this calculation, we estimated that females of large Cretaceous ammonites may have laid 10 to 100 million eggs. The overwhelming abundance of planktonic cephalopod hatchlings implies the great ecological importance of the juveniles as plankton in Cretaceous oceans. Ammonites, belemnites and coincidentally, large filter-feeding fishes went extinct at the end of the Cretaceous. This suggests a trophic relationship between ammonoid juveniles and large filter-feeding fishes, pointing at a possible ecological importance of ammonoid juveniles. We suggest that holoplanktonic gastropods resumed the ecological roles of extinct cephalopods in marine food webs, considering their similar size range, conch morphologies and trophic role. The rise of this new plankton may be linked with the rise of planktivorous chondrichthyans and baleen whales, which represent an ecologically related biotic replacement.



Speaker

# S25 - Mesozoic palaeontology and palaeoenvironments of Indochina

#### **Oral communications**

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#### Poster



#### Bookending Indochina: a comparison of terrestrial lacustrine Late Mesozoic deposits in Australia and China

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During the Mesozoic, low latitude Indochina had largely red-bed deposition, but was bookended in the higher latitudes by terrestrial environments in Australia and China. A comparison between these freshwater lacustrine deposits reveals some remarkable similarities. The Australian Upper Jurassic Talbragar Fossil Fish Bed and Lower Cretaceous Koonwarra Fossil Beds share many features with the Upper Jurassic Daohugou Biota and the Lower Cretaceous Jehol Biota in China. Research into sedimentary environments, plant, insect and fish faunas, has uncovered many common features.

There is a dominant small fish in all areas; *Lycoptera* in China, compared to *Waldmanichthys* in Koonwarra and *Cavenderichthys* in Talbragar. There are similar spiders in all deposits, and many similar insects. Common plants include Ginkgos, broad leafed conifers such as *Podozamites* /Araucariaceae, other conifers, cycads, horsetail ferns and other ferns. Both Jehol Biota and Koonwarra deposits contain an early angiosperm.

Details of the morphology of the fish fauna in Talbragar and Koonwarria are currently being updated. The families Luisiellidae, Archaeomenidae and Coccolepididae are represented at both sites and will be illustrated in this talk.

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Speaker
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#### Depositional environments and bivalve assemblages in the Triassic shallow marine facies in the northern part of Vietnam

Toshifumi Komatsu \*<sup>1</sup>, Takumi Maekawa <sup>2</sup>, Yasunari Shigeta <sup>3</sup>, Julien Legrand <sup>4</sup>, Takanobu Tsuihiji <sup>5</sup>, Phong Nguyen Duc <sup>6</sup>, Hung Dinh Doan <sup>7</sup>

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In northern Vietnam, fossiliferous Triassic shallow marine deposits are distributed in the Song Hien, An Chau and Song Da sedimentary basins. These marine deposits, which consist mainly of tidal flat, shoreface, shelf, slope and basin siliciclastics and/or carbonates, yield abundant bivalves and age-diagnostic ammonoids and conodonts.

We examined the paleontology and sedimentology of several type and key sections of the Lower Triassic Hong Ngai Formation (Induan-Olenekian) in the Song Hien Basin; the Lower Triassic Lang Son Formation (Induan-lower Olenekian), Bac Thuy Formation (Upper Induan- Olenekian) and the Middle Triassic Na Khuat Formation (Anisian to Ladinian) in the An Chau Basin; and the Lower Triassic Co Noi Formation (Induan-Olenekian), Middle Triassic Dong Giao Formation (Anisian) and the Upper Triassic Suoi Bang Formation (Carnian to Norian) in the Song Da Basin. Over 100 bivalve species were identified. The faunal compositions of bivalves were relatively similar among sedimentary basins, and were characterized by Early Triassic *Claraia* and *Eumorphotis*, Middle Triassic *Costatoria*, *Trigonodus* and *Hoernesia*, and Late Triassic *Costatoria* and *Halobia*. Abundant *Unionites*, *Bakevellia* and *Pteria* were found locally in the Lower to Upper Triassic shelf deposits. The Early Triassic bivalve assemblage was generally dominated by epifauna. *Claraia* and *Eumorphotis* were the most diversified groups in the Induan to early Olenekian, and almost all of the *Claraia* species were distributed in the lower shoreface, shelf and basin environments. Infaunal and semi-infaunal bivalves flourished during the Middle to Late Triassic. Thus, compared to epifaunal bivalves, the infaunal bivalves showed a remarkable delay in recovering from the end-Permian mass extinction.

*Costatoria* is a dominant genus in marine bivalve assemblages that diversified during the Middle to Late Triassic. Only one species, *C. costata*, was reported from the Lower Triassic (Olenekian) Co Noi Fm, four species in this genus were found in the shelf mudstones of the Middle Triassic (Ladinian) Na Khuat Fm. In the Upper Triassic (Carnian) Suoi Bang Fm, shelf mudstones yielded at least four *Costatoria* species. An *in situ* preserved *Costatoria* sp. A was found in intertidal deposits, and *Costatoria* sp. A and B were predominant in the shoreface sandstone of the Suoi Bang Fm.



<sup>&</sup>lt;sup>°</sup> Speaker

#### New macro- and microfloral assemblages obtained from the Ninh Binh and Quang Tri Provinces, and their correlation with Lower Mesozoic floras and palynostratigraphy of Vietnam

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After the Late Paleozoic extinction event, Mesozoic Biota repeated recovery, survival and extinctions until forming the fundamental structures of present floras. The Late Triassic to Cretaceous was also a period of great ecological changes on the continent with the apparition of angiosperms. In Asia, Mesozoic sediments have been extensively studied for Paleontology and comparative Biostratigraphy mainly in Japan, China and Mongolia. However, paleontological and sedimentological research is still late in Vietnam where precise age of most Late Triassic to Cretaceous terrestrial strata remains doubtful. Komatsu and collaborators are performing a series of studies about molluscan faunas and paleoenvironments of Vietnam for several years. Mesozoic Paleobotany and Palynology of Vietnam is mainly represented by French-Vietnamese works with the description of the Carnian to Norian Hongay (=Hong Gai) and Quang Nam Floras in North Vietnam, but palynological reports remain very few in comparison with adjacent areas as for example coeval strata of the Khorat Group in Thailand and Laos.

We report here a Flora newly obtained from the Upper Triassic (Carnian) Suoi Bang Formation in Me area of Ninh Binh Province, North Vietnam and the Lower-Middle Jurassic Nam Po Formation in Quang Tri Province of North Central Vietnam. The Suoi Bang Formation is divided into a mainly shallow marine lower part, and an upper part dominated by nonmarine deposits intercalating with coal beds where we could recover a rich macro- and microfloristic assemblage. Composition of the Flora is coherent with the age recently determined from the molluscan fauna and permits to propose a paleoenvironmental reconstruction for the area. Samples for palynological analysis were also taken from the Nam Po Formation composed mainly of terrestrial red beds, which contains leaf impressions.

We compare these new macro- and microfloral data with previously described floras of Vietnam and eastern Asia, in particular the Norian Nariwa Flora (Okayama Prefecture) and the Carnian Mine Flora (Yamaguchi Prefecture) of South Japan, and the late Triassic Xujiahe Flora (Sichuan Basin) of South China. These results about Vietnamese paleofloras increase our comprehension of vegetational changes that occurred during the Early Mesozoic in the Southwest Pacific region, and give new data for comparison with Asian and Gondwanan floras.



<sup>\*</sup> Speaker

#### Bio- and chemo-stratigraphic indexes for global correlation of the Smithian-Spathian boundary in Vietnam and Japan

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The Lower Triassic (Olenekian) Bac Thuy Formation, which crops out in Lang Son Province, northeastern Vietnam, consists mainly of fossiliferous siliciclastic and carbonate rocks that were deposited around an isolated platform in the southern part of the Nanpanjian Basin of the South China block. The formation is divided into four conodont biozones (e.g. the Novispathodus ex gr. pingdingshanensis Biozone) of the upper Dienerian to lower Spathian, and contains middle Smithian to early Spathian ammonoids. The Smithian-Spathian boundary (SSB), indicated by the first occurrence of Tirolites cf. cassianus, is included in the Nv. ex gr. pingdingshanensis Biozone. The uppermost Smithian Xenoceltites variocostatus beds, which consist mainly of organic-rich dark gray bedded limestone and mudstone, are characterized by monospecific fossil and ichnofossil assemblages. A positive excursion of  $\delta^{13}C_{carb}$  with a maximum value of +5 is recorded around the SSB;  $\delta^{13}C_{carb}$  values show a decrease across the SSB. A similar carbon isotope curve is recorded in the Panthalassa area. The Taho Formation in Ehime Prefecture, Southwest Japan, consists mainly of carbonates that accumulated in western Panthalassa and contains abundant Early Triassic conodont elements. The Olenekian conodont biostratigraphy of the formation is similar to that of the Bac Thuy Formation, and the SSB in the Taho Formation probably falls within the Nv. pingdingshanensis Biozone. The values of  $\delta^{13}C_{carb}$  gradually increase and reach a maximum of +5 in the Nv. pingdingshanensis Biozone, then gradually decline until the lowermost Spathian Nv. brevissimus Biozone. Those carbon isotope excursions can probably be attributed to global expansion of marine anoxia during the latest Smithian to earliest Spathian, and are useful for global correlation of the SSB.



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#### A new Early Cretaceous megatrack site in Korea

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South Korea has become globally famous for various tetrapod footprints (turtles, lizards, pterosaurs, dinosaurs, birds, and mammals) from the Cretaceous strata. Here we report the first Early Cretaceous megatrack site from the Sanbukdong Formation of an unnamed small basin in the west of Gunsan City, North Jeolla Province. The track site (720 m2, designated as a National Monument in 2014) produced 425 tracks. Among them, eleven ornithopod and three theropod trackways (189 tracks) were measured and mapped in detail. Most of ornithopod tracks are large (32 cm ~ 51 cm in length) and very similar to pes imprints of Caririchnium lotus from China in that the general track dimensions and large heel pad impressions are typically longer than wide. They are attributable to basal hadrosauroids based on their stratigraphic and geographic occurrence as well as skeletal evidence in Korea. Eleven ornithopod trackways show gregarious behaviour and two main directions of movements. Based on palaeocurrent analysis at the site, two directional movements were interpreted as that one group went back and forth along the lacustrine margin and the other group came to the lakeshore probably to drink water or any other purposes. One trackway consists of 39 consecutive tracks with the distance of 39 m, representing the longest Early Cretaceous ornithopod trackway ever found in Korea. Sanbukdong ornithopod tracks suggest that basal hadorsauroids had the same growth pattern as derived hadrosaurids such as a brief period where it was very rapid. They also support independently that the majority of Early Cretaceous basal hadrosauroids were smaller than Late Cretaceous hadrosaurids in body size. Two theropod trackways consist of large tracks (more than 40 cm in length) and closely resemble Irenesauripus glenrosensis from the Lower Cretaceous of Texas which was inferred to be of Acrocanthosaurus origin. It is reasonable that they are attributable to carcharodontosaurids because their skeletal materials were already reported from the Early Cretaceous strata in China and Korea. This new megatrack site indicates that large ornithopod and theropod dinosaurs lived in the Early Cretaceous in Korea and strengthens previous hypotheses of their existence based on only isolated teeth.



Speaker

#### S26 - Microorganism evolution and interaction with biogeochemical cycles and climate

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#### Long term changes in ocean chemistry (especially in S concentration) may have contributed to phytoplankton radiation

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During the Mesozoic Era, dinoflagellates, coccolithophorids and diatoms became prominent primary producers in the oceans, succeeding an earlier biota dominated by green algae and cyanobacteria. This transition occurred during an interval marked by increasing sulfate concentration in seawater. This is also a time when predators became more aggressive and likely also influenced the selection of algal clades. Extant algae (i.e., the cyanobacterium *Synechococcus* sp., the green alga *Tetraselmis suecica*, the diatom *Thalassiosira weissflogii*, the dinoflagellate *Protoceratium reticulatum* and the coccolithophorid *Emiliania huxleyi*), were cultured in media with different  $[SO_4^{2^-}]$ . The cyanobacterium and the green alga showed no growth response to varying  $[SO_4^{2^-}]$ . By contrast, the three chlorophyll a+c algae showed improved growth with higher  $[SO_4^{2^-}]$ , but only up to 10 mM. The chlorophyll a+c algae, but not the green alga or cyanobacterium, also showed lower C:S with higher  $[SO_4^{2^-}]$ . When the same experiment was repeated in the presence of a ciliate predator (*Euplotes* sp.), *T. suecica* and *T. weissflogii* increased their specific growth rate in most treatments, whereas the growth rate of *Synechococcus* sp. was not affected or decreased in the presence of grazers.

In a third experiment, the algae were grown in conditions approximating Mesozoic/Cenozoic and Paleozoic seawater. In these treatments, sulfate availability, nitrogen source, metal availability and PCO2 varied. The organic composition of cells grown in the Paleozoic medium was appreciably different from that of Mesozoic/Cenozoic cells. It is noteworthy that the outcome of our treatment was different if the algal species were cultured together or separately. In general, the "Mesozoic/Cenozoic cells", in the multispecific cultures, were enriched in protein and had a lower C:N ratio, which the literature suggests makes them better food for grazers. We hypothesize that this change in algal cell composition, determined by changes in ambient chemistry, fueled predatory activities and thus may have contributed to favor the rise to prominence of those algal clades that were better equipped to respond to this grazing pressure.

Collectively, our results suggest that secular increase in seawater  $[SO_4^{2-}]$ , possibly in association with the other concomitant changes in ocean chemistry, may have facilitated the evolutionary expansion of chlorophyll a+c phytoplankton, although probably not to the exclusion of other biological and environmental factors.



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# Phytoplankton evolution and diversification of the marine biosphere

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The quantity (primary productivity) and quality (stoichiometry) of phytoplankton have been critical to marine biodiversification through the Phanerozoic. Based on the theory of ecological stoichiometry, stoichiometrically-imbalanced food exhibits high C:P ratios and consumers must therefore initially expend more energy upfront to respire carbon and obtain inorganic nutrients like phosphorus, whereas stoichiometrically-balanced food is characterized by much lower C:P ratios. Increasing food quality (low C:P ratios) would therefore leave more energy for biosphere "energetics" (biomass, metabolism, food requirements), reproduction, and presumably micro- and macro-evolution. Enhanced nutrient runoff to the oceans is indicated by the behavior of strontium isotopes while the emplacement of Large Igneous Provinces (LIPs) exhibits a 30-to- 60-myr cyclicity that correlates with pulses of biodiversification. Mafic volcanics are thought to be especially phosphorus-rich and LIP periodicity brackets the 32-myr periodicity reported for weathering fluxes and marine phosphorus burial.

The parallelism of the fossil record of phytoplankton and the marine biodiversity curve implicates nutrient availability and phytoplankton evolution as critical to the diversification of the marine biosphere. Based on cultivation experiments of modern taxa, acritarchs were characterized by high C:P ratios whereas coccolithophorids, dinoflagellates, and diatoms of the Meso-Cenozoic, when the Modern Fauna exhibits its tremendous expansion, possessed low C:P ratios. Acritarchs are cysts that resist inimical conditions like low nutrient levels and which are preservable, unlike their free-living counterparts. The decline of acritarch diversity through the early-to-middle Paleozoic and the near disappearance of the group from the fossil record during and after the Permo-Carboniferous, despite the return of conditions during much of the Mesozoic that resembled those of the earlier Paleozoic (e.g., high sea level) indicates increasing nutrient runoff associated with tectonism and the spread of deep-rooting terrestrial forests that enhanced weathering during the later Paleozoic. The Permo-Carboniferous would therefore appear transitional between the Paleozoic and Mesozoic in terms of nutrient availability and primary productivity. Similar conditions obtained during the Neogene, when diatoms diversified explosively, and may offer clues to Permo-Carboniferous conditions.



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# Evolution of siliceous plankton and radiolarite - its relation with the carbon and silicon cycles and global climate

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A recent paper hypothesizes that a steep drop of dissolved silica (DSi) in the ocean occurred around 190 Ma due to the evolution of diatoms. Although molecular clock analyses suggest a 250 Ma origin of diatoms, the fossil record of this group, compared to radiolarians, is very scarce and quantitatively insignificant throughout the Mesozoic. Radiolarians exist in the fossil record since the early Cambrian, but formed radiolarites as the dominant (default) oceanic sediment in low and mid latitudes from middle Ordovician to Late Cretaceous (Turonian). Based on the advances in radiolarian biochronology, continuous radiolarite sequences are being discovered in circum-Pacific accreted terranes of Panthalassa and in remnants of Neotethys from Turkey to the Himalayas. None of these radiolarites, even in the best preserved assemblages, contain diatoms. In marginal basins (e.g. Jurassic of Umbria-Marche, Cretaceous Chalk) the abundance of biogenic chert vs. carbonate co-varies with  $\partial^{13}C_{carb}$ , reflecting advantage for radiolarians (and diatoms) over carbonate producers at higher trophic levels.

We conclude from Si- and O- stable isotope measurements in Mesozoic radiolarian silica that the world ocean was less under-saturated in DSi and other nutrients than in Cenozoic-Modern times, resulting in better preservation of radiolarians and/or in a higher productivity. This is especially true for the Triassic-Jurassic and can be explained by warmer/more humid continental climates brought about by Pangea beak-up. It resulted in increased continental weathering, producing a higher input of DSi and other nutrients to the ocean.

During the Late Cretaceous, planktonic foraminifera began to compete with radiolarians for food. Radiolarites continued to form essentially during OAEs and in coastal upwelling areas until the Eocene warm period.

The quantitative demise of radiolarites and the widespread appearance of diatomites is coeval with the stepwise descent into icehouse climate, lowering continental weathering, hence, reducing riverine DSi input. Although radiolarian evolution seems to have responded to DSi- and nutrient-starvation by lowering test weight and hosting symbionts, they are less efficient silica precipitators than diatoms in cooler, low-DSi waters. Today diatoms largely dominate the world ocean's silica precipitation. Radiolarian-rich sediments are essentially restricted to tropical upwelling areas. Diatoms are also efficient exporters of organic carbon. It has been argued that increased upwelling during ice ages could have spurted diatom productivity, resulting in cold periods due to increased drawdown of atmospheric CO<sub>2</sub>.



<sup>&</sup>lt;sup>\*</sup> Speaker

#### The impact of sulfur on the biocalcifier *Emiliania huxleyi* (Prymnesiophyceae). Implications for biocalcification crises in the ocean

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Major environmental disruptions such as biocalcification crises (BC) in the ocean could be induced by the impact of naturally occurring (volcanic) and/or anthropogenic sulfur (S) emissions. S is transformed into the atmosphere and deposited in surface oceans in the form of sulfuric acid (HSO) that dissociates in sea water inducing a decrease in pH and alkalinity (Ocean Acidification OA). In addition to the role of OA, increase of sulfates (SO) in the sea water could directly inhibit the biocalcification process, as has been observed for abiotic calcite precipitation in laboratory experiments. This hypothesis was tested using the coccolithophore Emiliania huxleyi (Ehux) as a model calcifying organism. This study analyzes the impact of SO concentrations increment, simulating the effects of volcanism or current anthropogenic contributions on: i) the growth, biocalcification and organic-inorganic Carbon (POC and PIC) ii) the elemental composition and iii) S isotopic signature of Ehux coccoliths. An innovative approach including : culture and growth of Ehux clones in artificial seawater and totally controlled conditions, a theoretical model, the internal composition mapping the calcitic structure of a coccolith obtained by a particle accelerator (synchrotron) and S isotopic fractionation in very small samples obtained by Multiple Collector Inductively Coupled Plasma Mass Spectrometry (MC-ICPMS Neptune). Culture experiments revealed an inhibition of the biocalcification at high SO concentration (fourfold the concentration in current ocean). Synchrotron analyses of coccoliths showed that S is incorporated into calcite as SO with a heterogeneous distribution. Ehux's calcite has a very negative and atypical S fractionation compared to other biocalcifiers, indicating a very peculiar S assimilation by the cell as well as incorporation into calcite controlled internally by the cell and very little dependent on the external source of S (seawater). This strong biological control opens new perspectives to better understand the S cycle at the cell scale including mechanisms of uptake from seawater SO, use in metabolic processes and incorporation into calcite, as well as mechanisms of release of dimethylsulfoniopropionate (DMSP) which is a precursor of the climatically active gas dimethyl sulfide (DMS).

These results also indicate that *Ehux* shows a high resilience to a very wide range of SO, suggesting that seawater SO might have been a key factor in the evolution of these calcareous organisms. In contrast, the incorporation of S into calcite and detrimental effect on biocalcification supports the hypothesis that the most massive S inputs might have contributed to past and present BC. In the context of climate change, not only CO but also S emissions must be taken into account to understand not only their effects on global warming but also their impact on OA and BC.

<sup>•</sup> Speaker



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# Triassic – Jurassic boundary event recorded in Pacific pelagic sites

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The Triassic-Jurassic boundary (TJB) event has been studied as one of the major mass extinction events during Phanerozoic time. In western Pacific region, TJB bioevents are well recorded in deep-sea sedimentary rock, marked by the extinction of conodonts, an important radiolarian faunal turnover and a negative excursion in organic Carbon isotope record. In this study we focused on high-resolution (100yr) geochemical and stratigraphic studies on the pelagic T-J boundary strata mainly from SW Japan and New Zealand. We also analyzed Os and Sr isotopic ratios to estimate effects of volcanism (e.g. CAMP) and/or extraterrestrial impact. Several bio- and geochemical events have been detected through a 0.2 my interval across the deep-sea TJB. In a chronological order these are as follows:

1: ocean acidification event and negative excursion of organic carbon isotopes

2: late Triassic conodont extinction and positive carbon isotope shift

3: radiolarian faunal turnover characterised by the first appearance of Jurassic species and morphotypes.

During events 1 and 3, bloom of opportunistic species such as spherical-shaped radiolarians are observed. Few radiolarian genera such as *Canoptum* are persistant and occasionally dominate in marginal sites and upwelling areas of the Paleopacific. During event 2 a positive shift of <sup>187</sup>Os/<sup>188</sup>Os values and high values of Sr isotopes occur. During event 3 no remarkable change in Os and C-isotopes values occurs before the TJB. On the other hand, event 3 is characterized by low Sr isotopic ratios and high contents of alkaline elements. No remarkable short- or long- term negative shifts of Os isotope values across the TJB sequences have been detected so far. This means that no clear extraterrestrial impact record existed at that time, and the CAMP only had a weak effect during these events.

In summary, taking all data into consideration, we suggest that the late Triassic ocean acidification decreased primary production leading to the extinction of marine organisms. Positive shifts of Os and C-isotope ratios coupled with high values of Sr isotopes indicate a high influx of terrigenous materials into the Paleopacific ocean. Finally, the T-J faunal turnover of Radiolaria occurred during alkaline-rich periods, where only genera having high-tolerance to environmental (pH) change of the ocean survived.



Speaker

#### Upper Paleozoic radiolarian cherts within accretionary complexes in Southwest Japan: Increase of chert accumulation in the middle Cisuralian, Permian

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Distribution and scale of chert accumulation have changed through the Earth History. Those of biogenic chert might record environmental change of the history. An accumulation of a large amount of chert during the late Paleozoic, especially middle Permian, is known as the Middle Permian Chert Event. The Permian paleogeography is characterized by super continent and super ocean, namely the Pangea and the Panthalassa. The initiation of the chert accumulation has been studied in detail near the northwestern Pangea; however, a few studies have focused on that in the Panthalassa.

Jurassic accretionary complexes in Southwest Japan (e.g., Tamba-Mino-Ashio and Chichibu composite terranes) contain upper Paleozoic radiolarian cherts that had deposited in the central Panthalassa. I compiled age distributions of these cherts in the previous studies to understand the Permian chert accumulation in the central Panthalassa.

The compilation revealed that the amount of cherts increased in the middle Cisuralian (early Permian). The previous studies pointed out the Middle Permian Chert Event in the northwestern Pangea started in the middle Cisuralian. Thus, chert accumulation in the central Panthalassa coincided roughly with that in the northwestern Pangea, although the former consists mainly of radiolarian cherts whereas the latter consists mainly of specular cherts.

Faunal turnover in the middle Cisuralian has been recognized in several taxa, such as ammonoid, conodont, brachiopod, and fusulinid, by the previous studies. In addition to these nektons and benthos, this study indicates that radiolarian, planktonic protozoan, had changed at least in abundance in the middle Cisuralian.



Speaker

#### Calcareous nannofossil fluxes and calcium isotopes across the Paleocene-Eocene Thermal Maximum

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The Paleocene-Eocene Thermal Maximum (PETM; ~56 Ma), is one of the most severe greenhouse warming events in Earth's history. Thousands of petagrams of carbon were released in the atmosphereocean system in a few thousand years, ultimately causing ocean acidification (OA). The gradual sequestration of this light carbon took place in the aftermath of the event, during the recovery phase, where calcium carbonate saturation was greater than pre-event levels, over approximately 200000 years. Silicate weathering is thought to be one of the fundamental negative feedbacks that triggered the input of carbonate ions (CO3-) in the oceans. This should lead to an increase in pelagic carbonate production, however a major crisis is reported in literature. This is a paradox, since the production of pelagic carbonate is directly related to the carbonate saturation state and alkalinity of the oceans. Here, we present new data for calcareous nannofossil (CN) fluxes and calcium isotopes measured on planktonic foraminifera to evaluate pelagic carbonate production across the PETM. Calcareous nannofossils were particularly sensitive to paleoenvironemental changes induced by the hyperthermal event; a significant turnover is reported in all the basins as well as a reorganization of the planktonic communities. If the overall response of calcareous nannofossils to the PETM is reasonably known, systematic analyses to quantify the fluxes of different sources of pelagic carbonate (coccoliths, nannoliths and planktonic foraminifera) have never been performed to date. Here, we present nannofossils fluxes (nannofossils/m<sup>2</sup>/year) at Site ODP 1209, located in the Pacific Ocean (Shatsky Rise). Additionally, we measured the calcium isotope composition of the planktonic foraminifer Morozovella velascoensis to track changes in seawater geochemistry across the event. Across the PETM, some taxa which are particularly widespread during the PETM (e.g., Rhomboaster spp., Discoaster araneus group) are interpreted as malformed phenotypes due to stressful conditions through the event. However, our data show that in term of fluxes, deformed morphotypes are never abundant while the majority of the taxa do not present any kind of deformation. Through the comparison of calcareous nannofossil fluxes, carbon and calcium isotopes, we show how interactions between carbon and calcium cycles affected the pelagic carbonate production through the PETM.

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#### Heterocystous Nitrogen-fixing Cyanobacteria from the Tonian Period and their implication for geobiological feedbacks

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The origin of cyanobacteria (or oxyphotobacteria) had profound and transformative impacts on carbon, nitrogen, and oxygen cycles in the Earth system. Cyanobacteria are the ultimate ancestor of all plastids and for much of the Earth history they were the only source of biogenic oxygen and a major source of fixed carbon and nitrogen. One important clade of cyanobacteria (subsections IV and V) includes complex members that are characterized by differentiated multicellularity with specialized nitrogen-fixing (or diazotrophic) heterocysts and encysting akinetes. However, molecular clock estimates of the divergence time of this clade are highly variable, ranging from ~2000 Ma to ~500 Ma, and the Precambrian fossil record of heterocystous cyanobacteria is limited and contested. Here we report a new filamentous cyanobacterium, Anhuithrix magna, from the Tonian (~1000–720 Ma) Liulaobei Formation in North China. A. magna has exceptionally large cell size and shows evidence for binary fission (for filament elongation), hormogonia (for reproduction and dispersal), akinetes (for survival in adverse conditions), and by implication diazotrophic heterocysts. The new fossils provide a key calibration for the divergence of cyanobacterial subsections IV+ V, place a firm constraint on the evolution of akinetes and heterocysts, and attest to the evolution of cellular differentiation among multicellular cyanobacteria in the Tonian Period. We also speculate that the blossom of heterocystous cyanobacteria in Tonian oceans may have been an evolutionary response to the increasing availability of bioessential metals (i.e., Fe, Mo, and V) due to the contraction of mid-depth euxinic waters and the rise in atmospheric oxygen levels during the Neoproterozoic Oxygenation Event. Thus, not only did cyanobacteria played a significant role in regulating the carbon and nitrogen cycles and surface Earth redox conditions, their own evolutionary trajectory was modulated by the very oxygen ultimately produced by themselves, highlighting the complex geobiological feedbacks between the biosphere and geosphere.



Speaker

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# Pyrite formation from FeS and H<sub>2</sub>S – a novel type of energy metabolism

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Braunschweig

The exergonic reaction of iron sulfide (FeS) and hydrogen sulfide to pyrite (FeS<sub>2</sub>) has been postulated to have been one of the earliest forms of energy metabolism on Earth. Since the Archean, pyrite has formed extensively in marine and freshwater sediments and is of major importance for the global iron and sulfur cycles. To date, sedimentary pyrite formation was considered a purely geochemical reaction with no evidence of involvement of biological activity. Here, we present freshwater and marine enrichment cultures growing with 5 mM FeS, 5 mM H<sub>2</sub>S, and CO<sub>2</sub> as their sole substrates. Cultures grew to cell densities of 106 – 107 cells mL–1 and consumed sulfide within nine months of incubation. Transformation of FeS and H<sub>2</sub>S to FeS<sub>2</sub> was followed by <sup>57</sup>Fe Mössbauer spectroscopy and showed a clear biological activity profile with a maximum at 30°C and decreasing activities towards 4°C and 60°C. The formation of methane also followed a clear biological activity profile. Addition of penicillin or bromoethanesulfonate inhibited pyrite and methane production, which points towards a syntrophically coupled process. This was supported by a parallel phylogenetic analysis based on 16S rRNA genes, which identified one archaeal and six bacterial OTUs. The archaeal OTU was most closely related to the hydrogenotrophic Methanospirillum spp. while the bacterial OTUs were most closely related to sulfate-reducing Deltaproteobacteria, Firmicutes, and uncultured Actinobacteria. Our enrichments are the first biotic system able to conserve energy from FeS transformation to pyrite and may represent a potential window into a possible primordial iron-sulfur world.



Speaker

#### Testing morphological trends of long range planktonic foraminifera species, example from the Late Cretaceous *Pseudotextularia nuttalli* lineage

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Planktonic foraminifera are unicellular marine organisms that constitute a major part of pelagic marine sediments. Their widespread distribution and rapid evolution make them excellent as biostratigraphic markers. However, some species has exceptionally long range of occurrence, showing either long morphological stability or gradual phyletic evolution. One example for exceptionally long evolutionary history (i.e. Turonian-Maastrichtian) is the common cosmopolitan planktonic foraminifera *Pseudotextularia nuttalli*. Its conspicuous morphology makes it one of the taxonomically recognizable species. Yet, comparison between Santonian and Maastrichtian forms reveal distinct morphological changes.

In this study, we have used image processing techniques to characterize shell growth pattern (depth-height and width-height ratios through different growth stages) of *P. nuttalli*, across the Santonian-Maastrichtian interval. DSDP and ODP long cores from two locations representing normal tropical-subtropical pelagic sequences were compared with a core from southern Israel representing high productivity sequence of upwelling conditions. Timing of morphological changes across these different oceanic provinces will resolve some of Late Cretaceous biostratigraphic uncertainties.

Comparison between end members of *P. nuttalli* lineage *Planoheterohelix globulosa* and Pseudotextularia elegans, shows a gradient of increasing depth-height proportions between this species continuing through all ontogeny stages. Therefore, different shell growth pattern is a visible property corresponding with evolutionary trends along this lineage.

In the normal tropical-subtropical pelagic sequences, *P. nuttalli* specimens collected from older strata were smaller compared with the ones collected from younger periods. This was most prominent in depth-height ratio of the adult form (later growth stage). While in the high productivity sequence of Israel all specimens were less developed, with smaller shell size similar to the primitive form.

Nevertheless, since the increase in depth-height proportions between primitive and more developed forms is consistent with increasing proportions within *P. nuttalli* lineage the separation between Santonian primitive form and the more develop Campanian-Maastrichtian forms has the potential to become an important stratigraphic biomarker.



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#### Sulfate incorporation in foraminifera cell and test : mechanisms and validation of a proxy for past seawater composition

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Foraminifers present the interesting feature of precipitating a mineral carbonate test that holds crucial information on their living conditions in their elemental and isotopic composition. The overwhelming presence of foraminiferal tests in the geological record make them the perfect material to study earth paleoclimate history and foraminifera interaction with biogeochemical cycles, and specifically in the carbon cycle and climate regulation.

During earth history, several episodes of biomineralization crisis, due to oceanic acidification triggered by volcanic catastrophic episodes, have affected foraminifera. Among other realeased volcanic gas,  $SO_2$  input in large quantities in the earth atmosphere during volcanic crisis is followed by dissolution and oxidation in the ocean and leads to water acidification. In this process, it produces sulphates ( $SO_4^{2^2}$ -), an ion that at high concentration has been shown to inhibit calcite formation in abiotic conditions.

In order to investigate the impact of  $SO_2$  and  $SO_4^{2-}$  on biocalcification by foraminifers, and the way  $SO_4^{2-}$  is being incorporated in foraminiferal test, we led a multidisciplinary approach combining foraminiferal culture experiments, isotopic labeling, nanoscale imaging, and bulk concentration and isotopic composition of the sulfur associated to carbonates (CAS) in foraminiferal test.

Benthic foraminifers were cultured in controlled conditions in labelled media at two different sulfate concentration. Because among foraminifers, the Rotaliida and the Miliolida orders present different calcification strategies, we cultured several species of foraminifers belonging to these two orders. The cultures were long enough to allow chambers formation or juveniles asexual production in the labelled media. We developed a preparation protocol permitting to observe simultaneously the cell ultrastructure and its interface with the test. Our results provide crucial new information on the modalities of sulfur incorporation in the foraminifers cell and test, on the origin of that sulfur, and on the effect of its variation on the test geochemical composition. Our results give new insights validating the measure of CAS concentration and isotopic composition in foraminiferal carbonates as proxies for past seawater sulphate concentration. Such proxies are crucial to explore how the sulfur and carbon cycles interact during biocalcification crises associated with massive volcanic events.



<sup>&</sup>lt;sup>\*</sup> Speaker

#### Global paleoclimatic *vs.* local endogenic impact on short-lived Lager Benthic Foraminifer-rhodoid photozoan carbonates in Central America and the Caribbean

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Late Cretaceous – Cenozoic carbonate-producing paleo-environments in the oceanic areas of the Caribbean Plate were short-lived (1-10 Ma), particularly in arc-related settings along intra-oceanic subduction zones, areas largely floored by a CLIP-type (Caribbean Large Igneous Province) thickened oceanic crust. These oceanic basements reached the photic zone due to tectonic uplift or volcanic activity. Subaerial edifices were affected by tropical weathering, producing high discharge of clays, volcanic ash and dissolved nutrients, creating unfavorable conditions for the growth of chlorozoan carbonates.

Punctuated (short-lived, small-scaled) chlorozoan carbonate paleo-environments are characterized by rapid appearance/disappearance of stable conditions for rock-forming LBF (Larger Benthic Foraminera) and rhodophycean algae, rudists in the Upper Cretaceous and corals in the Oligocene-Miocene. These banks are fundamentally different from long-lived large carbonate shelves set along passive margins.

Here we evaluate the biotic response of these carbonate systems to global, eustatic sealevel and paleoclimatic change vs. local endogenic processes, based on some examples.

• Middle Campanian rudist reefs and LBF-bioclastic limestones encroach on the accreted and uplifted Nicoya Complex and Santa Elena intraoceancic arc, while other areas of S-Central America accumulate pelagic limestones. Subsequent subsidence and perhaps a fast and short-lived eustatic sea-level rise caused return to deep water sedimentation in the late Campanian.

• The Selandian-Thanetian Barra Honda Limestone of the N-Costa Rica forearc area unconformably rests on Upper Cretaceous-Danian deep water formations that were tectonically uplifted and partly eroded. The relatively low and then rising late Paleocene eustatic sealevel may have favored a thick LBF-bearing, mostly micritic carbonate formation. The sudden demise of this platform is brought about by a combination of tectonic subsidence, eustatic sealevel rise, and eutrophication due to renewed arc activity and intense weathering during the Early Eocene Thermal Optimum.

• Lower Eocene shallow carbonates are dominated by rhodophycean algae and mollusks. With rare exceptions in deeper water facies, LBF are absent in S-Central America and the S-Caribbean, probably owing to very warm surface waters and eutrophication.

• Middle-Upper Eocene LBF-rhodophycean carbonates are very common throughout the Caribbean Plate. Often they rest with an angular unconformity on older, deep water formations. Regional tectonic uplift has been invoked together with cooling climatic conditions. Short term eustatic changes may have triggered appearance/disappearance of carbonate banks.

• Late Oligocene banks are rich in LBF and sometimes host coral reefs. Again, tectonic uplift can be invoked for the onset of carbonate banks, whereas short term glacioeustatic sealevel rises may have fostered keep-up growth of buildups.

In conclusion, paleoclimatic and eustatic sealevel variations come second in their influence on the development of punctuated chlorozoan carbonates of the tectonically active Caribbean Plate.



<sup>&</sup>lt;sup>\*</sup> Speaker

# Planktic foraminiferal test morphological abnormalities from pre-evaporitic Messinian sediments (Chelif Basin, Algeria)

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Remarkable morphological abnormalities have been observed on numerous planktic foraminiferal tests from pre-evaporitic Messinian marly-diatomitic deposits from Ain Merane region (Chelif Basin, Algeria). These abnormalities are quite diversified and have been recognized in several different species. Abnormal tests have long been documented for living and fossil benthic foraminifera and, in less extended, for planktic foraminifera, and can be induced by environmental stress factors (e.g. heavy metal pollution, salinity and/or pH fluctuations, oxygen-depleted conditions, high nutrient injections, rapid and extreme climatic variations). In order to test their potential environmental significance in a context of Messinian presalinity crisis, we have quantified their percentages and correlated them with other paleoenvironmental proxies (warm/cold species percentages, oxygen stable isotopes). The rate of morphological abnormalities varies between 0.33 and 10%, with maxima values targeting specific levels characterized by sharp increasing of warm species abundance and decreasing of  $\delta^{18}$ O values. The combining data set suggest several episodes of extreme stressful conditions of seawater column in the Chelif basin, preceding the Messian salinity crisis. These may be linked to severe stratification of seawater column, likely related to transient episodes of reduction of North Atlantic water inflow and/or of increase fresh water input into Chelif basin.



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#### Dimorphism of the Permian Albaillellaria (Radiolaria): Morphologic characters and lineage

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The Radiolaria belong to the Rhizaria along with the Cercozoa and Foraminifera. Some living Rhizaria, such as the Foraminifera and Phaeodaria, are known to have dimorphism, caused by alternating generations in their life cycles. This phenomenon has been studied in detail in the case of living benthic foraminifers. The dimorphism is also found in the Permian Albaillellaria, which had been considered to belong the Radiolaria. The dimorphic pairs of the Albaillellaria comprise normal and swollen types. Because of the rarity of swollen type specimens, morphologic characters of the Albaillellaria dimorphism are not clarified yet. We obtained abundant swollen type specimens of *Albaillella sinuata* (early Permian Albaillellaria) from Japan. We observed and analyzed biometrically these specimens to clarify its morphological characters. Furthermore, we compiled previous occurrences of Albaillellaria dimorphism to speculate its development in lineage.

Our observational and biometric results indicated that 1) the normal and swollen types are clearly dividable and 2) the swollen-type is characterized by a swollen apical portion and a shorter overall height compared to the normal-type.

The Albaillellaria dimorphism is known in two families Follicucullidae and Albaillellidae. A compilation of previous occurrences of the swollen type indicated that the dimorphism developed on a different lineage of both families. Therefore, the dimorphism is a common phenomenon that extends beyond the Albaillellaria families. In addition, from a morphological standpoint, Albaillellaria genera for which swollen types are absent or rare have simpler shells than other genera with dimorphic pairs.



Speaker

# Tectonic forcing of phytoplankton evolution, marine biodiversificaiton, and biogeochemical cycles

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The quantity (primary productivity) and quality (stoichiometry) of food (i.e., phytoplankton) at the base of food pyramids have been critical to marine biodiversification throughout the Phanerozoic Eon. Based on the theory of ecological stoichiometry developed for trophic cascades, increasing the phosphorus content of phytoplankton decreased the amount of energy consumers must expend to respire excess carbon to obtain inorganic nutrients like phosphorus, thereby leaving more energy for reproduction and, presumably, micro- and potentially macroevo- lution. Tectonism associated with the emplacement of large igneous provinces (LIPs) therefore enhanced the input of phosphorus from the continents to the oceans on approximately 30-to-60-million-year periodicities, stimulating primary productivity and the pelagic rain of organic matter, thereby affecting redox conditions and phosphorus availability.

We tested these hypotheses by conducting preliminary cross-correlations of currently available paleoenvironmental and biodiversity data using the statistical freeware PAST (PAleontological STatistics). We used data binned or interpolated on 1-myr intervals for preliminary cross- correlations. Cross-correlations between log percent carbon, LIPs, percent phosphorus, genera origination, and  $\delta^{34}$ S all exhibit statistically significant (p< 0.05) small-to-moderate positive cross-correlations of ±0.2 or greater for ~30-to-60 myr durations, and would likely have been stronger if not for variation of methods of compilation and temporal resolution of the different data bases of various investigators. LIP and <sup>87</sup>Sr/<sup>86</sup>Sr are negatively correlated, as might be expected. <sup>87</sup>Sr/<sup>86</sup>Sr and log percent carbon are negatively cross-correlated for all durations; possibly, <sup>87</sup>Sr/<sup>86</sup>Sr reflects the negative impact of tectonism (uplift) indirectly on carbon burial via sea level fall. Much shorter (glacial scale?) and longer (tectonic scale?) cross-correlations resulted in some cases, suggesting that the also same processes may also act on these time scales. These findings appear to cross-correlate with cycles of marine biodiversification on similar time scales.

The impact of these biogeochemical processes on marine biodiversification spans geologically long intervals of time. However, these processes appear to be scale-dependent since Oceanic Anoxic Events and mass extinction result from similar processes occurring with much greater intensities on geologically much shorter time scales.



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# S27 - Neogene continental environments in Africa and Eurasia

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## Clay minerals of the upper Miocene in Toros-Menalla (Chad) and implications for the palaeoenvironments

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The Djourab Erg Northern Chad contains a significant number of palaeontological sites. In particular the sector of Toros-Menalla has yielded more than half of the fossil vertebrate remains discovered to date, including the remains of the hominid Sahelanthropus tchadensis (Toumai). Available palaeoenvironmental reconstructions suggest a mosaic landscape consisting of a juxtaposition of rivers, lakes, wooded savannah, grassy meadows and deserts. For this study, 92 samples were collected in the Upper Miocene sedimentary formation of Toros-Menalla. The samples cover the different lithologies corresponding to lacustrine (diatomites) to peri-lacustrine (clayey sandstone) environments. Mineralogical tracers, and in particular the clay assemblages, are investigated to precise the palaeoenvironmental conditions in the sector of Toros-Menalla. The sediment mineralogy comprises clay minerals, quartz, K-feldspar and plagioclase, amphibole and calcite. Its fine < 2 microns fraction consists of kaolinite and smectite with some illite, fresh chlorite and chlorite degraded into vermiculite. The smectite is rich in swelling layers with a marked expansion from 16.9 to 17.8 å under glycolation. The position of the (060) reflection indicates its dioctahedral character. Smectites may be classified as AI-Fe dioctahedral minerals such as montmorillonite or beidelite, common weathering products under moderate hydrolysis conditions. Kaolinite is evidenced by a wide reflection at 7.15 å that disappears after 500°C heating. It corresponds to an advanced stage of hydrolysis after a complete leaching of interlayer cations. The relative abundance of smectite and kaolinite, measured by their intensity ratios on glycolated X-ray runs (17å/7å), display strong variations over the studied sequence. They mostly reflect changes in the weathering conditions during the Upper Miocene and consequently environmental changes experienced by hominids in Chad, between drier (high smectite/kaolinite ratio) and wetter (low ratio) conditions. The mineralogical interpretation will be coupled with a micropalaeontological study to confirm the environmental variations at Toros-Menalla.



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# Fossils of putative Haplochromini (Teleostei: Cichlidae) from the late Miocene Palaeolake Waril (Central Kenya, East African Rift system)

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At present, the family Cichlidae represents one of the most species-rich groups of tropical freshwater fishes, with hotspots of diversity in the East African Great Lakes: Lakes Tanganyika, Malawi and Victoria. Fossil cichlids from East Africa have the potential to offer unique insights into the evolutionary history of these radiations. Here we present two new fossil cichlid species from the upper Miocene (9-10 Ma) Palaeolake Waril in Central Kenya (East African Rift System). The two fossil species display a unique combination of morphological characters not found in any modern cichlid, which suggests that they belong to an extinct genus. Comparative analysis based on a comprehensive dataset of meristic, osteological and otolith data for extant cichlids from East Africa indicates that the new fossil genus occupies an intermediate position between two of the modern tribes among the East African cichlids: the virtually pan-African Oreochromini and the Haplochromini. However, the morphology of otoliths found in situ in one of the fossil specimens and also the caudal fin osteology point towards a closer relationship with the Haplochromini. The two fossil species can be distinguished from each other by their oral jaw dentition, which is tricuspid in one and conical in the other. Today's Haplochromini are famous for their numerous adaptations to multiple food resources and niches. They represent the most speciose group among the East African cichlids, and account for the huge cichlid species diversity found in Lakes Malawi and Victoria. The dentition of the two fossil species indicates that the adaptations leading to species diversification, such as feeding specialisations, already played a role in the late Miocene, i.e. relatively early in the evolutionary history of the Haplochromini. Moreover, we assess the possible total number of haplochromine species within Palaeolake Waril in the light of its late Miocene palaeoenvironmental setting in the East African Rift system, and taking into account its age and size (surface area 35-40 km<sup>2</sup>).

Speaker

#### Palaeoenvironments of the Ahaggar, Southern Algeria, and newly discovered faunas

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The Neogene-Quaternary of the Ahaggar, Southern Algeria, is poorly understood in contrast to the nearby area of Tassili n'Ajjer which includes the extensively studied early Palaeolithic site of Tihoudaine. Research carried out in the region in the early 1980's led to the discovery of the locality of Tan Kena in the Illizi region which is older than 2 Ma. More recently, surveys have led to the discovery of well-fossilised faunal remains in the Ahaggar, including Afilal and Silet and further north at the sites of Arak and In Salah. Near Atakor there is a Middle Miocene locality which has yielded remains of a small Rhinocerotidae, proboscideans and crocodiles. Previous studies in Southern Algeria indicated that the regional palaeoclimate fluctuated between arid and sub-humid conditions, interpreted as local expressions of the glacial-interglacial cycles that affected the high latitudes during the Quaternary. However, the Ahaggar, being a mountainous area culminating at nearly 3000 metres altitude at Atakor, evidently enjoyed a diversity of climatic conditions which differed from the regional 'saharan' palaeoclimates of the lower-lying country surrounding it. The newly discovered localities will throw light on climatic changes in a mountainous region in the heart of the World's largest desert and will yield evidence of early human activities in the region, as well as information about the installation of desert conditions in the Sahara during the Miocene.

Speaker

#### First occurrence of *Amphiorycteropus gaudryi* (Major, 1888) in Kerassia (Euboea, Greece)

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Cranial and postcranial material of *Amphiorycteropus gaudryi* (Orycteropodidae, Tubulidentata) from the Upper Miocene locality of Kerassia in Greece is described here for the first time. The material consists of one skull fragment, two hemimandibles, a humerus, a sacrum, a cuneiform, a metatarsal and four phalanges. The fossils are attributed to *A. gaudryi* (Major, 1888), the most common species of Orycteropodidae in the Late Miocene of Greece. The excavations took place in two phases, one in 1982 by H. van der Bruijn, A. van der Meulen and K. Doukas, and one since 1992 by George Theodorou, funded by NKUA Research Account projects 70/4/1397, 70/3/2842 and 70/3/3922. The material is stored in Museum of Palaeontology and Geology of Athens (AMPG).

The specimens add important new insights on the variation of the morphological characters of the species. The occurrence of this species in Kerassia supports the fact that there are important differences in the fauna of this locality from the classical fauna of Pikermi. The morphology of the teeth and the postcranial material preserve features that allow us to make some reliable assumptions about the ecology of the species. Morphological and biometrical comparison with the other *Amphiorycteropus* species gives us the opportunity to discriminate better the diagnostic features of the genus.

We believe that this new material offers noteworthy evidence concerning the evolutionary history of Tubulidentata and the Late Miocene faunas of Greece.

Speaker

## New fossil cichlids from the middle-to-upper Miocene of Kenya: evidence for the first fossil representative of the Etiini

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The cichlid fishes constitute one of the most speciose families of vertebrates, with about 1800 extant species having been recognized to date. They inhabit tropical freshwater environments, and more than two-thirds of all living species are endemic to Africa. Most African cichlids belong to the lineage Haplotilapiini. Many haplotilapiine species are found in the African Great Lakes region, and constitute an iconic example of adaptive radiation due to their diversity and adaptability. However, little information can be drawn from the fossil record regarding their evolution, due to the scarcity of fossils. Here we present three new cichlid species, from the middle-to-upper Miocene site Rebekka of the Ngorora Formation (10-12 Ma) in the Tugen Hills of Kenya. The specimens are preserved in green laminated siltstone and are articulated and nearly complete. The three species resemble each other meristically, but differ with regard to particular morphometric characters and the morphology of certain bones of the head. They possess two supraneural bones and tricuspid teeth of various sizes, the largest of which were most probably situated in the outermost row of the dentition. A few other haplotilapiine taxa may possess one or the other of these characters, but this combination is found only in the extant lineage Etiini. Today's Etiini comprise a single species, Etia nguti, and this taxon is sister to the rest of the Haplotilapiini. Owing to a number of similarities between the fossil taxa, and differences between them and E. nguti, these new species are attributed to a new genus. Nevertheless, African cichlids are famous for their high degree of homoplasy, and taxa that are distantly related (as inferred from DNA data) may be morphologically very similar. Therefore, pending the emergence of additional corroborative data, the new fossil species are referred to here as cf. Etiini. Assuming that the assignment is confirmed, it implies that the Ettini were more diverse in the past, which in turn raises questions regarding the decline of this clade. The discovery also has biogeographical implications: E. nguti is currently restricted to the river Mamfue system in Cameroon, West Africa. The inclusion of the new fossils within the Etiini would reinforce the hypothesis that a connection existed between the hydrological basins of East and West Africa during the Miocene.



Speaker

# Dietary diversity in the earliest Miocene ruminant guild from Montaigu-le-Blin/Saint-Gérand-le-Puy (France) inferred from Dental Microwear Texture Analysis

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Earliest Miocene faunas are crucial for understanding the establishment of modern communities, following the Microbunodon dispersal Event and the environmental fragmentation linked to the Oi-1 glaciation. Montaigu-le-Blin and Saint-Gérand-le-Puy (Allier, France) are world famous localities that yielded very abundant and well-preserved earliest Miocene vertebrate fossils (including birds, reptiles and mammals). No less than six species of ruminants (Mammalia: Artiodactyla) have been previously described in these geographically close sites: Dremotherium feignouxi Geoffroy Saint-Hilaire, 1833; "Dremotherium" lemanense (Pomel, 1853); Amphitragulus elegans Pomel, 1853; Pomelomeryx gracilis (Pomel, 1853); Pomelomeryx boulangeri (Pomel, 1853); and Oriomeryx major (Viret, 1929). This represents one of the oldest ruminant guilds composed only of Pecora (derived ruminants possessing four stomach chambers). Two size categories can be distinguished: Pomelomeryx species are very small (< 10 kg) while the other species are larger (> 15 kg). When considering dental morphology, species of Dremotherium and P. gracilis display more selenodont molars than the other species. Here we study the dietary diversity within this early pecoran guild to understand better the potential partitioning of ecological niches related to differences in dental morphology and body size. We made molds of the molars of about hundred specimens of ruminants from Montaigu-le-Blin and Saint-Gérand- le-Puy using the collections of the Naturhistorisches Museum Basel (Switzerland). We scanned the shearing enamel facets of the molars using a white-light confocal microscope to reconstruct a high resolution 3D model of the enamel surface. We compiled several dental microwear textural parameters (complexity, anisotropy, heterogeneity of complexity, and textural fill volume) that are known to distinguish mammals with different diets in modern ecosystems. The preliminary results indicate dietary differences between D. feignouxi and A. elegans : the former differs from the latter by higher anisotropy and textural fill volume and lower heterogeneity, suggesting a diet richer in tough plants. This study will provide original data to understand better the interspecific competition in a group that flourished during the Oligo-Miocene transition and that is currently the most diverse and abundant herbivorous group of large mammals with more tan 200 extant species.



Speaker

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## Taxonomy and ecology of the fossil freshwater molluscs from Late Miocene palaeolake Obweruka in the Albertine Basin (Uganda)

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From Late Miocene (Tortonian, 8 - 9 Ma) to Late Pliocene (Piacenzian, 2.5 Ma) times, a gigantic lake, Palaeolake Obweruka, occupied the Albertine Basin. This palaeolake was geomorphologically similar to Modern Lake Tanganyika and in addition it shares the occurrence of thallasoid (marine-like) molluscan faunas. Former research on this palaeolake revealed that evolution gave rise to three different thalassoid malacofaunas, each preceded by extinction. This conclusion was based on the study of fossil collections far from the north Lake Albert (Kaiso, Nkondo areas). Over the past few years fossil-bearing deposits were discovered north of Lake Albert, dating from the earliest lake stage (8-9 Ma), from which evidence had previously been lacking. In the present study, the fossil molluscan assemblages from these deposits are treated. The deposits have yielded a diverse molluscan community (15 species) dominated by viviparids (Neothauma) and unionids (Coelatura), that lived in a vast but relatively shallow lake. Eight of the species are new to science. Assemblages from the subsequent deeper lake stage (7 - 4.5 Ma) contain species that were found in other parts of the basin during earlier investigations. A total of 22 species is described from the two assemblages. The major scientific importance of the earlier assemblage is that it consists for a large part of hitherto undescribed thalassoid endemics, representing evidence for a first thalassoid evolutionary escalation at the very onset of the lake. It is clear that the four thalassoid molluscan faunas of Palaeolake Obweruka represent rapid escalatory punctuations, each preceded by a major environmental shift and extinction.



Speaker

## Can species of Oreochromini (Cichlidae, Teleostei) be distinguished based on the morphological characters of the hard parts alone?

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With more than 2000 species, cichlids are one of the most diverse groups of freshwater fishes on our planet, but their fossil record is sparse. Recently discovered fossil cichlids from the middle Miocene of Kenya promise to provide important taxonomic information relating to the early evolutionary history of African cichlids. However, identification of fossil cichlids is difficult, because species determination in extant cichlids is based mainly on delicate structures and soft- tissue characters, which are seldom preserved in the fossil record. In this case study, we set out to determine whether the morphological characters of hard parts can provide sufficient taxonomic information for correct species identification. We used 17 species of extant Oreochromis (53 specimens), 12 species of Sarotherodon (44 specimens), and one species of Iranocichla (two specimens). All studied species belong to the Oreochromini, which is one of the most diverse tribes of the East African cichlids. Based on X-rays of all 99 specimens, nine established meristic characters were analysed. In addition, new morphometric characters derived from features of the caudal skeleton were introduced, more specifically the angles of the hypural plates 1-4 and the length of hypural plate 5. Moreover, remarkable intraspecific variation of the caudal skeleton elements was observed in 12 species, mainly in relation to modification or fusion of the hypural plates. Uni- and multivariate statistical analyses were conducted for 24 species. The outcome reveals that five species of Oreochromis and two species of Sarotherodon can be distinguished from more than 80% of the remainder by their meristic characters. In addition, four species of Oreochromis and two of Sarotherodon could be differentiated based on the angles of the hypural plates 1–4. Of these, O. aureus and S. caroli are especially noteworthy, as they could be separated using angles of hypural plate 3 and hypural plate 2, but could not be differentiated based on the traditional meristic characters. We conclude that species identification in both extant and fossil Oreochromini is, at least in some instances, possible based solely on hard parts. The new results will contribute to correct taxonomic identification of fossil cichlids. Such information will provide a better understanding of the palaeoenvironmental settings of the middle Miocene of Kenya and will shed new light on the evolutionary history of African cichlids.



<sup>&</sup>lt;sup>°</sup> Speaker

#### The earliest record of the Oreochromini (Cichlidae: Pisces) from a Miocene lacustrine deposit in the East African Rift Valley

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The Oreochromini are an important clade within the family Cichlidae, with nearly pan- African distribution. Today's Oreochromini encompass a total of 10 genera and 63 species. However, their fossil record is paltry. Only two extinct species of the modern genus Oreochromis and a single extinct species of the modern genus Sarotherodon have been described, with ages from 4 to 6 Ma for Oreochromis and 12 Ma for Sarotherodon. Here we introduce the oldest known fossil record of Oreochromis, based on eight excellently preserved skeletons from the middle Miocene site of Kabchore (12.5 Ma), which is part of the Ngorora fish Lagerstätte (Tugen Hills, Central Kenya). Its systematic assignment is based on a unique character combination including a divided lateral line, tricuspid teeth and a distinctive pattern of body scales, together with certain meristic traits. To further elucidate its taxonomic position, a new data base including nine meristic traits of all 10 modern oreochromine genera (42 species, 181 specimens) was compiled and a principal coordinates analysis (PCoA) was conducted. The outcome clearly confirms the interpretation of the new fossil as Oreochromis. In addition, the new fossil species closely resembles Sarotherodon martyni Van Couvering, 1982, which was found in the same area (Tugen Hills) and is of similar age (12 Ma). The two fossil species differ significantly from each other in the length of the posterior lateral line segment, and the shape of the premaxillary bone, but display similar body proportions, meristic traits and a distinctive squamation, with smallsized ventral scales and large flank scales. It can thus be concluded that S. martyni represents a species of Oreochromis rather than Sarotherodon. It appears that the middle Miocene lakes in the Central Kenya Rift, as represented by the site Kabchore, played an important role in the evolution of the East African cichlids. This might be related to the occurrence of deep rift lakes in this area, providing ecological opportunities for freshwater fishes that were capable to adapt to the repeatedly changing palaeoenvironmental conditions at that time. Our new fossil also has important implications for divergence time estimates for the East African cichlids, because the previously used "oldest" species of the Oreochromini, i.e. O. lorenzoi Carnevale et al, 2003, is of late Miocene age, and hence significantly younger than our new find.



<sup>\*</sup> Speaker

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#### Palaeoenvironmental evolution of the Neogene Zahle palaeolake (Bekaa Valley, Lebanon)

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Neogene sedimentary rocks of the Bekaa Valley (Lebanon) show continuous exposures, little lateral facies changes, little post-depositional diagenetic alteration and extremely high content of microfossils. We studied these deposits in the area of Zahle (western margin of the Bekaa Valley) from a palaeoenvironmental point of view through detailed sedimentological and micropalaeontological analyses. This lacustrine sequence comrises up to 150 m of alternating fossiliferous yellowish marls and limestone, grading upwards into silty limestone and dark marls rich in ashes, lignites and palaeosol structures representing a shallowing depositional sequence in a lacustrine context. These sediments contain a wellpreserved and diverse microfossil assemblage composed of five species of charophytes, eleven species of freshwater and terrestrial molluscs, two species of ostracods, as well as vertebrate remains. Many of the fossils recovered from these deposits have living counterparts. Some fossil taxa have been reported from several European and Asiatic localities ranging in age from Miocene to Pliocene. The palaeoenvironmental characteristics and evolution of these deposits are inferred through a detailed facies analysis and by comparing the occurrence of the complete fossil assemblage throughout the studied sections with the ecological requirements of their nearest living relatives. Our results suggest that during the Miocene the Bekaa Valley was occupied by a relatively deep, stable, oligotrophic freshwater lake that evolved to a very shallow and eutrophic lake with a dense palustrine vegetation belt. The palaeolake ultimately regressed to the south due to climatic changes and tectonic stresses leaving the lacustrine deposits exposed in the area of Zahle as an erosional surface. This study also provides valuable data about the palaeogeographic distribution of Neogene lacustrine flora and fauna from Lebanon and the entire Middle East region.



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## Environmental reconstruction of the West Nile during the Mio-Pliocene transition based on mammalian faunas

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Recent surveys in the West Nile (Uganda) by the Uganda Palaeontology Expedition indicate that most of the sediments infilling the Albertine Graben in the region are of Miocene Age. They underlie a relatively thin but widespread layer of Pleistocene conglomerates and soils which are younger than a widespread lateritic ironstone horizon of Late Pliocene or Plio-Pleistocene age. Four major areas (Jupakombe, Marama, Gengere, Jupadwonga) comprising over two dozen biochronologically significant fossil occurrences have been identified. They contain Mio-Pliocene molluscs and mammals equivalent in age to late Pre-Obweruka, and Early Obweruka phases in the southern parts of the Albertine Basin. Four other localities (Pacego, Atara, Alwi-Atara, Alwi-Pateng) presumably of Lower Pliocene age yielded few age-diagnostic fossils. There is widespread evidence of an important phase of laterite pedogenesis which formed the Atara Ferricrete, pre-dating the Pleistocene deposits, which, in places, contain reworked blocks of this ferricrete.

Among the Mio-Pliocene localities, only two, Marama and Jupakombe, have yielded mammalian remains including a large deinothere, *Deinotherium bozasi*, which is common in the Eastern Rift Valley in deposits ranging in age from ca 7 Ma to ca 1.8 Ma; thick-enamelled proboscidean (*Tetralophodon* ?); Hipparion sp. an equid with low-crowned cheek teeth; *Ceratotherium praecox* known also from East-African sites dated between ca 7.5 and 4.2 Ma. At Jupakombe 7, remains of *Stegodon* or Primelephas have also been found associated with the suid *Sivachoerus devauxi* suggesting an age of 7 Ma or older.

Some stable isotope analysis ( $\delta^{13}$ C and  $\delta^{18}$ O) were also performed on mammalian dental enamel fragments for determining the diets and the ecophysiology and then reconstructing the environmental and thus the climatic conditions. The first results obtained on dental remains of equids, rhinocerotids, deinotheriids and gomphotheriids indicate the presence of tropical grasses and forested zones in the West Nile ecosystem in the Mio-Pliocene.

These discoveries are particularly important as they permit comparisons with the southern part of the Albert Basin, and between the Albertine Rift and the Gregory Rift in Kenya. Moreover, the deposits span a time period (late Miocene/early Pliocene) which is potentially interesting for understanding the dichotomy between great apes and humans. Finally, the area is close to the equatorial tropical forest zone of Africa and offers new possibilities for palaeontological surveys.



<sup>\*</sup> Speaker

#### **Elephant evolution revisited**

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For much of their evolutionary history, the Elephantidae were a much more diverse and widespread group than today, with only three extant species in tropical Africa and Asia (the African savannah elephant Loxodonta africana, the African forest elephant L. cyclotis, and the Asian elephant Elephas maximus). The elephantids have often been cited as examples of rapid evolutionary rate and phyletic morphological evolution. However, palaeontologists have historically relied heavily on fossil molars, which are subject to substantial intraspecific variability that arises from a peculiar mode of dental wear and replacement, as well as prevalent parallelism throughout their evolutionary history. This has made the elephantids resistant to robust phylogenetic analysis. Ancient DNA evidence has recently implied an apparently close phylogenetic relationship of Palaeoloxodon (the extinct Eurasian straight-tusked elephant) to Loxodonta, in opposition to the traditional morphology-based phylogeny which strongly favours Palaeoloxodon as closely related to Elephas. This further highlights the pressing need for a thorough reappraisal of elephantid systematics, from their early radiation in the African late Neogene through the Pleistocene to modern taxa. Initial phylogenetic inferences from a new morphological character matrix, based on first-hand examination of fossil and extant craniodental specimens, is presented, with many ingroup and outgroup species incorporated into a comprehensive phylogenetic study for the first time. The analysis broadly recovers the traditional morphological phylogenetic hypotheses of elephantids, while suggesting that several fossil species from Africa and Asia require further scrutiny. Further work is also needed to understand the phylogenetic and palaeobiogeographic background of elephantid origins. Finally, the analysis demonstrates the advantage of more extensive morphological character sampling, compared to restricted datasets which derive exclusively from isolated fossil elements.



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Speaker

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#### Diversity of Miocene rodents and palaeoenvironmental reconstructions in Eastern and Southern Africa

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During the Neogene climatic fluctuations in Africa caused faunal, floral and environmental changes. Since the 1990's, surveys have been conducted in Uganda and Namibia by UPE and NPE members during which abundant fossil remains dated from the lower Miocene (20.5-19 Ma) were recovered. Although much research has been done on several groups (primates, tragulids, hyracoids, suids, gastropods for example), few studies have been realised on lower Miocene micromammals from East Africa apart from those of Lavocat in 1973. So, it is essential to renew palaeontological studies of this group (comparative anatomy, systematics, taxonomy) and to compare Ugandan fossils with the Namibian material from the same time span. The fossil remains studied belong to four families of rodents: Bathyergidae, Diamantomyidae and the anomaluroid rodents (Anomaluridae and Nonanomaluridae). They have been found in the volcano-sedimentary sites of Napak (19-20.5 Ma) and the fluviatile deposits at Moroto (Middle Miocene-17 Ma) in Uganda, and in the fluvio-paludal sites of the Namib Desert (Grillental, Langental, Elisabethfeld, lower Miocene). Despite the great geographic distance between these sites, there are some similarities in their respective faunas. Bathyergids and diamantomyids are found in both areas, with one species in common: Diamantomys luederitzi. Among the bathyergids, the species Renefossor songhorensis (Uganda) and Bathyergoides neotertiarius (Namibia) have comparable characteristics, probably indicating the occupation of similar ecological niches (large fossorial rodent niche). The main difference between the two regions is the presence of anomaluroid rodents only in the Ugandan sites. This group is essentially found in forested environments, suggesting a more closed habitat at Napak and Moroto than in the Namibian sites. However, the presence of bathyergids and diamantomyids indicates the presence of more open landscape, characterized by a mosaic environment in Uganda and humid woodland at Grillental, Langental and Elisabethfeld, which is very different from the present day desert. These preliminary palaeoenvironmental interpretations will be compared and tested with the results of the ongoing geochemical analyses.



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<sup>&</sup>lt;sup>'</sup> Speaker

# Combination of dental microwear texture analyses with stable carbon isotopes in Bovidae from the Shungura Formation, Lower Omo Valley, Ethiopia: implications for environmental reconstruction during the Plio-Pleistocene

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The Shungura Formation (Lower Omo Valley, Ethiopia) constitutes the most complete stratigraphic and palaeontological record for the upper Pliocene - lower Pleistocene of Africa, and it has yielded a large collection of fossil bovids in which the two most abundant tribes are Tragelaphini and Reduncini. We used a multi-proxy approach to reconstruct precisely the diet and habitat preferences of these bovids for better understanding the environmental conditions that prevailed during the Plio-Pleistocene in this valley. We compared dental microwear texture analyses (3D DMTA) with the published  $\delta$ 13C values of tooth enamel in these two tribes between 3 Ma and 1.7 Ma. Dental microwear provides a short-term dietary signal of the physical properties (hardness, toughness and abrasiveness) of the last food items consumed by an individual. The carbon isotopic composition of tooth enamel varies following the proportion of C3 to C4 plants consumed during the period of enamel mineralization. The results indicate that tragelaphines and reduncines from the Shungura Formation had a diet dominated by browsing with a consumption of C4 dicots at around 2.8 Ma. The tragelaphines maintained a mixed-feeding dietary niche, with varying proportions of C3 versus C4 inputs from 2.8 Ma to > 2 Ma. The reduncines had flexible diets ranging from browsing to mixed feeding from 2.8 Ma to 2.3 Ma. They were more engaged in C4 grazing than the tragelaphines around 2.3 Ma and 1.8 Ma. Our results highlight the importance of a multi-proxy approach to determine precisely herbivorous diets and illustrates how these proxies offer slightly different, complementary perspectives on the ecology of fossil organisms.



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Speaker

#### Note on the palaeoecology of the genus Deinotherium

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Aspects of the Eastern European deinothere palaeoecology were previously presented by B. Tarabuchin and V.I. Svistun, based on morpho-functional analyses, but also on taphonomic data.

The strong skull flattening and eye migration to the top of the skull are related to adaptations for an aquatic life. On the skulls of *Deinotherium proavum* (Eichwald 1831) from Pripicenii Răze, si (Moldova) and *D. levius* Jourdan 1861 from Guseatin (Ukraine), well-developed bounding crests are present on the cheekbone. Facing posteriorly and downwards, they would include the *processus condyloides*, limited the antero-posterior movements of the mandible and protected its extension while the tusks were submitted to great forces.

The tusks of the mandible of *D. proavum* from Pripicenii Răzeşi (Moldova) show signs of intense usage, not only at the tips, but also on the lateral-longitudinal sectors, on both the facial and lingual sides.

Koenigswald highlights the deinotherian pattern of mastication, serving to cut by scissoring. The consumption of steppe or floodplain vegetation is excluded in these animals.

The *processus odontoideus* on the epistropheus of *D. proavum* from Pripicenii Răze, si ends with a downward-pointing hook that attaches to the anterior end of the ventral arch of the atlas – evidence of performing up and down movements with the mandible and the entire head and also from behind: in these cases with great forces.

The hip bones and rib structures indicate that the chest and belly were of huge size; the relatively straight vertebrae were less curved than in the elephants. These features suggest an aquatic life.

The limbs of deinotheres were slightly withdrawn laterally, allowing ample lateral movements. The relatively strong development of the deltoid crest on the humerus and the flattening of the femur indicate that the deinotheriids were good swimmers.

Based on the above, we can conclude as logical the fact that deinotheres inhabited rivers, lakes, and shallow lagoons that were covered in abundant algae and floating islands of plant rhizomes. Their diet was dominated by floating palustral plants and their juicy roots. Deinotheres could certainly move on dry land, where they could stay for long periods of time.



Speaker

## Plant-animal interactions from the perspective of ichnology: case study of Jesuitengraben (Oligocene, Czech Republic)

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Plant-animal interactions (PAI) are a topic that is being rapidly evolving in paleontological sciences. It has a pivotal role in the reconstruction of palaeoecosystems and also provides a significant contribution to evolutionary biology.

However, an appropriate terminological approach is necessary for correct interpretation. This is currently a major problem, as there is a combination of different classification criteria, preventing the possibility of a clear correlation. Formally, the least correct option is the strictly **zoological (= entomological) approach**, when fossil evidences of PAI were described on the basis of a neontological comparison and they were given names of recent taxa, at best only with the addition of attribute "fossilis". Because the hypotheses about the specific creator of a given fossil are often misleading or unprovable, a number of authors use a **functional morphological approach**, where different types of PAI are divided into groups according to the type of life signs of the fossil creator. A more detailed method of classifying PAI, based on comparative morphology, was the establishment of functional food groups. Recently, an **ichnological approach** has been promoted, where fossils are referred to by the nomenclature names used in the description of the fossils traces. However, this classification method can be also confusing, especially if the ICZN rules are not followed properly during defining diagnoses and if the utilized types of signs cannot be considered as valid ichnotaxobasis. The result has benn the creation of numerous so-called form-genera that will require a thorough revision in the future. At present, about 80 ichnogenera of PAI are described, about 220 ichnospecies respectively, but the validity of more than 70% of these cannot be confirmed.

For the particular study of PAI, the Jesuitengraben locality, one of the most productive sites of Oligocene terrestrial flora in Northern Bohemia, was selected. A total of 168 potential PAIs were identified in the collection of 419 fossil leaves gathered for a BSc thesis. The process of identification is currently underway and the following ichnogenera have already been confirmed: *Phagophytichnus* ispp., *Paleoovoidus* isp., *Stigmellites* isp., many others remain undetermined. The aim of the present research is not only ichnological description of the collected fossil material, but also an intended taxonomic revision of selected PAI groups in the future.

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# New morphological and biometrical data on the carpal and metacarpal bones of *Dihoplus pikermiensis* and "*Diceros*" *neumayri* (Perissodactyla, Rhinocerotidae) from the Late Miocene of Greece

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The locality of Pikermi (Attica, Greece) has yielded a remarkably rich Late Miocene vertebrate fauna, which is considered to be part of the Subparatethyan or Greco-Iranian Zoogeographic Province. Among the Order Perissodactyla, the Family Rhinocerotidae has encountered some complex taxonomic problems due to its high uniformity. Species taxonomy has mainly been based on cranial and dental characters. In this work, we used carpal (scaphoids, unciforms) and metacarpal (McII, McIII, McIV) bones of the two partly sympatric horned rhinocerotid species of the Pikermian fauna, "Diceros" neumayri and Dihoplus pikermiensis. Morphological differences, concerning mostly the articular facets of the bones, and biometrical data are described and used for the attribution of the studied samples to the respective species. Further, a detailed comparison with material excavated from the Turolian sites of Halmyropotamos and Kerassia (Euboea) and other Late Miocene Greek localities is attempted in order to examine potential faunal differences. However, due to the small amount of the studied material, additional study of the postcranial elements is required, so that more integrated knowledge on the species taxonomy can be acquired.

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#### Late Miocene Vertebrates from Tizi N'Tadderht near Skoura, Ouarzazate Basin, Morocco

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The Neogene record of large vertebrates in North-Western Africa is poor, no significant assemblage being known in Morocco between the Middle Miocene of Beni Mellal and the latest Pliocene of Ahl al Oughlam. The newly recognized fossiliferous area of Tizi N'Tadderht helps to fill this gap, due to collections made by the authors and by amateur collectors. It adds to the importance of the Ouarzazate Basin, famous for its Palaeogene deposits that document the early history of African faunas. The sediments are not richly fossiliferous but several specimens rank among the best from the African Late Miocene. The fauna includes an ostrich cf. Struthio sp, a turtle cf. Centrochelys sp., a skull of Crocodylus cf. niloticus, and a diverse fauna of large mammals. It includes three hipparions (a small form not previously reported from Africa, aff. Cremohipparion periafricanum, cf. Hippotherium primigenium, and an Hippotheriini indet., not 'Eurygnathohippus '); two species of rhinos (cf. Ceratotherium sp. and probably an elasmotheriine, including a complete skull); a Proboscidean cf. Tetralophodon sp., also including an almost complete skull; a large Giraffidae cf. 'Palaeotragus ' germaini from Algerian and Tunisian sites of Vallesian-equivalent age; and two bovids (one likely related to the Eastern Mediterranean Prostrepsiceros, and a caprine recently described as a new taxon, Skouraia helicoides). Rare remains of carnivores are present also. The detailed stratigraphy of the area has not been worked out but we assume, given the small extent of the deposits and their coarse nature suggesting rapid deposition, that the entire collection can be regarded as roughly isochronous. The similarities of the crocodile with the living species and the derived features of Skouraia are more in agreement with the European Turolian Mammal age, but no elasmotheriine has yet been identified from African and European sites of this age. An interesting aspect of the Skoura fauna is its contribution to the biogeographic history of this poorly documented region: Skouraia is clearly of Northern origin, whereas the crocodile and the elasmotheriine are certainly African. Anthracotheres are noticeably absent, as in Western Algeria. In any case, this original fauna hints at how much remains to be learned about Neogene mammalian faunas from Africa.



Speaker

# S28 - New trends in stratigraphy - Stratigraphic section (SGF) session

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#### Carbon isotope stratigraphy: a tool for chronostratigraphic calibration of Middle–Upper Jurassic radiolarian-bearing rocks of Tethys

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This research concerns the potential of a well-calibrated  $\delta^{13}$ C isotopic curve, recently established in low latitude areas, as a tool for stratigraphic correlationacross deep-pelagic siliceous successions and to test the viability of using the carbon isotopes curve to resolve major biostratigraphic uncertainties of UAZones of Interrad WG, especially at the Middle–Upper Jurassic transition.

Over the years, this zonation has been widely used as a reference for biostratigraphic work worldwide, despite some disparities in the stratigraphic range of some characteristic species. This zonation provides itself a good relative timescale; actually, no better alternative biostratigraphic schemes have been presented up to day. However, its correlation to the stages, via the co-occurrence of radiolarians and ammonites is still fragmentary. In particular, this correlation is quite imprecise for the time of most widespread radiolarite deposition (Bathonian–Oxfordian) because no other fossils coexist with radiolarians. An exception is found in the western basins (namely the Subbetic Realm) where nannofossils occur and the carbonate content of these siliceous facies is higher. We have conducted stable isotope stratigraphy (C, O) in the same sections that provide radiolarian and nannofossil stratigraphy to overcome the correlation problem.

This research presents a chemostratigraphic correlation between the carbon isotope curve of reference proposed for the Bajocian–Kimmeridgian (based on data from the pelagic Subbetic seamounts in Spain and the Subalpine Basin in France) and sixteen localities across the western Tethys where siliceous and radiolarian-bearing deposits are recorded. These are from west to east: Site 534A (central Atlantic), Jarropa, S. Harana, Ricote, Cuver (Subbetic Basin), Terminelleto (Umbria-Marche Apennines), Breggia, Tignale (Lombardian Basin, Southern Alps), Ceniga, Costton delle Vette (Trento Plateau, Southern Alps), Ardo (Belluno Basin,Southern Alps), Mangart (eastern Southern Alps) and the Krížna Unit (Tatra Mountains)

Another important topic, beside the biochronologic information, is the great potential for paleoenvironmental and paleoclimatic interpretation of these siliceous deposits. In that way, the evolution of the biosphere, lithologic, and preservational shifts, can directly be compared to parameters recording regional and/or global physico-chemical processes. The combination of several disciplines (biostratigraphy, stable isotope chemostratigraphy and geochemistry) may eventually help to overcome these fundamental problems in the future and lead to a more consistent model of the Middle-late Jurassic paleoenvironmental/paleoclimatic evolution. At the same time the benefit of this contribution would be in a more coherent chronostratigraphic correlation of radiolarian biochronozones in the framework of the International Subcomission of Jurassic Stratigraphy.



<sup>&</sup>lt;sup>\*</sup> Speaker

#### Palynostratigraphy and oceanic anoxic environmental study of the Toarcian-Bathonian age rocks, Chichali Nala, Central Punjab, Pakistan

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The Shinawari Formation of Toarcian–Bathonian age exposed in the Chichali Nala, Surghar Range has been studied for palynostratigraphy and oceanic anoxic events. The mix carbonate siliciclastic stratigraphic units are composed of limestone, marls, sandstone, organic rich shale, coal, siltstone, and cherts. The color of limestone is grey to dark grey on fresh surface, fine to medium grained and richly fossiliferous, while the marl is reddish to reddish grey in color. The sandstone is brown, grey, and cream in color while shale is black, carbonaceous, and green in color. Based on the identification of flora (pollen and spores), the palynostratigraphy of the Shinawari Formation is established. The identified palynomorphs correspond to two assemblage biozones which include Callialasporites turbatus assemblage biozone (CTUABZ I) of Toracian-Bajocian age and the Callialasporites trilobatus assemblage biozone (CTLABZ II) of Bajocian-middle Bathonian age. The deposition of black shales in the exposed studied section suggests the record of anoxic event. The anoxic bottom water conditions are also reflected in studied section by the enrichment of pyrite nodules in the carbonate beds and the presence in organic rich shale. The  $\delta^{13}$ C values of the bulk organic matter in shale samples show overall lightening in the  $\delta^{13}$ C from Sample SS1 to SS7 and afterward the  $\delta^{13}$ C values recovers from samples SS8 to SS20. However, the primary isotopic values of carbonates are overprinted by diagenesis while the isotopic signals from carbonaceous shales clearly depict anoxic conditions. Furthermore, the palynostratigraphic age constraints the isotope excursion as Toarcian and allow to correlated with the Toarcian Anoxic Events in eastern Tethys.



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# Biostratigraphic makers for defining GSSP levels in the Carboniferous: how to make it a success?

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The definition of global stratotype sections and points (GSSPs) is one of the main tasks of the International Commission on Stratigraphy over the last decades. GSSPs have been defined only for 3 of 7 stages in the Carboniferous, and some of those show shortcomings. Why is it so difficult in the Carboniferous?

The Carboniferous is a time of rapid and profound environmental changes. As a positive effect for biostratigraphers, diverse and often short-ranging taxa evolved in different marine and continental biota, increasing the availability of reliable boundary markers. But these changes also triggered faunal provincialisms, which hamper global correlation.

The FAD of the conodont *Siphonodella sulcata* defines the base of the Carboniferous in the La Serre GSSP since 1991. Stratigraphic studies in the last decades showed not only problems related to the section itself, but also to the boundary taxon for which different species concepts are in use. It results in the subjective placement of the boundary. This shows the general need of a well-constrained intraspecific variability.

The attempt to define the base of the Serpukhovian stage is an interesting example. This criterion that the task group proposed to test in 2003 (FO of the conodont *Lochriea ziegleri*) shifts the potential base of the stage into the upper part of the Visean. The next steps would have been to demonstrate an isochronous first occurrence in various regions and to correlate the FO to other faunal groups. However, the discussion has quickly turned into a battle for potential GSSP sections, which is based on a today still unproven assumption. Hence, this situation endangers the reliable definition of the boundary and results in stratigraphic tentativeness, if not chaos.

In contrast, a success story is the base of the Visean Stage defined by the FAD of the foraminifer *Eoparastaffella simplex*. Global correlation is achieved via a taxon widely distributed in shallow water facies and its correlation to the FO of deeper water organisms via its transport in calciturbidtes, The limit is also well constrained in terms of sequence stratigraphy.

Hence biostratigraphic markers can be powerful tools in the Carboniferous, as seen in different fossil groups. However, for a solid global correlation, the prerequisites are clear phylogenies and species concepts, consideration of different taxa, and the integration of non-biostratigraphic markers and palaeoenvironmental studies.



<sup>&</sup>lt;sup>•</sup> Speaker

#### Multiproxy chronostratigraphy of the Lower Cambrian Byrd Group, Central Transantarctic Mountains

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We present the first multiproxy chronostratigraphic assessment of the early-mid Cambrian Byrd Group from the Central Transantarctic Mountains, East Antarctica. This region was sutured to southern Australia throughout the Cambrian and is an integral, but poorly understood, region of East Gondwana. Two in-situ autochthonous stratigraphic sections were measured in the Holyoake Range (HRA and HRSE) intersecting up to ~350 m of biohermal, oolitic and lagoonal carbonātes of the upper Shackleton Limestone and the overlying dark nodular carbonates of the Holyoake Formation.

Biostratigraphically significant faunas from HRA include moderately diverse phosphatized steinkerns of hyoliths and numerous long-ranging helcionelloid taxa, organophosphatic tommotiids, linguliform brachiopods and disarticulated chancelloriids. The presence of key taxa such as, *Cambroclavus absonus, Cupitheca holocyclata* along with brachiopods *Schizopholis yorkensis* and *Eodicellomus elkaniformis*, and fragments of the bradoriid *Spinospitella coronata* are age diagnostic and enable close correlation to the new Series 2 Stages 3–4 *Dailyatia odyssei* Zone of South Australia. Accessory taxa such as *Pojetaia runnegari* and *Mackinnonia rostrata* strengthen this age assessment along with *Dailyatia ajax* towards the base of the section.

Chemostratigraphic data from the HRA section is discontinuous, but initial carbon isotope results show a +2.0  $\delta^{13}$ C plateau, similar to global post-CARE values that span much of Series 2, Stage 3 of the Cambrian. A trilobite fauna at the top of the HRSE section including *Estaingia*, *Discomesites*, and *Holyoakia*, occurs some 50 m above a major negative excursion (peak at -5.0  $\delta^{13}$ C) which is interpreted as the ROECE, and suggests a late Cambrian Series 2, Stage 4 age for this stratigraphic section.



Speaker

#### The Bartonian Stage in the Alum Bay section (Hampshire Basin, UK) revisited: a multidisciplinary study

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The base of the Bartonian Stage remains undefined. The Alum Bay section (Isle of Wight) is the parastratotype section of the Bartonian unit Stratotype located in the Hampshire Basin. The level chosen for the base of the unit Bartonian Stage, in the type area, is a single bed rich in *Nummulites prestwichianus*. Unfortunately this bed is scarcely correlatable outside of the Hampshire Basin.

Previous biostratigraphic studies were based on dinocysts, foraminifera and calcareous nannofossils in the Alum Bay section (Bujak et al. 1970; Murray and Wright 1974; Aubry 1983, 1986). Dinoflagellates show a taxonomic turnover with *Rhombodinium draco* occurring just above the bed with abundant *N. prestwichianus* at several localities in the Hampshire Basin. However, this is not consistent outside this region. Magnetostratigraphic interpretation by Dawber et al. (2011) identified the C18n chron in the Alum Bay section, and the NP16-17 boundary and the *N. prestwichianus* bed within the underlying reversed chron. Nonetheless, their interpretation is difficult to reconcile with the nannofossil record.

Our integrated approach includes physical stratigraphy (sedimentology, magnetostratigraphy) and biostratigraphy (benthic micro and macro foraminifera, planktonic foraminifera, calcareous nannofossils and dinocysts). In spite of their rarity and discontinuous occurrence, our calcareous nannofossil results allow the recognition of new secondary events that improved the biostratigraphic resolution of the Alum Bay section with the identification of the CNE14-CNE15 transition of the Agnini et al. 2014 Zonation.

Our interdisciplinary effort provides new information for consideration in the discussion and definition of the GSSP for the base of the Bartonian.



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#### Mesozoic radiolarian biochronology – current status and future directions

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Mesozoic radiolarian biochronologic scales have been developed since the 1970s and most of them reached their present day status in the 1990s. The degree of temporal resolution, in average, corresponds to substage level and is sufficient to provide a meaningful framework for general geological studies. A great majority of zonal schemes were elaborated in low-latitude sections but are applicable in high-latitudes as well, because an adequate number of species occur worldwide.

As proven over the years of their application, the reliable radiolarian subdivisions are those based on the assemblage concept. The biochronologically significant assemblages may be defined either empirically or quantitatively by using the Unitary Association Method. The more species are included, the easier is the correlation of an assemblage over large geographic distances and with less than optimal preservation. Interval zones defined exclusively with FADs and LADs of marker taxa are not appropriate for the radiolarian stratigraphic record, which is highly incomplete due to facies restrictions and variable degree of preservation. Yet the evolutionary FADs and LADs within securely recognized lineages are extremely valuable. The well-documented first phyletic appearances, rare for the moment, are the most suitable datums to pinpoint the limit between two consecutive zones.

In the forthcoming years, particular studies will focus on zonal division of under-explored time intervals and on improved calibration to chronostratigraphy. Two objectives that need a joint effort of the international community of radiolarian researchers are considered. The first objective, achievable in a relatively short time, is to compile a composite Mesozoic zonation, which would provide a single reference standard for radiolarian dating at a global scale. The second objective is to refine the radiolarian zonal schemes, which, in certain intervals, have already attained the resolution comparable to that of the standard ammonite zones. To increase the degree of precision and accuracy to this level through the entire Mesozoic is a long-term goal that requires additional high-resolution sampling and emphasis on detailed documentation of evolutionary FADs and LADs in different phylogenetic lineages.



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## Biostratigraphic review of the synextensionnal Upper Aptian-Early Albian boundary from Sidi Salem–Messella structure (Northeastern of Tunisia)

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Despite several studies based on ammonite's data, especially in Fahden area, the Aptian- Albian boundary was for a long-time difficult to identify along the foreland basin of Tunisian Atlas.

During our study on the Sidi Salem–Messella structure, northeastern part of the Tunisian dorsal, the revision of the Aptian-Albian series provides new information on this boundary interval. The Djebel Sidi Salem structure preserves a complete recording of Aptian-Albian interval with no sign of redeposition; the section presents a rich fauna of planktic foraminifera.

It leads to a chronological appearance of index species giving six zones from Gargasian to middle Albian: "Ticinella algerianus Zone", "Ticinella trocoidea Zone", "Planomalina cheniourensis Zone", "Paraticinella eubejaouensis/Ticinella roberti Zone", "Hedbergella planispira Zone" and "Ticinella primula Zone". Pt. eubejaouensis has never been identified yet in the Sidi Salem-Messella series, since the lower Albian was often considered as incomplete. This species is a real find in this studied section. This later shows a very remarkable abundance and even an exclusive presence in some samples, here, the "Pt. eubejaouensis Total/Abundant Range Zone" allows to identify the Upper Albian boundary and proves the continued sedimentation of the Aptian-Albian boundary thus a non-generalization of the famous notion of "Lower Albian hiatus" at least at the Sidi Salem- Messella structure.

This work suggests a close relationship between sedimentary recording and tectonic event. The extensional tectonic activity is associated with ENE- trending normal faults that are associated with significant thickness and/or facies variations comprising abundant syntectonic sequences. Normal faults controlled the Aptian Albian sedimentation where the deposits were thicker and showed growth strata architectures in the hanging wall. The biostratigraphic correlation of the Aptian-Albian provides listric extensional growth faults draws the structural architecture of the south Tethyan margin in Northern Tunisian Atlas. Therefore, the tectonic and structural works come to reinforce the biostratigraphic and sedimentological data by explaining the geodynamic evolution of Sidi Salem-Messella structure in tilted blocks during Aptian-Albian crisis with a continuous sedimentation in an open marine environment allowing to a considerable biostratigraphic resolution of the Upper Aptian-Iower Albian boundary.

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# The Jurassic/Cretaceous boundary and phyletic analysis of radiolarian *Loopus-Pseudodictyomitra* and *Vallupus* lineages

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The Global Boundary Stratotype Section and Point (GSSP) of the Jurassic/ Cretaceous boundary (JKB) is the last among the GSSPs in the Phanerozoic. It is defined as the base of the Berriasian Stage. The formal definition was decided in 2016 to use the base of the *Calpionella alpina* Subzone as the primary marker by the Berriasian Working Group in the International Subcommission on Cretaceous Stratigraphy. The definition is satisfactorily applicable for shallow marine deposits within the western Tethys, north Atlantic and central-south America. Unfortunately, the primary marker taxon cannot be found in the Pacific and circum-Pacific regions since the distribution of *Calpionella* is limited to the western Tethys, north Atlantic and central-south America. To determine the base of the Berriasian outside of these regions, alternative markers are needed.

Radiolarians are good candidates for defining the JKB because they are wide spread and can be found both shallow and deep sedimentary facies. Pelagic sequences across the JKB have been reported in ODP/IODP sites in the western Pacific and land sections in Japan, the Philippines, southern Tibet, Iran and others. Evolutionary lineages of several radiolarian taxa across the JKB are reviewed and suitable bioevents, which are approximate to the JKB, are presented. These lineages include the radiolarian genera: *Archaeodictyomitra, Cinguloturris, Complexapora, Eucyrtidiellum, Hemicryptocapsa, Hsuum, Loopus, Mirifusus, Neorelumbra, Pantanellium, Podocapsa, Pseudodictyomitra, Ristola, Tethysetta, Thanarla, and Vallupus*.

A radiolarian zonal scheme was proposed for the entire Jurassic and lower Cretaceous in the western Pacific and Japan. In defining zones evolutionary first appearance biohorizons (EFABs) are selected as much as possible. The JKB is located within the *Pseudodictyomitra carpatica* Zone, of which base is defined by the EFAB of Pseudodictyomitra carpatica and of which top is defined the EFAB of *Cecrops septemporatus*. Our current research revealed that one of the most important lineages for defining the JKB is the Loopus-Pseudodictyomitra lineage. Detailed morphological analysis of Loopus and *Pseudodictyomitra* species and their stratigraphic distributions are presented. In addition to this lineage, the *Vallupus* lineage is also useful within the *Vallupus* territory or tropical realm. The relationship between the JKB and these lineages is discussed.



<sup>&</sup>lt;sup>°</sup> Speaker

## Testing the global correlation and resolution of Early Jurassic ammonoid zonal schemes using quantitative biostratigraphic methods

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Since Oppel's first zonal scheme in Northwest Europe, Jurassic ammonoids are a prime target group of biostratigraphic research. Recognition of their provincialism led to introduction of regional zonations. Mediterranean (western Tethyan), North and South American zonal schemes have been developed after the northwest European standard, using traditional approaches. Their correlation is fraught with problems arising from differences among coeval assemblages in biogeographic provinces and diachronous first and last appearance datum (FAD and LAD) of some diagnostic taxa.

In addition, the achieved resolution also appears different: biohorizons are in prevalent use in northwest Europe, horizons are less universally accepted but subzones are common subdivisions in the Mediterranean schemes, whereas infrazonal units are rarely applied in either North or South America. Such difference may result from the longer history of study in Europe or, alternatively, it may reflect longer ranges of species in open oceanic habitats and/or frequent migration events as opposed to true evolutionary events recorded in epicontinental seas.

Here we use quantitative biostratigraphic methods to (i) refine the interregional correlations and assess their uncertainty, and (ii) evaluate the resolving power of ammonoid biostratigraphy in different regions. Our focus is on the Early Jurassic, specifically the Sinemurian and Pliensbachian stages that are not affected by major extinction events and subsequent recovery intervals. A dataset was compiled from stratigraphic distribution of taxa in key sections from North and South America, western Tethys and northwest Europe. Among the various quantitative biostratigraphic methods, we employ Unitary Association (UA), Constrained Optimization (CONOP) and Horizon Annealing (HA). The three techniques differ in both their goals and approach to resolve contradictions: UA seeks the temporal order of sets of cooccurring taxa, CONOP aims to approximate the true sequence of FADs and LADs, whereas HA establishes the temporal sequence of collection horizons from individual sections.

Our first results permit an evaluation of previously suggested correlation between regional zonations, demonstrate the achievable resolution in different areas on the basis of available data, highlight the need of further studies in the underrepresented East Pacific realm, and demonstrate the utility of quantitative methods to advance Jurassic ammonoid biostratigraphy.



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## Synthesis of the palynological content of the Lower Cretaceous continental deposits in France: stratigraphic implications

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A first attempt at a biostratigraphic synthesis of the palynological content of French Lower Cretaceous continental deposits is the subject of this paper. Palynomorphs listed in previous studies on Berriasian–Albian non-marine palynology have been taken into account, gathering 360 species of pollen grains and spores altogether. In addition, 70 samples have been recovered from outcrops of argillaceous rocks, mostly corresponding to the Purbeck and Wealden facies of southern England. The samples concerned are from the departments of Charente- Maritime, Charente, Savoie (Berriasian, Valanginian, Albian), Oise, Seine-Maritime, Pas-de- Calais (Hauterivian–Barremian), and Isère (Aptian). Early Cretaceous miospores are commonly long-ranging; hence, it is necessary to consider fluctuations in their abundance within palynological assemblages if they are to have any biostratigraphic value. Lower Berriasian assemblages are often dominated by gymnosperm pollen grains, associated with anemiaceous spores such as Cicatricosisporites australiensis and C. hughesii. These taxa are also found in younger strata, but upper Berriasian–Valanginian assemblages are characterized by containing more abundant lygodiaceous verrucate spores associated with the appearance of gleicheniaceous Clavifera triplex from the Valanginian onwards. Many genera have been erected to accommodate Mesozoic verrucate spores. The considerable overlap between diagnoses diminishes the stratigraphic significance of the constituent species. Only the genera Concavissimisporites and Trilobosporites are considered useful here. Hauterivian-Barremian assemblages are similar to those of the Valanginian, but differ in the reduction in numbers of verrucate spores and a commensurate increase in abundance of Cicatricosisporites and Appendicisporites associated with the first occurrences of monoaperturate angiosperm pollen grains, such as Clavatipollenites hughesii, within Barremian deposits of northern France. Considered to be more typical of Albian assemblages, Clavatipollenites rotundus has been recovered from lower Aptian deposits in south-eastern France. Aptian palynofloras are also characterized by the appearance of other monoaperturate pollen forms, such as Retimonocolpites. Very little information is available on French Albian assemblages. They are defined by the diversification of dicotyledonous tri- and polyaperturate pollen grains associated with the virtual disappearance of lygodiaceous verrucate spores.



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#### Mapping network flows through sedimentary deposits based on fossil assemblages: a case study from the Quaternary of the Po Plain (Italy)

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Understanding the biosedimentary response of marginal marine systems to sea-level changes is critical in both theoretical and applied contexts. At the basin-level, effects of sea-level change are generally evaluated based on a sequence-stratigraphic interpretation of the sediment succession. Here we explore the modular structure of a depositional basin, independently of the sequence stratigraphic interpretation, by mapping information flows directly through the succession. We present a case study on the latest Quaternary biosedimentary record of the Po Plain. Past investigations of multiple cores from this region demonstrated that macro-benthic assemblages vary predictably in response to sea-level fluctuations. This makes it possible to quantify information flows across a network of nodes representing both core samples (641) and taxa (361), retrieved from 22 cores, and joined by 6069 weighted edges indicating local interactions. This network was examined using a clustering method known as the Map Equation. The resulted network partitioning comprised of 71 modules ranging from 213 to 1 node in size, with the 13 largest modules including 75% of total nodes. Each module appears to be preferentially located relative to depositional profile of the basin (either landward or seaward) as well as restricted to certain depths. However, spatial interpretation of the modules is not straightforward. Goodman and Kruskal's Tau index (tau) suggested a strong correlation of the modules with the species' ecosystem (n=346; tau = 0.7;  $p < 10^{-10}$ 0.05). In contrast, there was at most weak correlation with the sequence stratigraphic attributes of the core samples such as facies associations, depositional systems, parasequences, and systems tracts. Resampling of the network links accompanied by significant clustering (100 iterations; CI= 90) indicates that the resulted partitioning is robust (75% of nodes belong to the significant nucleus of its module), suggesting the presence of a modular structure that cannot be fully explained by the underlying sequence stratigraphic interpretation. Our case study illustrates how a networks-based analysis may reveals some modular patterns in the basin structure that cannot be retrieved from standard methods. Mapping information flows through sedimentary successions may allow us a better interpretation of the role of relative sea-level changes in shaping the basin structure and provide a more precise interpretation of the fossil and rock record.

IPC 5

Speaker

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#### Late Cretaceous – Paleocene chronostratigraphy of the Gulf of Guinea: Evidences from dinoflagellate cysts

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The establishment of the connexion between the South and the Central Atlantic Oceans triggered important paleoceanographic and paleoclimatic changes. These changes were decisive for the development of the modern climate system. However, the precise timing of the paleoceanographic evolution of the South Atlantic is still debated. Improving the chronological constraints is essential to decipher the complex evolution of the paleoceanographic and paleoclimatic conditions. The Ocean Drilling Program (ODP) Leg 159 drilled the Ivory Coast – Ghana continental margin to better understand the evolution of the South Atlantic opening. Although several previous works have focussed on the stratigraphic assignment of the ODP Hole 959D from the ODP Leg 159, the position of some stage boundaries is still discussed. This study focus on the dinocyst biostratigraphy of the Cretaceous and Paleocene deposits of the ODP Hole 959D. A chronostratigraphic synthesis for the Late Cretaceous and the Paleocene of the Ivory Coast – Ghana continental margin is proposed for the ODP Hole 959D. The Late Cretaceous stage boundaries are consistent with previous studies. However, the Maastrichtian/Danian boundary is revised in the new chronostratigraphic scheme. Based on the First Occurrence (FO) of *Carpatella cornuta* and *Danea californica* it is placed much lower than previously thought. The base of the Thanetian is recognized from the FO of *Adnatosphaeridium multispinosum* and *Aeroligera gippingensis*.



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#### SYRACO, an automated recognition system of nannofossils applied to biostratigraphy: Advantages and Limitations

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Calcareous nannofossils are very small calcitic remains of marine microorganism (3 to 40  $\mu$ m). They are generally abundant worldwide, well diversified and have been present in the fossil record since the middle Triassic. The extensive documentation of their stratigraphic distribution in the pelagic and hemipelagic realms has made them one of the most used microfossil groups in petroleum biostratigraphy.

During the last decade, the improvements in computing performances associated to dedicated algorithms allowed the development of software assisting biostratigraphers in their time consuming task of fossil markers investigation. SYRACO (SYsteme de Reconnaissance Automatique des COccolithes), a tool originally created for paleoceanographic studies by L. Beaufort and D. Dollfus (CNRS-CEREGE), is an automated microscope designed to automatically scan a sample and to classify in real-time nannofossils in different morphogroups. It is based on convolutional neural networks and statistical classification of morphometric parameters. The system allows the user to directly cross check the species determination in the sample at the corresponding coordinates.

The biostratigraphic team of Total S.A. initiated a collaboration with the CEREGE to adapt the system to the industry constraints and, consequently, to extend the species spectrum to be recognized. In order to do this, a large database of calcareous nannofossils images was created for the whole Cenozoic and some Cretaceous and Jurassic horizons. It is composed of about 40,000 specimens split into ~100 morphogroups that contain thousands of species.

We tested the applicability of the system on conventional samples (cores, ditch cuttings) to compare the quality and the time spent with or without the system. The results on two West African wellbores shows that the expert interpreted in the same samples, the same Last Downhole Occurrences (LDO) and First Downhole Occurrences (FDO) of Early/Mid-Miocene marker species. Abundance fluctuations (acmes) were also recognized. The analysis showed that an expert using SYRACO complete up to twice as much work in the same period of time. The main advantage of the system is to efficiently sort nannofossils/non-nannofossils, even in sand rich intervals, allowing the specialist to focus on species determination. Moreover morphometry extracted from specimens can also be a complementary argument to correlate wellbores andrefine local/regional bioevents.

The system is operational and the image database is continuously fed. Recent progresses (sample preparation, circular polarization, image processing, algorithms/architectures...) are expected to reach better results on detection, classification and potential application to other fossil groups in the coming years.



<sup>&</sup>lt;sup>\*</sup> Speaker

#### Successive appearances of *Globorotalia truncatulinoides* (foraminifera) as a biostratigraphic tool in Northwestern Arabian Sea (last 100 000 years)

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The hydrography of the northwest part of the Arabian Sea, off Oman coasts, is largely influenced by the monsoon climate regime that switches between NE (triggered by winter monsoons) and SW (triggered by summer monsoons) dominant winds (Bourget, 2009).

This oceanic area is considered to be among the most productive oceanic zones, mainly due to upwelling phenomenons related to the monsoon dynamics (Singh, 2011). It directly impacts the primary production and the planktonic assemblages among which planktonic foraminifera communities (Ivanova, 2003).

These later are used as key proxies to reconstruct past oceanic conditions thanks to their preservation in marine sediments, and constitute also major stratigraphic tools along quaternary sedimentary archives. Indeed, their shells are the support of numerous geochemical analyses (such as isotopic measurements, radiocarbon datings, elemental ratio, ...). Radiocarbon datings are time consuming and expensive tools that constrain strongly the establishment or refinement of time scales.

Here we use a biostratigraphical approach based on the simple determination of the appearances of the foraminifera species, *Globorotalia truncatulinoides*. By counting the absolute abundance of this species in four different cores sampled in the northern part of the Arabian Sea coupled to radiocarbon datings, we identified a stratigraphic correspondence between the appearances of this foraminiferan in the four cores used in this study and the Heinrich events 1,4 and 6 (H1, H4, H6). Those events are brief periods of iceberg discharge into the northern part of the Atlantic Ocean shown to have an effect on lower latitudes (Schulz, 1998).

Stadials are defined by a well stirred water column (Reichart, 2004) which might have a benefic effect on the reproductive success of *G. truncatulinoides* that reproduce into subsurface waters after a time spent at greater depths (Kemle-von M'ucke, 1999).

This study appears to overlap the *G. truncatulinoides* abundances data of other cores in the region (Reichart, 1998; Reichart, 2004). It could thus be a support for the hypothesis that this planktonic foraminiferan can be used as a biostratigraphic tool in order to obtain key dates in the study of cores from the northwestern Arabian Sea.



#### Neogene paleoenvironmental evolution of Guercif basin (Morocco): implications for the evolution of the South Rifian Corridor

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Biostratigraphic and paleoenvironmental results are presented from Neogene deposits in the Guercif Basin, located at the southern margin of the Rifian Corridor in Morocco. This corridor was the main marine passageway which connected the Mediterranean with the Atlantic during late Miocene. The samples were taken from a geological section located at the southwestern part of the basin. The section can be divided in three lithological units, dated from the Tortonian to the Messinian. The lithostratigraphical continuity between the late Tortonian and the Messinian are confirmed by the succession of planktonic foraminifera (eg., Globorotalia menardii group, right coiling) from the upper Tortonian, (eg., Globorotalia miotumida group, left coiling) to the Messinian. The diversity of benthic foraminifera is significant in the studied geological section, with 41 species assigned to 26 genera. Five successive assemblages of benthic foraminifera were defined, each one characteristic a different paleoenvironment. The Tortonian calcarenitic units were deposited in a shallow neritic (infralittoral) environment, especially marked by the species Ammonia beccarii accompanied by Nonion commune and Textularia sagittula. The environment gradually evolves to a deep epibathyal environment, evidenced by the presence of an association of Uvigerinids at the base of the marks sandstones levels. The intermediate upper Tortonian unit is marked by an association of Lenticulinids and by an alteration of gypsiferous marks and sandstones suggesting rather a circalittoral environment. Finally the Messinian gypsiferous marls were first deposited in circalittoral identified by an association of Lenticulinids. The cooccurrence of A. beccarii and Cibicides lobatulus rather suggest an infralittoral environment. The upper Messinian sediments are unconformably covered by Pliocene continental deposits, which are devoid of foraminifera. At this time the connection between the Mediterranean Sea and the Atlantic Ocean was interrupted through the South Rifian Corridor. This closure contributed to the installation of the conditions of the Messinian salinity crisis.



Speaker

## Biostratigraphy and Paleoenvironment of the upper Cretaceous sediments of the Gagra-Java zone and Okriba-Khreitian subzone (Georgia) on the basis planktonic foraminifers

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The studied region includes the Late Cretaceous sediments of the the Gagra-Java zone, Okriba-Khreiti and Dzirula subzones of the greater Caucasus (Western Georgia). For the Odishi- Okriba facies type (Tskhenis tskali, Rioni and Tsachkhura river basins (vil. Gordi (r. Tskhenis tskali), vil. Nokalakevi, r. Abasha, r. Tskhunkuri (r. Rioni basin), vil. Gogna) in the interval of Turonian-Santonian characterized by the presence of volcanic rocks formed on the general background of carbonate sedimentation.

These given possibility complexes were compared with complexes of macrofauna and nannoplancton.

I. Complex *Marginotruncana pseudolinneiana* and *Marginotruncana schneegansi* are found together with mollusks of the *Inoceramus lamarcki* zone and corresponds to the nannoplankton zone of *Tetralithus pyramidus*. The complex is dated as early Turonian.

II. Complex *Marginotruncana coronata* corresponds to a mollusks zone of *Inoceramus sturmi* and nannoplankton zone of *Marthasterites furcatus*. The age is determined as early Coniacian.

III. Complex *Marginotruncana sigali* and *Marginotruncana renzi* (Mtavari Suite). Stratigraphically the given complex corresponds to the *Inoceramus involutus* zone. It is dated as Upper Coniacian.

IV. Complex *Globotruncana arca* is characterized by the abundance of index-species and it corresponds to the layer with *Micraster schroederi* and the nannoplanlankton zone of *Tetralithus aculeus*. It is dated as early Campanian.

V. Complex *Globotruncana ventricosa* corresponds to the layers with *Belemnitella mucronata* and corresponds to a zone of *Tetralithus aculeus* and a part of *Tetralithus trifidus* by nannoplankton. The age is determined as Middle Campanian.

With the help of the carried out analyses it is possible to judge, that in the Upper Cretaceous period a warm tropical climate can be inferred, where temperature of water varied from  $15 \circ C$  to  $27 \circ C$ , and depth of the basin from 80m to 250.



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### Coiling ratio of *Globorotalia truncatulinoides*: a robust stratigraphic tool in the North East-Atlantic during the Holocene

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Coiling ratios of planktonic foraminifera are commonly used in paleoceanographic studies to build stratigraphic sequences (e.g. *Neogloboquadrina pachyderma* sinistral form). Bolli (1950, 1951) noticed that such an exercise is especially possible with the species *Globorotalia truncatulinoides* because the ratio of sinistral *vs* dextral shells strongly varied in time and space. Since, this stratigraphic tool has been used by many authors mainly to tie cores in the same area and to determine stratigraphic correspondences (Ericson *et al.* 1954, Nagapta 1957). In Holocene sequences of the North East Atlantic ocean, authors usually use coiling ratio of *G.truncatulinoides* to identify a warm period (between 6 and 10 ka) marked by increases of sinistral form occurrences (Pujol 1980, Auffret *et al.* 1996, Zaragosi *et al.* 2000).

In this study, we consider changes in the coiling ratio of *G. truncatulinoides* over the last 15 000 years thanks to a collection and combination of ten marine sediment cores distributed from the Rockall trough to the southern Iberian Peninsula. This regional compilation aims at improving the accuracy of this stratigraphic tool. Preliminary results allow us to identify a marked change in *G. truncatulinoides* populations at 10 ka, with sinistral forms reaching up to 80%. This transient event which can extend to the mid Holocene depending on the considered site is characterized by a multi-step structure. Accurate datings of this interval will allow obtaining a robust stratigraphic tool for the Holocene.

As counts of the two coiling forms of *G. truncatulinoides* are quite easy and do not imply high instrumental costs, such a study demonstrates that a robust stratigraphic framework can be efficiently obtained for Holocene marine archives on this basis.



28 // Poster

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# Visean (Carboniferous) foraminiferal biostratigraphic succession of South China

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Foraminifers were very abundant, widely distributed, and had high diversities and evolutionary rates in the Carboniferous. It has special significance for division of shallow-water facies strata, and the Tournaisian–Visean boundary is defined by the FAD of the benthic foraminifer *Eoparastaffella simplex*, within the *Eoparastaffella ovalis –E. simplex* evolutionary lineage. The South China has the best Visean strata and the Global Stratotype Section and Point (GSSP) for the base of the Visean Stage has been defined here. Four typical sections of Visean Stage, which are the Beian section from Pengchong, Liuzhou, Guangxi Province, Shangsi section from Dushan, Yashui A and B sections from Huishui, Guizhou Province, have been studied. Data collected allowed us to perform systematic paleontology and biostratigraphy based on foraminifers. From this study and previous works, seven foraminiferal zones in the Visean Stage of the Carboniferous in South China have been recognized, which are, from the bottom to the top, the *Eoparastaffella simplex* Zone, *Viseidiscus/Planoarchaediscus* Zone, *Paraarchaediscus* Zone, *Pojarkovella nibelis* Zone, *Koskinotextularia* Zone, *Bradyina* Zone and *Janischewskina* Zone.

All the foraminiferal zones are interval zones. The lower boundary of each zone is marked by the first appearance of the index taxon of the zone, and its upper boundary coincides with the first appearance of the index taxon of the next zone. (1) *Eoparastaffella simplex* Zone is widely recorded in the word. (2) *Viseidiscus/Planoarchaediscus* Zone. The lower boundary of this zone is defined by the appearance of the first primitive archaediscids, such as *Viseidiscus, Planoarchaediscus*. This zone can be correlated with the MFZ 10 in Western Europe. (3) *Paraarchaediscus* Zone can be broadly correlated with the MFZ 11 in Western Europe. (4) *Pojarkovella nibelis* Zone can be correlated with the lower part of the MFZ 12. (5) *Koskinotextularia* Zone can be correlated with the upper part of the MFZ 12. (6) *Bradyina* Zone can be broadly correlated with the MFZ 14. (7) *Janischewskina* Zone. The upper boundary of this zone is marked by the first appearance of *'Millerella ' tortula*. This zone can be broadly correlated with the lower part of the MFZ 15.

This work has established and perfected the foraminiferal biostratigraphic succession in the Visean Stage of South China and provided a reasonable biostratigraphic correlation with Western Europe.

IPC 5

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#### **S29 - Palaeobiodiversity of Southeast Asia**

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#### Investigation of the occurrences of Monitor Lizards (Varanus sp.) from Late Pleistocene to Holocene in continental South-East Asia

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Several Late Pleistocene and Holocene South-East Asian archaeological deposits are known to contain important osteological assemblages of Monitor lizards (*Varanus* sp.). This taxon could be of primary interest for paleoenvironmental and paleobiodiversity questions as it is nowadays represented by several species occupying different ecological niches (dry and moist forest, proximity of water flows...). However the archaeological remains of these lizards were never fully investigated from an anatomical point of view and the issue of their specific identification remains poorly resolved.

We tried to solve this issue by performing an anatomical study of the skeletons of modern *Varanus* species occurring in the Sunda region in order to define osteological characters allowing for their identification in the fossil record.

The results of this investigation are then used to study fossil *Varanus* from two Late Pleistocene and Holocene Thai archaeological deposits situated in the northern and in the peninsular part of the country, the sites of Doi Pha Kan shelter and Moh Khiew cave. The obtained data provide information about the past distribution of the different species occurring in this area as well as paleoenvironmental information concerning the surroundings of the deposits.

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### The *Khoratpithecus*-bearing fauna from the Central Basin of Myanmar: faunal composition, biochronology and biogeographic affinities

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The area of Magway (Central Basin of Myanmar) has yielded in 2011 a late Miocene fauna comprising the hominoid primate *Khoratpithecus*, a Pongo relative. Here we present new data collected by the Myanmar-French Paleontological Expedition further documenting the biodiversity of this fauna. This assemblage comprises the equid Hipparion s.l., the proboscideans Tetralophodon and Stegolophodon, 4 suoids including Tetraconodon minor, Propotamochoerus cf. hysudricus, cf. Hippopotamodon sivalense, the rhinocerotid Brachypotherium perimense, a chalicotheriinae, the giraffid Bramatherium, the tragulid Dorcatherium, the anthracotheres Merycopotamus medioximus and Microbunodon as well as the bovids Selenoportax and Helicoportax. This faunal assemblage mostly comprises taxa identical or very close to the representatives of the late Miocene Nagri fauna of the Siwaliks of Pakistan, suggesting that no major barrier was blocking faunal dispersals in Southern Asia during the late Miocene and reinforcing the claim that Southern Asia was a bioprovince during the late Miocene. Biochronological data using the Siwaliks of Pakistan as a reference date this fauna from the early late Miocene and bracket its age between 10.5 and 8.5 Ma which roughly corresponds to the temporal extension of the Nagri Formation. Preliminary isotopic data acquired on the large mammals of the fauna show no sign of C4 plant consumption. These new data suggest that the vegetation in the Central Basin of Myanmar was contrasting with that of the Siwaliks of Pakistan where C4 plants have been identified as early as 10 Ma and point to a delayed emergence of environments dominated by C4 plants in Myanmar.



### Early to Middle Permian ostracods (crustaceans) of Indochina terrane, central and northeastern Thailand: implication for palaeobiogeography

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During the Permian, areas on the western rim of Indochina terrane were parts of the Paleotethys; therefore, the Permian rocks exposed in central and northeastern Thailand are composed mainly of limestones with less siliciclastic rocks. Diversified fossils such as fusulinaceans, corals, brachiopods, conodonts recovered from these limestones and shales have been recorded for more than 50 years. Recently ostracods are recovered from limestones of Saraburi Group. Seventeen sections of Lower to Middle Permian located in Loei, Phetchabun, Nakhon Sawan, and Lopburi provinces were investigated. More than 200 species are identified, most are endemic. The ostracod assemblages including Bairdiidae, Acratiidae, Sigilloidae, Geroiidae, Cytherideidae, Cavellinidae, Polycopidae, Aparchitidae, Kloedenelidae, Knoxitidae, Paraparchitidae, Kirkbyidae, Amphissitidae, Youngiellidae, Hollinellidae, Coelonellidae are typical shallow marine species inhabiting on marginal marine to exterior platform environments. Thirty-one species are known from other sites within Paleotethys region and are also benthic inhabitants. Provincialism index suggests that the Early Permian ostracods from Thailand have close relationships with those reported from Eastern China, and the Middle Permian ones have relationships with Tunisia, South China, and Eastern China species.



Speaker

#### Biodiversity decreasing in peninsular Southeast Asia: The message of Holocene turtles from the central plain of Thailand

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With more than 40 extant terrestrial and freshwater turtles, Southeast Asia is currently a hot spot of turtle biodiversity. However, the distribution areas of most species are decreasing as a consequence of human activities. The causes of this decline are multiple: habitat and natural resources destruction, introduction of invasive species, hunting, etc. However, historical data are still lacking for a detailed understanding of that global trend as well as for forecasting its evolution in the future. Indeed, while interviews can provide a rather good appreciation of the decline of biodiversity over the last few decades; nothing is known about the dynamic of turtle biodiversity over the Holocene. This lack of data is especially damaging in strongly anthropized areas, as the central plain of Thailand, which is now dominated by agricultural landscape. In order to solve these issues, we investigated three archaeological localities in the Thai central plain which provided assemblages of turtle remains ranging from Late Metal Ages to the Dvaravati periods. Most of the studied archaeological assemblages showed a very high species richness. Species such as Malayemys cf macrocephala, Cuora amboinensis, Heosemys annandalei, Heosemys grandis, Indotestudo elongata, Siebenrockiella crassicolis, Amyda cartilaginea were among the most abundant. We also found several plates and a skull fragment belonging to a species of the genus Batagur and a few plates belonging to the genus Geochelone. These two taxa are absent from living turtle assemblages in the central plain but are present in Myanmar, Cambodia, Indonesia or Southern Thailand for Batagur and far in the West for Geochelone (Myanmar) respectively. Batagur sp. is usually found in coastal areas and its presence inland until the first millenium is interpreted in regard of the rapid and recent geomorphological evolution of the gulf of Thailand. Cutting traces showed that most turtles were used as food resources at these times, suggesting that turtle hunting was a common practice. Furthermore, occurence of holes in the peripheral plates of some specimens from Kheed Khin (Saraburi province) suggests that some specimens were kept captive alive or transported. This study shows that investigation of recent fossil localities allows for a better understanding of the role of past human populations in the alteration of the biodiversity through time, and for a more accurate estimation of the rates of species extinction.



<sup>&</sup>lt;sup>°</sup> Speaker

# Freshwater hybodont sharks as biostratigraphic tools for the Early Cretaceous of Southeast Asia

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Dating and correlation in non-marine environment are notoriously difficult due to the absence of many biostratigraphic markers, usually restricted to the marine environment (i.e. ammonites and foraminifers). The dating and correlation of the Upper Jurassic/Lower Cretaceous Khorat Group in Thailand and adjacent areas relied mostly on palynological data. Vertebrates have also yielded valuable information and recently, the use of hybodont sharks allowed locating the position of the Jurassic/Cretaceous boundary in the Phu Kradung Formation. Freshwater hybodont sharks allow also biostratigraphic correlations outside the Thai Khorat Plateau. The first example was the recovery on Kut Island, situated 200 km south of the southernmost border of the Khorat Plateau in the Gulf of Thailand, of Heteroptychodus kokutensis and Isanodus paladeji, which allowed correlating the island's vertebrate beds with the Sao Khua Formation, although in the Geological Map of Thailand the fossiliferous sites were attributed to the Phu Kradung Formation. The second example was the recovery of a shark fauna including Heteroptychodus steinmanni, Hybodus aequitridentatus, Khoratodus foreyi, Thaiodus ruchae and Acrorhizodus khoratensis in the Napai Basin in the Guangxi Zhuang Autonomous Region, South China. This fauna allowed correlating the Chinese Xinlong Formation with the Thai Khok Kruat Formation. However, to maximise the biostratigraphic use of hybodont sharks, a refined taxonomic study of some taxa is needed. Since the erection of Heteroptychodus kokutensis in 2010, it has sometimes been difficult to separate this species from H. steinmanni. New material discovered in Pahang of Peninsular Malaysia, as well as in various sites in Thailand, including Pra Prong on the southern margin of the Khorat Plateau, offers the opportunity to revise the genus Heteroptychodus and to test whether or not H. kokutensis and H. steinmanni co-existed in the upper part of the Sao Khua Formation. Similar problems still exist with Isanodus in that I. paladeji and I. nongbualamphuensis are known from the Sao Khua fauna but the new material from Malaysia now calls their distinction into question. A full taxonomic revision of the genera Heteroptychodus and Isanodus is therefore necessary before a reliable biostratigraphic scale based on hybodont sharks can be established for the non-marine Cretaceous of Southeast Asia. The deciphering of their phylogenetic relationships will also vastly improve our understanding of the colonization patterns of freshwater environments by these sharks.

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<sup>&</sup>lt;sup>\*</sup> Speaker

#### New data about the braincase of *Thaiichthys* (Holostei: Lepisosteformes) from the Early Cretaceous of NE Thailand

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Since the resurrection of the Holostei by Lance Grande in 2010, much progress has been done in the understanding of the content and intrarelationships within this clade of actinopterygian fishes. In particular, it has been shown that the living gars (Lepisosteidae) are rooted in a clade of Mesozoic fishes previously integrated in the 'Lepidotes – Semionotus' complex. Most recent phylogenies of ginglymodians identify two inclusive clades, the Semionotiformes and the Lepisosteiformes. The content of both clades and in particular the identity of the basal-most lepisosteiforms varies from one study to another. Among these basal taxa are several genera found in the Late Jurassic and Early Cretaceous of northeasten Thailand and of Laos, notably *Thaiichthys, Isanichthys* and *Lanxangichthys*.

Recently published phylogenies are based on data matrix containing relatively few characters associated with the braincase. Those, moreover, are poorly known for a majority of genera for preservational reasons. Most of these characters concern presence vs absence of specific ossifications (intercalary, basisphenoid) or of anatomical structures (posterior myodome, posttemporal fossa, etc.). Braincase features, however, potentially contain a strong phylogenetic signal because they are supposedly less affected by superficial adaptative constraints and we hypothesize that the discovery of new anatomical structures in this part of the skeleton will help us to better resolve the relationships among the clade.

Here we provide new information about the anatomy of the braincase of *Thaiichthys* buddhabutrensis, a fish from the basal Cretaceous of NE Thailand, on the basis of a CT reconstruction. *T.* buddhabutrensis is known by several hundred specimens showing all kinds of preservation, from completely articulated specimens to isolated braincases. In all recent phylogenies, *T.* buddhabutrensis is resolved as one of the basal lepisosteiforms but in a more crownward position than *Isanichthys* and *Lanxangichthys*. The braincase has already been superficially described on the base of 3D preserved specimens, but it is expected that the tomographic reconstruction will provide insight into anatomical structures that, by comparison with the gars, contain a phylogenetic signal.



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#### The late Pleistocene (MIS 4) mammal assemblage of Tham Prakai Phet (Thailand): a new biochronological benchmark for mainland Southeast Asia

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The Tham Prakai Phet (literally, "the cave of glittering diamonds") is a long karstic cavity formed in a Permian dolomitic limestone, located in the Chaiyaphum Province, Northeastern Thailand. The presence of large mammal fossils in the deposits has been reported in the 1990s'. Subsequent surveys performed between 2011-2013 by a team from the Palaeontological Research and Education Centre and from the Mahasarakham University led to the discovery of additional isolated teeth. Here, we present the results of the first excavation conducted between 2014 and 2015 in a small gallery of the network that preserved breccia deposits, containing a dense quantity of faunal remains. More than 1,000 fossil remains were collected from a 4m2 excavation. This rich collection of mammal fossils is composed mostly of isolated teeth and few badly preserved bones. Palaeontological analysis reveals a high diversity of taxa including Primates, Carnivores, Artiodactyla, Perissodactyla and Rodents. The mammal association contained archaic species such as Ailuropoda melanoleuca baconi, Crocuta crocuta ultima, as well as taxa still extant today in the Indochinese subregion. Direct U-series and ESR dating analyses performed on three bovid teeth gave an age range between 56-79 ka. This now well dated mammal association provides a new biochronological benchmark for the Southeast Asian mammal record at the beginning of the Late Pleistocene. Additionally, isotope analyses ( $\delta^{13}$ C,  $\delta^{18}$ O,...) performed on tooth enamel samples provided further insights into the palaeoenvironmental conditions during MIS-4. Finally, taphonomic studies showed the important role played by rodents and carnivores in the constitution and modification of the mammal assemblage, in combination with gravity- flow deposit process.

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#### Fusulinids from the Changning-Menglian Belt, western Yunnan, China and their paleogeographic implications

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Palaeodiversity of benthic invertebrate fossils has been proven valuable in deciphering the complex tectonic evolution of the Tethyan domain. The Changning-Menglian belt in western Yunnan, China has been interpreted to be a suture of Tethys ocean and also a demarcation between faunas of Gondwana-affinity and Cathaysia-affinity during Permo-Carboniferous. Fusulinids in this belt, however, have been hitherto rarely dealt with detailed taxonomic and paleobiogeographic analysis, notwithstanding their spatiotemporal significance. We in present study update the taxonomic list of fusulinids in this belt, based on our collections and data in literature. Moreover, we compare, both qualitatively and statistically, the generic composition of fusulinids from this belt and their counterparts in Gondwana-derived blocks, e.g. Sibumasu region to its west, and South China, Indochina in Cathaysian region to its east. Late Carboniferous-Early Permian and Middle Permian have been emphasized as two time intervals for comparison, because they represent the crucial periods amid and posterior to Gondwana glaciation. Results reveal that Gzhelian-Sakmarian fusulinids in this belt markedly differ from those from Sibumasu region by much more diversified fusulinids and yielding characteristic elements of the Cathaysian region, e.g. Pseudoschwagerinids. However, the Roadian-Capitanian fusulinids in this belt turns to be outnumbered by their counterparts in the Sibumasu region, in terms of overall diversification and diversity of typically warm-water Neoschwagerinids and Verbeekinids. Compared with tropical Cathaysian region, fusulinids in this belt are consistently less diversified throughout late Carboniferous to Middle Permian, despite the taxonomic similarity between them. Therefore, the compositional feature of fusulinids from the Changning-Menglian belt probably signifies transitional environment between the blocks with Gondwana-affinity at southern mid-latitudes and tropical Cathaysian region during Permo-Carboniferous. This interpretation is also corroborated by lines of evidence from carbonate sediments and other fossil taxa, e.g. pollen and spores and corals. We believe this study sheds new light on the geological details of the Tethys recorded in this belt from the paleontological perspective.



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# Permian gastropods in Thailand: Implications for diversity and palaeobiogeography in Southeast Asia

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The first diverse Permian gastropod fauna in Thailand has recently been reported from the Tak Fa Formation, Northern Thailand. This formation belongs to the Indochina Block of Southeast Asia in which vast late Palaeozoic carbonate platform deposits crop out. The Middle Permian Tak Fa Limestone yielding the gastropod fauna is a fusulinid limestone. Its invertebrate fauna is locally strongly dominated by gastropods. Ca. 1,000 silicified gastropod specimens representing 40 species are present (about 30% of the taxa are new). The gastropod fauna is strongly dominated by the vetigastropod Anomphalus sp. followed by bellerophontoids and pleurotomarioids in abundance. Although this fauna contains several new species, most of the present genera are cosmopolitan. Additionally, a new, undescribed Early Permian gastropod assemblage from Southern Thailand, belonging to the Sibumasu block, is currently under study. It comprises approximately twenty species. Moreover, ongoing dissolution of limestone from three localities within central Thailand will provide important information on Permian gastropod faunas of Thailand. Gastropod faunas from Thailand are compared with those from Southeast Asia for instance with the Permian gastropod fauna from Perak, Malaysia and the Akasaka Limestone, Japan. On the species level, few taxa are shared whereas many genera are shared. Gastropod diversity as determined by species richness and rarefaction analyses is relatively high throughout these faunas from Southeast Asia reflecting that they are from tropical shallow water environments. A palaeobiogeographical analysis of gastropod faunas of Southeast Asia is planned when faunal analysis is completed and previous taxonomic assignments are revised. At this point, cosmopolitan taxa on the one hand and endemic taxa on the other hand hinder a meaningful analysis of palaeobiogeographical patterns.



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#### Ichnofossils from the Mesozoic lower formations of the Khorat Group: toward a better understanding of the continental ichnofacies from Thailand

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The Mesozoic continental formations of northeastern Thailand yield a large diversity of trace fossils, including vertebrate footprints, invertebrate productions and rhizoliths. The first trace fossils discovery from the Khorat Group was made by Buffetaut *et al.* in 1985. Hitherto some of these formations present a very reduced ichnofossil record.

Studies conducted on ichnofossils from Northeast Thailand usually referred to sites with tracks of vertebrates, principally dinosaurs. Until recently no fossil track had been reported from the Phu Kradung Formation, one of the oldest formation of the Khorat Group. In this study ichnofossils from seven localities in Northeast Thailand were studied, four of these sites belonging to the Phu Kradung Formation. The siltstone substrates of the Phu Kradung Formation preserve some singular and diverse vertebrate ichnofacies as well as exceptionally-preserved bone-beds, something unique in the fossil record of Southeast Asia. Ichnofossils from the underlying upper Nam Phong Formation as well as those from the overlying Phra Wihan Formation were also described and compared.

The ichnofauna of the upper Nam Phong Formation is represented by footprints of vertebrates corresponding to the *Grallator-Eubrontes* ichnotaxa continuum formed in a meandering river paleoenvironment.

The *Camborygma* crawfish burrows associated with rhizoliths and calcareous nodules from the lower part of the Phu Kradung Formation are characteristic of palaeosols from distal floodplain areas. In the upper part of the Formation, the *Mermia* ichnofacies indicates a change to an alluvial environment presenting characteristics of a continental lakeside margin.

The ichnofossil record from the Phra Wihan Formation corresponds to the ichnogenus *Grallator* associated to the ichnofacies *Palaeophycus*, a common ichnogenus of both lacustrine and fluvial environments.

The ichnofossils from the Phu Kradung and adjacent formations presented here provide a better understanding of the evolution of the various depositional systems of the lower part of the Khorat sequence as well as a better reconstruction of the living environments of fossil vertebrates from these Formations.

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#### Cenozoic fossil tortoises of Southeast Asia: palaeobiogeographical implications

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The fossil record of Paleogene tortoises (Testudinidae) is scarce in Southeast Asia. The oldest tortoise record is a few fragments from the late Middle Eocene Pondaung Formation, Myanmar. The Late Eocene – Early Oligocene Krabi Basin in Southern Peninsula of Thailand has yielded some fragments of shell that could also be referred to Testudinidae. During the Neogene, remains of tortoises are more commonly reported from this region. In particular, giant tortoises have been reported from India to Indonesian islands and referred to the extinct genus Megalochelys. Reported first from the Plio-Pleistocene beds of Siwaliks, India, *Megalochelys sivalensis* or affine forms have been recorded from the Early Pleistocene of the Bumiaya area, Central Java and in Sulawesi and Timor islands. Megalochelys is also present in peninsular Southeast Asia, notably in Thailand and more recently in the Lower Irrawady beds of Myanmar. Abundant and yet undescribed new specimens from Tha Chang sandpits (Nakhon Ratchasima Province, Thailand), are represented by isolated and fragmentary shell elements of several individuals. Variations in the shape of the epiplastra indicate that several morphotypes are present in Southeast Asia during the Plio-Pleistocene, which may correspond to different species, sexual dimorphism or intraspecific variations. Our examination of the material suggests that a unique group of giant tortoises was present throughout Southeast Asia and that they had a long distance dispersal on mainland and islands of Southeast Asia.



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## New dicynodonts (Therapsida, Anomodontia) from the Early Triassic of Laos: implications for the tetrapod recovery after the Permian–Triassic mass extinction and the paleobiogeography of Southeast Asian Blocks

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The dicynodonts are an emblematic group of herbivorous therapsids, which have survived the Permian–Triassic (PT) crisis. Laotian dicynodonts from stratigraphically well-constrained beds, using U–Pb on zircon dating, bring new insights into terrestrial faunas of Southeast Asia during the Early Triassic. They have already briefly been described but their phylogenetic relationships were never been investigated. Reexamination of the Laotian dicynodonts, three well-preserved skulls, indicates that they belong to two new species. Our phylogenetic analysis within Dicynodontia indicates that 1) gen. et sp. nov. 1 is closely related to some "Dicynodon" - grade taxa; and 2) gen. et sp. nov. 2 is a stem taxon to Kannemeyeriiformes. The phylogenetic affinities of these new Laotian dicynodonts allow to discuss about the recovery of the terrestrial tetrapods during the Early Triassic: the survival of a Permian lineage across the PT crisis and/or a rapid recovery with a new occurrence in the Early Triassic. The Laotian dicynodonts also shed new light on the debated paleogeographic issues concerning the evolution of Southeast Asia from the late Paleozoic to the early Mesozoic, particularly on the timing of the collision between the Indochina, the South China and the North China blocks. The Early Triassic age of the two new Laotian dicynodonts, their essentially terrestrial lifestyle, and the phylogenetic affinities between gen. et sp. nov. 2 and Early Triassic Chinese Kannemeyeriiformes, suppose a land connection between the Indochina Block and other dicynodont bearing continents as early as the Early Triassic.



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#### Zooarchaeology of small impoverished islands: Looking at microvertebrates from Bubog rockshelters (Ilin Island, Mindoro, Philippines)

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Small islands were a mandatory passage en route to Australia about 60,000 years ago. Little is known about the cultural adaptations in these faunal- and floral-impoverished environments. Ilin is one of the first small islands on the north of this migration path being located south of Mindoro main island in the Philippines. The archaeological record of two rockshelters, Bubog I and Bubog II both excavated since 2011 on Ilin Island, dates back to ca.30,000 kya and extends up to the mid-Holocene just before the arrival of Neolithic populations. Beyond the continuous presence of shell (Lim, 2016) and fish remains (Boulanger, 2015) resulting from foraging along the moving palaeoshoreline, the faunal assemblage recovered in these two sites is overwhelmingly dominated by the presently extinct giant cloud rat Crateromys paulus. Other rodents have also been recovered such as Anonymomys cf. mindorensis, Maxomys sp. and two rats namely Rattus everetti and Rattus mindorensis. Among the chiropterids, Acerodon cf. jubatus, Desmalopex microleucopterus, Styloctenium mindorensis, Hipposideros diadema, Pteropus sp., and Rhinolophus sp. have all been positively identified. These terrestrial/arboreal species not only document the evolution of past environments around the Late Pleistocene - early Holocene transition but also inform us on human subsistence strategies. Butchery marks were recorded, notably on a tibia of C. paulus, which was certainly is an interesting game on this small island considering its size. Some bones also showed burning patterns while there were also several bones that have indicators of digestion by birds. The anthropogenic origin of a part of this microvertebrate assemblage can then be at least suspected. This communication will discuss in detail those evidences of hunting and consumption of small mammals in relation to the ever changing palaeoenvironmental conditions.



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#### Non-avian theropod dinosaurs in Thailand & Southeast Asia: evolution and paleobiogeography

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In Southeast Asia, at least fourteen non-avian theropods have been reported so far. They are dominantly found from the northeastern Thailand, however, one bizarre theropod is described from Lao PDR, one reported from Malaysia and one recently reported from Myanmar. The temporal distribution of Southeast Asian theropod ranges from the Late Jurassic to Middle Cretaceous.

There are two large-bodied metriacanthosaurids (=sinraptorids) from the Phu Kradung Formation of Thailand. Seven non-avian theropods from the Sao Khua Formation of Thailand are described, including a small-bodied compsognathid, a spinosaurid *Siamosaurus suteethorni*, an ostrich-mimic dinosaur *Kinnareemimus khonkaenensis*, a large-bodied carcharodontosaurid; a possible basal coelurosaur *Siamotyrannus isanensis;* and two newly reported, undescribed mid- sized megaraptorans which look similar to *Fukuiraptor* from Japan. Two theropods from the Early Cretaceous Khok Kruat Formation of Thailand include an undescribed spinosaurid and an undescribed carcharodontosaurian. One spinosaurid from Laos named *Ichthyovenator laosensis* is recorded from the "Grès supérieurs" Formation which is equivalent to Khok Kruat Formation of Thailand. Recently two spinosaurid teeth from the late Early Cretaceous of Malay Peninsula are correspondingly reported. One coelurosaur and enantiornithine birds preserved in ambers were also reported from the mid-Cretaceous of Myanmar.

All non-avian theropod faunas from Southeast Asia belong to non-maniraptoran tetanurans (with exception of the coelurosaur and birds from Myanmar). They show greater similarity to Chinese plus Japanese theropods during the Early Cretaceous in the broad systematic term. During this time, megaraptorans can be found only in Japan, Australia, and Thailand, whereas tyrannosauroids can be found in China, Europe, and possibly Brazil and Australia. Spinosaurids, carcharodontosaurians, and some coelurosaurs were almost cosmopolitan.



Speaker

# The long-lived Lake Nanning and its endemic and non-endemic fossil biota

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Long-lived lakes are famous for the development of taxonomically and morphologically diverse endemic faunas, which usually radiated from a rootstock of only a few early colonisers. Examples of such radiations are known from several continents. Eocene? to Oligocene sediments of Lake Nanning in southern China (Guangxi Province) have yielded rich and diversified fossil biota. Although research on these fossils started in the early 20th century, Lake Nanning has not found its way onto the map of long-lived lakes. Providing an overview of the flora and fauna recorded from Lake Nanning, we intent to change this now.

Gastropods (Viviparidae, Stenothyridae), bivalves (Unionidae), ostracods and fish have successfully radiated in Lake Nanning, and developed a variety of endemic species, many of which still await formal description. Several mollusc species have developed peculiar morphologies, some of them reminiscent of (unrelated) marine taxa. Shell thickening, spines, carinae, nodes and restricted apertures in bivalves and gastropods are interpreted as armour to prevent predation by giant shell crushing carp. Four different, successive macro-mollusc associations are defined, which can likely be used for relative dating of the lake sediments. The molluscs of Lake Nanning are outstandingly well preserved and provide a great opportunity to study a remarkable endemic lake radiation, as well as life-life interactions with their predators.

In addition, a pilot palynology study has generated data on palaeoecology. Palynomorph assemblages from different lake stages are dominated by cool temperate conifer pollen and freshwater algae. This suggests that the sediments were deposited during or after Eocene–Oligocene cooling, and supports the biostratigraphy based on rare mammal finds. The presence of well-preserved palynomorphs throughout the succession makes the sediments of Lake Nanning one of the most important Oligocene climate archives of the region.



Speaker

## A possible glacial-interglacial stability of large mammal faunas in Southeast Asia

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The Pleistocene consisting of two major climatic conditions: the glacial and the interglacial, is characterized by the series of ice ages that occurred during its reign. Differences in environments and climate between these two events turn a landscape into an optimal habitat for specific land mammals, allowing only a survival of some wildlife species. Moreover, the climate change affects ecosystems in a variety of ways. Unlike Europe and North America, Southeast Asia is possibly less affected by the vegetational variability because the land is traditionally supposed to have not been covered by ice. However, the impacts of climate changes on the mammalian community during the Pleistocene are poorly known in this region and the vegetation has never been studied in details so far.

Since the last century, the biochronologic ordering by advanced radiometric datings has become available in some Pleistocene fossil sites across Southeast Asia. The Pleistocene mammalian assemblages consist of extinct and extant tropical forested taxa recognized as "Ailuropoda - Stegodon " faunal association that covers a long range of intervals (starting from Early to Late Pleistocene). The stratified fluviatile terrace of Khok Sung, Nakhon Ratchasima province, has yielded a very rich Pleistocene vertebrate fauna of Thailand, where abundant fossil mammals and reptiles (skulls, isolated teeth, and postcranial remains) were recovered. The Khok Sung fauna (dated as either 188 or 213 ka based on the paleomagnetic data and on the faunal comparisons) in northeastern Thailand comprises a diverse mammalian assemblage (at least 15 recognized species in 13 genera), relatively similar in composition to most of Pleistocene fossil sites in Southeast Asia. The chronological evidence and stable carbon isotope analysis of large mammal faunas suggest that C4 grasslands still existed and were inhabited by spotted hyaenas, Indian rhinoceroses, and several large bovid species through the Pleistocene glacial-interglacial stages, supporting the patterns of a long-term faunal stability across mainland Southeast Asia. Although the faunal stability during the glacial-interglacial cycles makes the biochronological context of "Ailuropoda -Stegodon" association difficult to be subdivided, changes in species composition are still debated (e.g., the disappearance of Gigantopithecus and Stegodon). Future investigations into more precise chronological constraints on the fossil sites and further studies on the species diversity and ecological interactions of Pleistocene mammal faunas may hold a clue to testing for the prevalence of faunal stability across mainland Southeast Asia.



Speaker

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#### An exceptional Late Jurassic vertebrate assemblage from the Phu Kradung Formation of Phu Noi, NE Thailand

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The Phu Noi site was discovered in 2008 by a villager from Ban Din Chi in Kham Muang District, Kalasin Province, NE Thailand. Since ten years, the excavations conducted by a joint team from the Department of Mineral Resources, Mahasarakham University (Thailand) and the Centre national de la recherche scientifique (France) have resulted in the discovery of a large number of fossils. Various vertebrate remains, including partially articulated carcasses, isolated skulls, lower jaws and postcranial elements, are accumulated over an area of more than 1000 m2. To date, more than 4000 bones have been collected. The bone bed lies in non-marine brown, grey and greenish mudstones, siltstones and fine sandstones in the lower part of the Phu Kradung Formation of the Khorat group. The deposits correspond to a crevasse splay and were formed under a seasonal climate with alternating semi-arid and wet seasons. The assemblage contains mamenchisaurid sauropods, sinraptorid theropods, small ornithopods, pterosaurs, teleosaurid crocodiles, eucryptodiran turtles, temnospondyl amphibians, lepisosteiformes fishes, hybodont and lonchidiid sharks. On the basis of the hybodont sharks, the xinjiangchelyid turtles and the teleosaurid crocodiles, a Late Jurassic age is suggested for the Phu Noi locality. Similarities with Late Jurassic vertebrate assemblages from China are apparent. Because of the abundance and diversity of the vertebrate remains it contains, the Phu Noi site is currently the most significant Mesozoic vertebrate locality in Thailand and more generally in Southeast Asia.



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#### Morphological diversity of spinosaurid teeth from the Pra Prong locality (Lower Cretaceous of eastern Thailand)

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The presence of spinosaurid dinosaurs in Asia was revealed in 1986 when teeth from the Sao Khua Formation of north-eastern Thailand were described as *Siamosaurus suteethorni*. Since then, abundant isolated spinosaurid teeth have been found in both the Barremian Sao Khua Formation and the Aptian Khok Kruat Formation of the Khorat Plateau. Although several morphotypes can be distinguished, all spinosaurid teeth hitherto reported from Thailand were characterized by the presence of well-marked ribs on both faces of the crown.

The recently discovered Pra Prong locality, in Sa Kaeo Province, is the only Early Cretaceous vertebrate locality currently known in eastern Thailand. It has yielded a diverse non-marine vertebrate assemblage comprising sharks, turtles, squamates, crocodiles and theropod ans sauropod dinosaurs. Teeth showing typical spinosaurid features (weak compression, mesiodistal rather than labiolingual curvature) are common at Pra Prong and two distinct morphotypes can be distinguished :

Teeth with a strongly ornamented crown, bearing up to 25 well-marked ridges on each face, and with a wrinkled enamel between the ridges and at the apex. These teeth are reminiscent of *Spinosaurus suteethorni*, but the higher number of ridges and indistinct carinae are reminiscent of some teeth from the Khok Kruat Formation.

Teeth with no ribbing of the crown. The enamel shows the fine wrinkling seen on most spinosaurid teeth. The carinae are well-marked. The mesial carina seems to be unserrated. The distal carina bears very small irregular serrations which disappear easily when the tooth is worn.

These two morphotypes are very different from each other, and strongly suggest that more than one spinosaurid taxon is present at Pra Prong. This is also what is suggested by a study of spinosaurid teeth from the Khok Kruat Formation. It should be pointed out that the morphotype without ribbing found at Pra Prong has so far never been reported from other localities, in Thailand or elsewhere.

Correlation of the Pra Prong site with the formations of the Khorat Group of north-eastern Thailand is not completely clear, although turtles seem to indicate similarities with the Sao Khua Formation. The spinosaur teeth from Pra Prong, however, seem to be different from those from the Sao Khua Formation. Whether this reflects slightly different geological ages or geographical separation in distinct sedimentary basins remains unclear.

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#### Middle Triassic ostracods (Crustacea) from northern Thailand: first insight into their diversity and paleoenvironmental significance

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Ostracods are micro-crustacean with a fossil record spanning from the base of the Ordovician to present days. Marine ostracods have been deeply affected by the end-Permian extinction, about 252 Ma ago, leading to the deep restructuration of neritic assemblages during the Triassic. It is assumed that their recovery was completed somewhere during the Anisian (Middle Triassic) but many issues are still unsolved regarding its mechanisms, timing and associated environments. Most of our knowledge on the Triassic ostracod communities is issued from the Alps, documenting the abundant and diversified faunas developing along the western margin of the Tethys lato sensu. Here we document an inedited assemblage retrieved from the Pha Kan Formation (Lampang Group) at the Wat Phra That Muang Kham section located in northern Thailand. It is composed of 29 species distributed among 14 genera, which constitute the first detailed report of Middle Triassic (Anisian) ostracods from the Sukhothai terrane and the first insight into diversity dynamics following the end-Permian extinction in this area. The ostracod characteristics document an important shift from siliciclastic to carbonate conditions, from a protected to an open marine environment, followed by a slight regressive trend upsection associated with repeated salinity fluctuations. The comparison with other localities worldwide suggests the importance of the Sukhothai terrane for the recognition of ostracods distribution pathways during the Triassic. The age of the Pha Kan Formation is still disputed, with propositions ranging from the Early Triassic (Scythian) to the Middle Triassic (Anisian). The abundance of genera which are typical of the Middle and Late Triassic (Nodobairdia, Triassocypris, Bektasia and Leviella) seems to rather document a relatively advanced recovery state, advocating for a Middle Triassic age. The absence of Cytheroidea might furthermore indicate a relatively early Anisian age (Aegean substage?) and that the newly-evolved typically Mesozoic cytheroids only reach the Sukhothai terrane later during the Anisian.



Speaker

#### Palaeobiodiversity of Mesozoic turtles in Southeast Asia

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Most Mesozoic turtle records in SE Asia are from Thailand, ranging from Late Triassic to Early Cretaceous. *Proganochelys ruchae* from the Late Triassic Huai Hin Lat Formation represents the oldest testudines from continental ecosystems in Asia. Basal eucryptodiran xinjiangchelyids and close relatives are reported from the Jurassic Khlong Min Formation in the southern peninsula (*Siamochelys peninsularis*) and the lower part of the Phu Kradung Formation on the Khorat Plateau, NE Thailand (*Phunoichelys thirakhupti* and a new xinjiangchelyid taxon). In the upper part of the Phu Kradung Formation, there are several morphotypes of large trionychoids, including *Basilochelys macrobios*. The Early Cretaceous Sao Khua and Khok Kruat formations have yielded trionychoids. The Sao Khua Formation contains four taxa of that group (the adocid *Isanemys srisuki*, the carettochelyid *Kizylkumemys* sp. and two other trionychoids). *K.* sp. and two adocids, including *Shachemys* sp. are recorded from the Khok Kruat Formation. A diverse turtle fauna has been discovered recently in eastern Thailand, including large trionychoids, a *Kizylkumemys* with keeled neurals, an *Isanemys* -like adocid and a eucryptodiran with smooth shell surface of uncertain affinities. This assemblage can be correlated with that from the Sao Khua Formation of the Khorat Group in NE Thailand.

A lateral equivalent of the Khok Kruat Formation on the eastern margin of the Khorat Basin, the Grès supérieurs Formation of Laos, has yielded *Shachemys laosiana* and *Kizylkumemys* sp. The turtle fauna from the Xinlong Formation of the Napai Basin, Guangxi Province, southern China, is similar to that from the Khok Kruat Formation in Thailand, suggesting a similar age and that both areas belonged to the same paleogeographical region.

The turtle assemblages from the lower part of the Phu Kradung Formation in NE Thailand have close affinities with those of the Late Jurassic of mainland Asia (China and Central Asia). On the contrary, those from the upper part of the Phu Kradung Formation and the Early Cretaceous Sao Khua and Khok Kruat formations, as well as those from the Grès supérieurs Formation and the Xinlong Formation are distinct and composed of trionychoids. They differ from the turtle fauna of the Jehol Biota in northeastern China but show some similarities with those from the peripheral regions of Asia, suggesting that SE Asia was more isolated from mainland Asia during the Early Cretaceous than earlier.

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### Mid-Holocene Pollen records of vegetation and climate change from the peat profile in Lake Chenyaohu, the plain of the lower reaches of Yangtze River

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The formation and evolution of Peatland is the research focus of Globle changes. It also the key carrier to the study of paleoclimate and the carbon cycle. This study will focus on the peatland in the plain of the lower reaches of Yangtze River since the middle Holocene and we hope to explore the formation and development of the peatland and their environmental controlling actors. Palynological analyses of a peat profile in the Lake Chenyaohu documented the vegetation history and climate change perfectly during the time of peat evolution. Since 6600 cal. aBP the evergreen and deciduous mixed broad-leaved forest dominated by *Quercus* developed in this area and the climate had turned into the warm and humid period. The peat began to develop since 5700 cal. aBP when the sediment environment changed to swamp facies. After 4850 cal. aBP the broad-leaved forest decreased rapidly, instead the land herbs, mainly the Poaceae, increased. In the meantime peat also disappeared. Based on the pollen vegetation was characterized by the human activities, we consider that human activities should be cause the end of peat evolution in this area meanwhile the nature environment did not changed. Our study provide a new important data and information for the researches on the relation between climate change and peatland formation and evelopment theories in the lower reaches of the Yangtze River.

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#### A late Pleistocene Hominin from Tham Prakai Phet (Chaiyaphum Province, Thailand) : preliminary analysis of an isolated upper premolar

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The excavation of a small chamber in the network of the Tham Prakai Phet site (Chaiyaphum Province, Thailand), conducted by the Palaeontological Research and Education Centre and the Mahasarakham University, provided a rich collection of more than 1,000 mammal teeth. The combined U/Th and ESR series dating analyses performed on dental material yielded an age bracket between 56 to 79 ka. Among the collection of fossil orang-outan (Pongo sp.) from this site, an isolated upper P3 (TPKP-SW-100) shows human features. Human fossils remains are scarce in mainland Southeast Asia sites and the taxonomic identification of isolated hominoid teeth is sometimes problematic due to the morpho-metrical similarities between Homo and Pongo. In this study, the morphological description of this premolar is based on microtomographic data with special attention for enamel-dentine junction (EDJ), distribution of enamel thickness, pulp cavity and roots canals configurations. The EDJ of TPKP-SW-100 exhibits a symmetric pentagonal outline mesiodistally compressed. This surface is relatively smooth with few crenulations and the only nonmetric trait corresponds to a low mesial transverse crest connecting the base of buccal and lingual cusps. The conformation at EDJ, as well as crown external size are included in the variation range of Asiatic Homo from middle to late Pleistocene and clearly exclude the taxonomical assignation of this tooth to Pongo sp.. Moreover, the condition of enamel thickness distribution of TPKP-SW-100, with a maximum of thickness on lingual and buccal parts, is conform to human pattern and distinguishes to that of orangoutans. Finally, this upper P3 shows three roots partially preserved, two buccals including one radicule and one lingual. This root configuration contrasts with Pongo sp. pattern and is rarely observed in humans. Although this first analysis does not allow to validate with confidence an attribution to archaic Homo sapiens or modern Homo sapiens, this tooth give some information about Homo biogeography during the Pleistocene in Asia. The further analyses could probably ascribe this specimen to a better species level.



Speaker

### Middle Permian fusulinid *Rugososchwagerina* (Xiaoxinzhaiella) from the Shan Plateau, Myanmar: systematics and paleogeography

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The eastern Myanmar has been well known for its Gondwanan provenance during late Paleozoic, thus is indispensable for understanding the dynamic gelogical evolution of the Gondwana- derived blocks in the context of Tethyan domain. Nevertheless, researches on Paleozoic fossils, especially fusulinids, of this crucial region have heretofore remained rather limited in published literature, which further renders their biostratigraphic and paleobiogeographic information ambiguous. We here present a systematic study on a special morphospecies of Rugososchwagerina from the Shan Plateau in eastern Myanmar and further discuss its paleobiogeographic significance. The studied materials were collected from the Thitsipin Formation of Plateau Limestone at Pindaya in western Shan Plateau. Fusuinids in the collection are overwhelmingly dominated by specimens morphologically rather similar to Rugososchwagerina. However, they can be differentiated from typical Rugososchwagerina from the type area in Sicily, Italy or South China by consistently dwarfed size at consecutive stages of ontogeny, rather tight elongate fusiform shape and essential absence of septal flution in juvenarium. Based on biostratigraphic correlation, the studied fusulinids is dated to be Middle Permian (late Roadian to Wordian) in age. Besides the Shan Plateau, specimens with such morphological feature and previously identified as Rugososchwagerina have been reported from Central Iran, South Afghanistan, Lhasa Block in Tibet and Baoshan Block in western Yunnan, China. We suggest that these specimens constitute a subgenus of Rugososchwagerina named R. (Xiaoxinzhaiella). The areas now known to yield this subgenus all belong to the so-called Cimmerian continents, which have been interpreted to rift from the northern Gondwana margin and drift across the Tethys ocean during late Paleozoic to Mesozoic, and now is accreted to Southeast Asia. The R. (Xiaoxinzhaiella) therefore very likely represents a geographic variation of Rugososchwagerina among the Gondwana-derived blocks. The dwarfism of this subgenus might reflect a response to not so optimal seasurface temperature for the prosperity of fusulinids in the sallow marine region at southern mid-latitudes where the Cimmerian blocks resided during the Middle Permian.



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#### Phylogenetic Position of an Ornithomimosaur Kinnareemimus khonkaenensis from the Early Cretaceous of Thailand

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A small-bodied ornithomimosaur *Kinnareemimus khonkaenensis* from the Early Cretaceous Sao Khua Formation of northeastern Thailand was first reported in 1999 then named in 2009 by Buffetaut et al. It is the only report of this group in Southeast Asia and was concluded to be a member of Ornithomimosauria more derived than *Harpymimus* and *Garudimimus* but more basal than *Archaeornithomimus*. *Kinnareemimus* has since then never been included in any cladistical analysis.

Here, the phylogenetic analyses for assessing the relationships of *Kinnareemimus* within Ornithomimosauria were done. The results suggested it might be a basal ornithomimosaur (104 taxa, 568 characters) or belongs to the subclade Deinocheiridae (98 taxa, 568 characters). Generally, the tree topologies agreed with previous studies, i.e. the Ornithomimosauria consists of the subclades Ornithomimidae and Deinocheiridae, and the basal forms. *Kinnareemimus* looks similar to *Garudimimus* in the shape of the fibula in proximal view. Its metatarsal III shows subarctometatarsalian condition which might have evolved independently from other ornithomimids. However, the basal position of *Kinnareemimus* could also be due to the immaturity and the incompleteness nature of this animal.

This study shows that the evolution of the arctometatarsalia condition in ornithomimosaurs was not a simple linear process. Furthermore, it appears that during the Early Cretaceous the basal ornithomimosaurs were more widespread than in the Late Cretaceous when they were restricted to central Asia and North America. *Kinnareemimus* is one of the oldest and more basal ornithomimosaurs. This indicates that Southeast Asia played an important role in the early radiation of the Ornithomimosauria.



Speaker

#### The reconstruction of the theropod dinosaur Siamotyrannus isanensis from the Early Cretaceous of Thailand

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*Siamotyrannus isanensis* is a large-bodied and informative theropod dinosaur from the Early Cretaceous Sao Khua Formation of Thailand. It was first interpreted as a basal member of the tyrannosaur lineage. This conclusion has been debated by various works, for example, it was found to belong to Metriacanthosauridae (=Sinraptoridae), basal Allosauroidea, might be a carcharodontosaurian, or even a basal coelurosaur. These affect the appearance of this theropod since then.

In the recent phylogenetic analysis which focused on non-coelurosaurian tetanurans (63 taxa 351 characters), *Siamotyrannus* was found to belong to Coelurosauria but uncertain position due to a small number of coelurosaurian representatives. In another analysis that focused mainly on Allosauroidea and Tyrannosauroidea (44 taxa 284 characters), *Siamotyrannus* was found to be a basal coelurosaur, more basal than the clade Tyrannosauroidea + 'derived' coelurosaurs. These results lead to the new reconstruction of *Siamotyrannus* in the present work.

In this present work, we review previous reconstructions of *Siamotyrannus* which mostly based on the Tyrannosaurs. For the new reconstruction, the general morphology such as skull shape, the ratio of maxilla-antorbital fenestra, the shape and size of teeth of theropods, the body shape, and the size and shape of the forelimbs are considered. Then the unique characters of each group are focused since we do not find any skull materials of this dinosaur. The reconstruction has been successful thanks to the collaborative work between the paleontologist and the paleo-artist/ illustrator.



Speaker

### A permineralized fertile segment of leptosporangiate fern *Dennstaedtia* (Dennstaedtiaceae) from the Late Cretaceous (Coniacian) of Hokkaido, Japan

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Fossil records are necessary for reconstructing the true fern (moniliophyte) phylogeny and understanding the character evolution pattern, even though the phylogenetic patterns of the living species are resolved using molecular characters. The family Dennstaedtiaceae comprise a clade nested in basal polypods and are estimated to have performed their early diversification during the Cretaceous. However, fossil records illustrating this early diversification process are still limited. The Cretaceous Yezo Group from Hokkaido, Japan yields abundant plant debris that are anatomically preserved in calcareous nodules contained in marine sediments at Asian continental margin. Nearly 140 species of vascular plants ever described since early 1900s contain fern fragments attributable to Osmundaceae, Gleicheniaceae, Matoniaceae, Schizaeaceae (s.l.), Cyatheaceae (s.l.), Loxomaceae and Dennstaedtiaceae (Nishida 2001). For the Dennstaedtiaceae only vegetative remains such as solenostelic dorsiventral rhizomes, petioles and distal rachides with a typical vascular configuration, and fragments of sterile leaves have been recovered. Here we report a well-preserved fertile segment that is attributable to the genus Dennstaedtia for the first time from Hokkaido as well as from the world. The specimen is a small segment embedded in a calcareous nodule collected from the Kashima Formation (Coniacian) of the Yezo Group. Preliminary X-ray CT observation helped to decide peeling directions that made us possible to reconstruct a 3D image based on obtained serial sections. The segment is pinnatiparted with one possible terminal and six lateral lobes each of which has single vein terminating an indusiate sorus. The identification is supported by the terminal sorus covered with an abaxial kidney- shaped indusium, the sporangium with a vertical incomplete annulus, and in situ Biretisporites - type spores. Sixty-four spores per sporangium are estimated. The spore is trilete, 42-45 $\mu$ m in diameter and has psilate surface. The new finding confirms the presence of Dennstaedtia, which has been predicted based on vegetative materials. Fragments of leaves and other vegetative parts similar to those of Hokkaido Dennstaedtia are widely reported worldwide including the Sothern Hemisphere during the Cretaceous. Evolution and phytogeography of Mesozoic ferns will be better clarified based on further fossil records.



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#### S30 - Palaeontology and geological heritage

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# Paleontology and geological heritage through 3D facies distribution models artistically recreated

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The generation of accurate and realistic 3D models of fossils, or even, in a broad sense, entire geomorphic structures where the biofacies distribution are essential to understand the geosedimentary structure itself, can serve to promote the paleontological heritage of a geosite. Here, we show implemented 3D Geomodels artistically recreated of a coral reef (atoll-type), which can be useful to promote and disseminate to general and specialised audience the paleo-scientific and didactic value of a geosite. We chose, the Santa Pola coral reef, one of the most significant geosites of southeastern Spain, since it is included in the Spanish Geosite Inventory (Geological and Mining Institute of Spain) and presents both a significant geo- and paleo-scientific and high didactic and tourism-recreational interest. Therefore, it is the perfect place to develop 3D geosedimentary models, where the geological and paleontological records are intimately connected. Also, we choose this geological structure because the current relief exhibit the original geomorphology of the atoll being possible to recognized the different geomorphic structures of the reef (reef-front with regularly spaced channels and buttresses, reef-slope with fan-shaped Halimeda packstones developed in front of the channels and lagoon and back-reef zone) - representative outcrops of international geoscientific interest can be recognized in several locations. Two different 3D Geomodels of different scales (entire geomorphic structure and best representative outcrop) have been implemented. The joint assessment of the digital elevation model (1 meter, LIDAR 2009, Generalitat Valenciana), the hydrographic network and the observational field data have allowed us to detect the most representative and less eroded outcrop (high potential use). We have been generated a high-resolution 3D model of this outcrop (Structure from Motion photogrammetric technique) based on Remotely Piloted Aircraft System images (Drone Phantom DJI 3 Advanced). After that, we have been produced a small-scale 3D Geomodel (printer Vulcanus Max 40, FDM, PLA material), where the facies distribution have been artistically recreated, highlighting the most significant geosedimentary and facies distribution characteristics of this emblematic fossil atoll coral reef.

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## Nilpena: an Ediacaran field laboratory in South Australia

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Fossils of the Ediacara biota were discovered in 1947-1949, from the Ediacara Mine area in the Flinders Ranges of South Australia, but not fully appreciated until diverse forms were described in 1957-1958. The early methods of field collection from surface slabs, out of context, limited interpretation of their palaeoecological and sedimentary context.

The late discovery of rich fossil deposits on Nilpena Pastoral Lease, in the 1980s, prompted a new approach to field research. By agreement with the landholders, this involved systematic excavation, reassembly, preparation and conservation of serial fossil-bearing sandstone beds on site, under a "no-collection" policy. The only exceptions are specimens collected from talus slopes as type and figured material or for display and lodged in the South Australian Museum Palaeontological Collections.

Unlike almost all other excavated fossil Lagerstäten, Ediacara fossil casts and counterpart moulds, on these silicified and ferruginous sandstones beds, are enhanced with exposure to desert conditions. Consequently, such Ediacaran excavation sites remain in stratigraphic context for future palaeoecological and taphonomic studies. Archiving for ongoing research and public interpretation is achieved using drone or ground based digital photography and replication by non-destructive casting and moulding. Field sites are monitored year-round with electronic security systems.

This approach has currently produced almost 400 sq. m. of serially excavated, inverted and reassembled Ediacaran fossil-bearing seafloor samples from 12 sites. Detailed preparation and description of these fossil-rich samples of benthic Ediacaran communities have been utilized for testing models for multiple projects in the last 15 years. Nilpena is being managed as an effective, outdoor field laboratory for palaeontologists and their graduate students from South Australian Museum, University of California, Riverside, the University of Adelaide and the University of South Australia, and other international research centres, as determined by our palaeontolgical team and the landholders. Nilpena is protected as a National Heritage Listed fossil site. Plans are in place for the linked areas of Nilpena and Ediacara Hills to be upgraded to National Park status, with interpretive facilities.

Interest by the general public is directed to the nearby scenic *Brachina Gorge Geological Trail* entitled: "A corridor through time", within the Ikara-Flinders Ranges National Park. Here visitors can self-guide or take interpretative tours through one of the world's best-preserved and most accessible Cryogenian, Ediacaran and Early Cambrian exposures, including the Global Stratotype Section and Point for the base of the Ediacaran Period, the first GSSP ever defined in the Southern Hemisphere.



<sup>&</sup>lt;sup>°</sup> Speaker

## Permian period geological heritage interpretation at the place of its discovery: Perm Regional Museum and Perm University Framework

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The abstract presents experience of the Permian Period geological heritage interpretation and current research at the place of its discovery – Perm Region in Urals, Russia – which still have outstanding significance in historical geology. Permian Period was discovered here by Scottish geologist Sir Roderick Murchison in 1841. Since 2009 regional government, scientific community and several museums leading by Perm Regional Museum have made a strategic shift in time scale perception through paleontological research and interdisciplinary interpretation. It was not so easy to start the program due to the "negative connotation" of the Permian mass-extinction in the minds of decision-makers, so we've made several step-by-step activities in scientific and museum fields to achieve change in minds. All these activities ultimately aim to shift the perception of the geological heritage interpretation *in situ* and *ex situ*. Firstly, interdisciplinary scientific research projects were developed at Perm Regional Museum and its paleontological branch – Museum of Permian Antiquities. Scientific re-attribution of geological and paleontological collections was followed by excavations and monitoring on four localities, as resumption after a 20-years break; with the support of Paleontological Institute of Russian Academy of Sciences. Excavations are accompanied by a public communication campaign.

Secondly, interdisciplinary educational programs on time scale perception were started, including the only one in Russia Children Paleontological Conference, with more than 500 participants annually, from 7 to 17 years old. Conference is held in close collaboration of Perm Regional Museum and Perm State University. 11 tourist routs of the mobile app "Discover the Permian Period!" across the city of Perm and Perm Region were developed by the museum, involving the network of small museums and localities.

Thirdly, Perm University have started a research project devoted to the identification of the potential of natural objects in terms of creating the Permian Geopark, based on the existing regional network of nature reserved areas of so-called "Main Permian Field" where most significant marine and terrestrial Upper-Permian outcrops are available for studying, representation and eco-education.



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## Conservation monitoring at the Joggins Fossil Cliffs UNESCO World Heritage Site – Ten years later

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The Joggins Fossil Cliffs UNSECO World Heritage Site (Joggins, Nova Scotia, Canada) was inscribed in 2008 for the outstanding universal value of the cliffs' fossil content, which promotes a deeper understanding of the life and times of the Pennsylvanian (Late Carboniferous). Since the inscription and opening of the Joggins Fossil Centre in 2008, there has been increased tourism to the site: approximately 25,000 people visit annually, which is at least three times higher than estimates from years preceding inscription. Effects of increased tourism activity continue to be closely monitored to ensure that the integrity of the property is not compromised.

The Joggins Fossil Institute (JFI) is a not-for-profit, charitable organization that administers the beach at Joggins, provides safety and interpretive services, carries out scientific research, and promotes educational programs that emphasize the importance of conserving natural heritage. JFI and its Scientific Advisory Committee have worked in conjunction with community groups and government agencies to ensure that the value of the cliffs is lasting and appreciated.

A monitoring program was created to report on the conservation status of the property to UNESCO. The program consists of three attributes: maintenance of the integrity of the fossil cliffs; continued strong level of scientific/public interest in the property; and conservation of the fossil record of biodiversity. Several qualitative and quantitative indicators are associated with each attribute and some of these include a review human impacts on the beach and cliffs; number of peer reviewed papers in scientific journals; and number of new specimens added to the collection. Data is gathered via collection, surveillance and surveys. UNESCO has noted that the most significant potential impact on the property is the removal of resources, specifically fossils. Therefore management plans address this concern through educational signage, beach monitoring and social media content. JFI's conservation monitoring program is evolving but has thus far provided useful data for Periodic Reporting to UNESCO.



## Scientific research and Nature Reserves: a win-win partnership, the example of the National Natural Geological Reserve of Haute-Provence, France

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The acquisition of knowledge is fundamental for an optimal and up-to-date management of Nature Reserves, and is part of the responsibilities of reserve managers. The acquired data (studies, inventories) on the sites are useful to the manager to evaluate (1) their scientific and heritage value, (2) their fragilities and protection needs, (3) their additional potential. Researchers can benefit from technical or even financial support, co-supervise student internships, and promote studies through scientific publications and congress. The National Natural Geological Reserve of Haute-Provence (RNNGHP) is known worldwide for its iconic paleontological sites and by the discovery of exceptional fossils. Numerous scientific studies have been initiated by the RNNGHP, such as the Castellane sirenians, the ammonites of the Digne slab, or the Barremian biostratigraphy and ammonites. Other studies are underway, and the recent discovery by the RNNGHP of another exceptional paleontological deposit (Albian plesiosaur and ammonites) has convinced its new administrator, the Departmental Council of the Alpes de Haute-Provence (CD04), to develop actions to improve knowledge and to promote them internationally. The CD04, is the leader of a cross-border European program Interreg V A France-Italy Alcotra: l'@venture géologique, which aims at developing tourism on the geological sites of the Haute-Provence-Mercantour (France) and the Cuneo Alpi Maritime (Italy) areas; this program includes the preparation of sites (accessibility and protection, e-discovery) and studies. The scientific part includes naturalist inventories, investigations for the preservation of palaeontological sites (Digne ammonites slab, La Robine ichthyosaur), 3D data acquisition (follow-up protocols). A Franco-Italian scientific council has been set up to support the project, which will be completed in 2020. The RNNGHP, with its wealth of exceptional paleobiodiversity, welcomes and cosupervises student internships on the theme of paleontology (Master 1 or 2 - for example, in 2017, a 6month M2 internship on Hauterivian biostratigraphy and ammonites, done in partnership with the Rennes 1 University). Other projects are being developed, which include PhDs programs.



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# The southern boundary of *Australopithecus africanus*: are the Buxton-Norlim Limeworks a false boundary for early hominins?

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In 1924 the Taung Child, type specimen for *Australopithecus africanus*, was discovered at the Buxton-Norlim Limeworks, near the town of Taung, South Africa. This discovery set the tone for the next 90+ years of research into human evolution and is the basis for the current field of PalaeoAnthropology. Subsequently multiple specimens of *A. africanus* have been recovered from sites further north in a region known as The Cradle of Humankind and at the site of Makapansgat (the northern limit of the species to date). In over 90 years of on again off again excavations the Taung Child is the only specimen of the species to be recovered from the Buxton- Norlim Limeworks. Research since 2010 has illustrated that the location where the Taung Child was recovered is in actuality not a cave deposit, but a pedogenic landscape deposit; furthermore all indications point to the collector being a large raptor. Here we review the current state of scientific research in comparison to the previous hypotheses and what the affect of large raptor hunting behavior has on where the Taung Child actually comes from.



# The Etches Collection- a new museum of Jurassic marine life in Kimmeridge, Dorset, UK

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In 2017 a new purpose built museum opened in Kimmeridge, Dorset that houses over 2000 fossil specimens collected by Steve Etches. This collection shows that the Kimmeridge Clay contains a very diverse fauna of well preserved fossils many with soft-part preservation. High- lights include an 'octopus', new species of fish, ammonites with aptychi, crocodiles, turtles, crinoids, starfish amongst others. Much of this collection now needs to be documented through scientific publication and these specimens are available for collaborative study with interested parties. A small fraction of the collection is online at http://www.theetchescollection.org/home. The museum is open every day and visiting palaeontologists and students are particularly welcome. Discounted rates are available. Steve Etchesis normally in attendance and will guide you through the collection. If you are interested in any specific fossil group do contact Steve at the Collection for a discussion and to expedite access.

Speaker

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## Managing geoheritage for research, conservation, and education at florissant fossil beds, Colorado, USA: a textbook example for North America

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The conservation, scientific research, and interpretation of paleontological and geologic resources at the Florissant Fossil beds demonstrate a multifaceted approach to effective geoheritage management. Assessment of paleontological assets includes ongoing inventory and monitoring of fossil sites, and surveying Florissant publications and collections at other museums to document taxonomic diversity. Conservation activities involve maintaining fossil collections at museums worldwide and developing new methods to conserve fragile fossiliferous shale and large in situ petrified tree stumps. With support from the University of Colorado, the site actively conducts ongoing scientific research, such as reconstruction of paleoclimate from fossil plants, which in turn provides information for educational media in the exhibit hall of a new visitor center and in website exhibits in which the research of University of Colorado scientists is featured. Recent innovative developments in collaboration with local parks include interpretive panels along a newly designated geologic trail, a geologic trail map and guide, mobile apps to describe geologic features in the field, the design of a geology curriculum for elementary school students, and various website applications that feature information about the fossils at various levels for students, teachers, and the public. International collaboration enables partnerships to share conservation methods with other petrified forest sites worldwide. Pursuit by government agencies for geopark designation for the area has been ongoing, but must garner better support from local communities, who stand to benefit economically from increased interest in the area. Human impacts from the site's geoheritage began during the homesteading era, and more recently include economic benefits for local communities and career-building opportunities for scientists and student interns. Florissant provides the single case study example of geoheritage assessment and management for North America in a new textbook on geoheritage efforts worldwide. The University of Colorado was directly involved in achieving protective status for the site and continues to provide support in achieving these goals by maintaining fossil collections and providing student involvement that has contributed to conservation and research management.



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Speaker

# Saving a piece of the Colombian's geoheritage: Organizing and characterizing the macrofossil collection of the Floresta Formation (Devonian, South America) at the National Pedagogic University

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Paleontological collections constitute an important component of our cultural and geoheritage. These ex-situ natural-history archives are valuable resources for scientific research, formal and non-formal education, tourism, recreation, and provides numerous indirect uses. Despite a renovated interest in nonrenewable geological assets, most paleontological collections in Colombia remain uncatalogued and housed under sub-optimal conditions. In addition, there is a lack of studies measuring the quality of those collections countrywide, thereby making it difficult to objectively assessing their heritage values and to justify the financial support needed for their maintenance and improvement. The macrofossil collection of the Devonian Floresta Formation at the National Pedagogic University (UPN) comprises around 700 specimens collected near the Floresta town in the Boyacá Province. This collection was assembled by undergraduate biology students through several school field trips to the area between 2012 and 2013. However, specimens were largely uncatalogued, stored in sub-optimal materials, and many specimens needed immediate curation to prevent deterioration. Here we present partial results of curation, databasing and general assessments of this paleontological collection. A comparison of the number of specimens in each major zoological group (i.e., brachiopods, mollusks, arthropods, cnidarians and bryozoan) with those reported in the most comprehensive paleontological study of the Floresta Formation indicates that our collection properly captures its macrofauna assemblage (r = 0.99, n = 5, p < 0.005). Furthermore, we found no significant differences in mean body size (shell length) between specimens of selected taxa in both collections (e.g., Acrospirifer olssoni, p = 0.9, iterations = 9999, uniform bootstrap). Although we are still in the early stages of our project, we expect that our curatorial efforts promote its use into scientific and education environments, as well as its appreciation by the members of the university, the academic community and the public in general.



**S30 // Ora** 

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# Natural Reserves for the Study and Protection of Paleobiodiversity in the Provence-Alpes-Côte d'Azur Region (PACA, SE France)

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In the southeastern France, the PACA Region has an exceptional paleobiodiversity. Many of the region's iconic and fragile deposits, coveted by fossil merchants, are now protected in 4 Natural Reserves (RN); by order of creation: Haute-Provence Geological RN (RNGHP), Luberon Geological RN (RNGL), RN of Sainte-Victoire (RNSV) and RN of Daluis (RND). The scientific research developed by the RN made it possible to increase the knowledge of the sites and to discover new remarkable deposits. Paleontological remains are spread over 300 m.y. and are associated with very varied paleoenvironments. For the Paleozoic, the Barles site (RNGHP) offers flora typical of the Limnical Stephanian basins (upper Pennsylvanian); the RND has just discovered Permian fossils previously unknown from the geosite, such as the grasshopper-leaf Permotettigonia gallica. The marine Mesozoic is much diversified: for example the new Albian site of Tartonne (RNGHP) shows exceptional ammonite fauna and vertebrate remains (plesiosaur, ichthyosaurs, selachians). The abundant ammonites have allowed the designation of several stratotypes (Barremian and Bathonian GSSP for the RNGHP, Aptian for the RNGL). The continental Campano-Maastrichtian of the RNSV, formerly known for its exceptional dinosaur egg deposits, is today a rich source of dinosaur bones. The Cenozoic, with highly diversified environments, is represented by the lagerstätten of Luberon, with a very abundant lacustrine ichthyofauna, remains of mammals (artiodactyls, Chiroptera), birds, insects (Diptera, Lepidoptera), vegetal remains (leaves, fruiting, flowers). The RNGL is also famous for its Oligocene mammals and birds footprints tracks. In Haute-Provence, marine Priabonian and Rupelian deposits show abundant invertebrate faunas and sometimes locally remains of mammals (sirenians in Taulanne). The Natural Reserves, formerly regarded as "locked up" areas, are, on the contrary, privileged territories for research. The diversity of their geoheritage contributes to enhance the region's attractiveness for geologypaleontology learning in the field. Scientific collaborations are facilitated by the implementation of technical, financial and scientific means.



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## New discoveries of *Rhabdodon* from the Campanian of the National Natural Reserve of Sainte-Victoire (Southeastern France)

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Historically, palaeontological researches conducted in the Réserve Naturelle nationale de Sainte-Victoire (Bouches-du-Rhône, SE France) has been directed, since 1940's, toward the dinosaurs nests, eggs and eggshells discovered, in droves, in the locality of Grand-Creux (near Roques-Hautes). Unfortunately, this research effort was strongly limited by economic and historical factors and, since 1994, by the protection regulation in effect on this natural geological reserve which is, also, classed as national heritage site. In the framework of the new Management Plan 2016-2020, the first palaontological long-term excavations are conducted in order to better know the local geoheritage and, thus, to improve its protection and conservation.

This study presents the preliminary results of excavations started in 2015 on the historical "eggs" locality of Grand-Creux, by a team composed of agents belonging to the Conseil départemental des Bouches-du-Rhône and the Muséum d'Histoire Naturelle d'Aix-en-Provence. If, without surprises, eggs has been discovered by hundreds, we report here for the first time the discovery of a number of partial skeletons and isolated elements belonging to the ornithopod *Rhabdodon*, to other dinosaurs (dromaeosaurids, abelisaurids and titanosaurs) and tortoises (*Solemys*). On this locality, *Rhabdodon* are represented by, at least, eight fragmentary individuals (small to medium-sized).

These discoveries include unknown elements such as cranial elements, cervical and sacral vertebrae, foreand hindlimbs, pelvic bones allowing a better understanding of Rhabdodon anatomy. This elements reveal an important morphological disparity observed between the two most complete individuals on the basis of pelvic and hindlimbs bones despite of the same dimension. This supports the consideration of a strong sexual dimorphism in *Rhabdodon*.

These new discoveries confirm the presence of a complex combination of features among specimens from the Provence. As such, they establish the basis for the recognition of the different types of dimorphism (interspecific, ontogenetic and, now, sexual) in order to better define the genus *Rhabdodon*, better estimate the French rhabdodontid diversity and improve understanding of the paleobiodiversity on the Ibero-Armorican island during the Late Cretaceous.

IPC 5

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## Two centuries of palaeontological research in the University of Liège, Belgium

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When the University of Liège was founded in 1817, geology and mineralogy were taught by H.-M. Gaëde then by A. Lévy, P.-A. Lesoinne, C.-P. Davreux and M. Gloesener in 1828-834. They all contributed to the building of the fossil collections but palaeontological research started with P.-C. Schmerling who described the Quaternary cave fauna, including the rest a child now considered as the first neanderthalian ever described. Geological research started with the arrival of A. Dumont in 1835 while L.-G. de Koninck was appointed to teach palaeontology in 1846. His expertise on fossil animals led him to produce impressive monographic publications on Belgian material but also on collections sent to him from all over the world. His Faune du Calcaire carbonifère de la Belgique is the most comprehensive study of Carboniferous invertebrates ever published. In 1857 G. Dewalque replaced Dumont and de Koninck on geology and palaeontology chairs and combined both their scientific views to produce very detailed research. His publication on Jurassic fossils is remarkable but his main achievements were his geological map of Belgium and his masterful Prodrome d'une description géologique de la Belgique. In parallel, he gathered a huge collection of fossils. Dewalque progressively delegated his teaching to his collaborators who eventually replaced him. A. Gilkinet was the first palaeobotanists to embrace the theory of evolution and worked on Devonian to Paleocene plants. M. Lohest published several contributions to the Palaeozoic fishes, including a mandible now interpreted as from an Ichthyostega -like tetrapod. J. Fraipont first entered the university as assistant of the biologist E. van Beneden and published papers on marine invertebrates before working on Devonian crinoids. He published several papers on Palaeozoic invertebrates, including the remarkable echinoderms from the Marbre Noir de Denée. Furthermore, Fraipont and Lohest described the human remains from the Spy cave where they demonstrated, for the first time in history, the co-occurrence of a fossil human species, Mousterian lithic industries and Pleistocene megafauna. After the death of J. Fraipont in 1909, palaeontology was taught by his son, C. Fraipont who continued his father's work on palaeoanthropology and created the Palaoeanthropology Doctorate. A. Renier was a palaeobotanist who dedicated his life to understand the palaeontology, and stratigraphy of the coal measures. He initiated the works of S. Leclercq, C. Fraipont's assistant before the war. In 1937 she was appointed as the female Professor in Belgium. Leclercq produced important monographies on Devonian plants and Carboniferous coal balls and was among the first to focus on the biological of her fossils. G. Ubaghs replaced C. Fraipont in 1946 and started to work on early echinoderms. He was charged to write the Echinoderm chapter in the Traité de Paléontologie and the Treatise of Invertebrate Palaeontology.



<sup>&</sup>lt;sup>\*</sup> Speaker

# The national geoheritage inventory in France, from knowledge to outreach

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In 2002, France established by law a "Natural Heritage Inventory" on its entire territory defined as "an inventory of ecological, fauna, flora, geological, mineralogical and paleontological resources". For the first time, geology or "geological sciences" are clearly mentioned and are now fully part of the Environmental Code. The State was committed to making an inventory, which has been officially launched in 2007.

To register a geological site in this inventory and to allow its official dissemination, two steps are required: first, each region proposes a list which is worked out by local partners specialized in geological science. Then each geological site identification is validated by the National Museum of Natural History which is in charge of the national scientific validation of informations. At the end of the process, they are disseminated on the website of the INPN (National Inventory of Natural Heritage, https://inpn.mnhn.fr/accueil/index) which is the national platform data promoting biodiversity and geodiversity in France.

On the eve of the 10th anniversary of its official launch, more than 1100 geosites are now available on the website, and more than 4000 geosites are expected at the end of the year. For each site, more than 100 fields can be filled in, including at least 30 required fields to obtain their validation at the national level. Each geosite is stored in a database with its geographical coordinates. An exchange standard has been defined to facilitate the circulation of the data. This standard corresponds to the INSPIRE convention and it can be downloaded on the internet.

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Speaker

# Urban palaeontology: a key tool for the protection and conservation of the Geoheritage in the Alto Ricaurte Province

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The Alto Ricaurte region of the Eastern Cordillera of Colombia is a remarkable province known for its cultural, historical and geological heritage. Over many years, geologists have recognized this area for the exquisite preservation of its fossils, especially ammonites and marine reptiles, which are found in one of the most complete Lower Cretaceous sequences in the world. One of the primary tasks of the Servicio Geológico Colombiano (SGC) is to safeguard Colombian geological and palaeontological heritage. Therefore, it has started working with the local Alto Ricaurte community on an integrated management plan for the region, currently focused on providing ongoing assistance for the successful implementation of a project focused on geological routes. This is a pioneering initiative in Colombia that promotes social appropriation of geological and heritage knowledge and the achievement of an alternative economic development.

In a first instance, the project attention was focused on the traditional incorporation of ammonites in the buildings together with heritage elements of the urban center of Villa de Leyva. This first geologicalheritage route is directed at a family audience with a scope covering groups of visitors and the local community, where they can understand the importance of the fossils under the following guidelines: ammonites as part of the identity of the municipality; the scientific value of ammonites; the encouragement of good practice for the paleontological heritage conservation; and fossils as a finite resource.

For the construction of this route, the heritage interest was assessed taking into account 210 possible sites of interest, and those where the fossils have been incorporated into historical architecture were selected based of the three following aspects: their aesthetic appearance; their conservation status; and the proximity to other points of cultural and paleontological interest. After considering the points with the highest scores, those which could be joined into main circuit, and two secondary walks, were selected so the audience can understand the paleontological ideas, the provenance of the ammonites included in the buildings, and the mode of life of living organism. Furthermore, considering that fossils are irreplaceable and significant source of palaeobiological information, the route aims to raise awareness about the loss of scientific value, which derives from the extraction of fossils, from the rocks that contained them.



<sup>&</sup>lt;sup>°</sup> Speaker

# Colombian geological and paleontological heritage geoconservation

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As part of a national strategy for geoconservation, the Colombian Geological Survey (SGC) is currently developing a National Inventory of Geological and Paleontological Heritage. A systematic inventory has been selected, based on the establishment of a geological framework prior to identification of sites of geological importance. This methodology allows an assessment of the geodiversity of the country. In addition, it constitutes an innovative selection strategy in Latin America, where inventories have not yet been carried out for this purpose.

The methodology for the inventory consists of two phases. The first is based on a bibliographic compilation related to the study area, and consultation with experts in the geosciences and with research experience in the region. As a result, a preliminary list of sites of national and/or international geological importance has been generated. The second phase comprises on-site assessment of their scientific, educational and tourism value; the assessment is registered on a form which contains information related to its identification, characterization, as well as its potential use for education, tourism and/or recreation, and degradation risk. After this quantitative assessment, the sites with a scientific value above 3.3 (out of 10) will be included in the National Inventory and will be designated as 'geotopes'. The methodology of inventory is a fundamental tool not only for the identification of geotopes (of national importance) and geosites (of international importance), but also for comparison between sites, thus allowing for both preservation and use.

The project began in 2016 in the geological province of the Eastern Cordillera, in the Department of Boyacá, where 99 sites of national geological importance have been identified. Of the geotopes identified to date, most are of stratigraphic interest (39%). The others are of geological interest related to paleontology (17%), geomorphology (16%), petrology (10%), mineralogy (6%), tectonics (5%), geochemistry (4%) and volcanology (3%). Of these 99 sites, at least three have an international scientific importance, and are being considered as possible geosites and thus worthy of recognition as global natural heritage for the whole of humanity. By the end of 2018, it is expected the SGC will have an inventory covering two other departments in Colombia, as well as an online database to visualize the inventory on the SGC website.



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## The paleontological heritage at the heart of the European cross border intereg V-A France-Italy Alcotra: the geological @dventure

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The departmental council of the Alpes de Haute-Provence, in charge of the Natural Geological Reserve of Haute-Provence (RNGHP), the largest in Europe, is leading the geological @dventure project which is supported by the European program Interreg V-A France-Italy ALCOTRA. The geological @dventure includes, on the French side, the department of the Alpes de Haute-Provence and, on the neighbouring Italian side, the sector of the Cuneo Province. Part of the area of the RNGHP is labelled as UNESCO Geopark.

It is intended to create a new geo-touristic destination. The project aims at developing, enhance and link several remarkable geosites, which are representative of the history of the Alps. This will allow making scientific culture accessible to as many people as possible, developing experiential tourism together with a fun and educational e-tour. Paleontology is, with the history of landscapes, at the heart of the @dventure. The remarkable paleontological sites of the RNGHP, such as the ammonite slab at Digne, will benefit from new studies to help monitoring and preserving them. Some studies have already been carried out, such as searching for voids under fossil rich outcrops using radar detection, or running a Digital Terrain Model (DTM) to assess fracturing, deformation and current stability of the outcrop. Future studies (mineralogy, geochemistry) will help to better understand and solve the weathering problems. These data will be used to set up the conservation and site development project. The results will then be used as a support for the mediation. The @dventure will also propose the discovery of world-famous sites: the fold of the Vélodrome and its beaches with bird footsteps, the site of the sirenians of Castellane, etc. On the Italian side, the Federico Sacco Foundation aims to make an inventory of the collection of this famous naturalist of the nineteenth-twentieth century, and who is one of the pioneers of alpine geotourism. F. Sacco, best known for his work on the history and the understanding of the Alps, was also interested in paleontology and he made many publications (Pliocene mollusks of the Piedmont, foraminifers, ichnofossils ... and on some vertebrates such as rhinoceros, crocodiles). The F. Sacco collection will soon be put on display in Fossano, his hometown. A French-Italian scientific council has been set up to support the @dventure and guarantee all the rigor necessary for quality mediation.

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## Main marine outcrops of interest for the paleontological heritage in the Iberian Peninsula and the Balearic Islands

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The main marine outcrops of interest for the paleontological heritage located in the Iberian Peninsula and in the Balearic Islands are described. These outcrops are relevant mainly for different reasons, some for having served to define stratotypes of stages or boundaries, others for their excellent fossil record that has allowed to define new species; as well as others for its good lithological development that has allowed high resolution studies on different events of extinction and evolution. Many of these outcrops have been protected for their great heritage interest. The most relevant sections of the Paleozoic are: Murero, Rio Luna, Arnao, Cabañeros, Checa, Sierra Norte de sevilla, Demués y Las Llacerías. The most relevant sections of the Mesozoic are: Sierra de Lúgar, Agua Larga, Cúber, Fuentelsaz, Escaño, Cañada Luenga, Rio Argos, Organyà y Olazagutia. The most relevant sections of the Cenozoic are: Caravaca, Zumaya, Ilerdiense, Arguis, Gorrondatxe, Caldera Fountain, Navazuelo, Sorbas-Ńijar, Casa del Pino, Estepona-San Pedro and Andaluciense.



Speaker

### Paleontological heritage and tourism: interpretation of patrimony in Brazilian museums of natural history

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This study investigated how the patrimonial interpretation happens in the Brazilian natural history museums with paleontological expositions under a touristic bias. The analysis fallows the interpretations principles purposed by Tilden (1957) and Beck and Cable (1998). This study aims to understand the interpretative medias available to communicate with the public in the museums. The methodology has a qualitative bias and are formed by exploratory investigation. Using documental/bibliographical search and interviews with subject experts and natural history managers. A total of eleven Brazilian museums from five States were analyzed. In each the interpretative medias were analyzed and the main public identified.. It was verified that, under many aspects, the Brazilian museums are even with the interpretations principles. This is mainly due the fact that Brazilian museums prioritize the development of responsible attitudes regarding the collection. This fallows the main museum interpretation objective, the patrimonial preservation. Regarding the personal medias, it is verified that all the museums had mediators to help the exposition interpretation. Besides that, the museums also offer thematic games, play activities, demonstrations, lectures and round tables. Regarding the impersonal media, the museums had many options in its expositions. Those are mainly visual and graphical communications, with panels, labels, subtitles, infographics. The icnographical material are composed by graphics, drawings, tridimensional models and dioramas. Few museums had digital media in its expositions. In general, the Brazilian museums of natural history significantly diffuse the paleontological patrimony for a public mainly composed by students and researchers, but with a low technology resources, far from advanced technological resource. Aiming the museums made a more attractive exposition to the general public and attract tourist, it is suggested the elaboration of an interpretative plan. Considering that Brazil have an expressive paleontological potential, not yet considered a touristic activity, new studies faced to this patrimony is recommended, aiming new discussions and suggestions of better interpretation practices faced to tourism development.

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# Rudists from the Moulin de la Roque section and other Santonian outcrops of the La Cadière-d'Azur Formation (Le Beausset basin, SE France) housed in the MCNB palaeontological collections

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Palaeontological collections of the Natural Sciences Museum of Barcelona (MCNB) preserve rudist bivalve fossils from several classical fossil localities from the Cretaceous of SE France. Among all the French localities represented in the collections, the specimens from Le Beausset basin deserve special consideration for their well preservation, quantity, and diversity. In the present work we have studied the rudist faunas belonging to the La Cadière-d'Azur Formation cropping out in the municipalities of La Cadièred'Azur, Le Castellet and Le Beausset.

The well-known La Cadière-d'Azur Formation forms a carbonated sedimentary lenticular body rich in rudist banks that was developed in a perideltaic environment of early Santonian age (Late Cretaceous). This formation extends from NE to SW forming an elongated strip of about 6 km in the central part of the Le Beausset basin. The rudist association recognized from our material of the Moulin de la Roque section (Le Castellet) consists of Hippurites matheroni, Hippurites socialis, Hippurites sublaevis, Hippuritella toucasi, Bournonia excavata, Praeradiolites caderensis, Praeradiolites toucasi, Praeradiolites cf. sinuatus, Radiolites galloprovincialis, and Radiolites squamosus. Among all these species represented, H. socialis, H. toucasi and R. galloprovincialis are the most abundant and the main bioconstructing organisms. Bournonia excavata and H. matheroni are also abundant, whereas the other species are poorly represented. The rudist assemblages from the La Cadière-d'Azur and Le Beausset localities are richer in terms of diversity, containing other species such as Hippuritella maestrei, Pseudovaccinites beaussetensis, Pseudovaccinites galloprovincialis, Biradiolites acuticostatus, and Biradiolites fissicostatus. Thus, the MCNB palaeontological collections hold a well representation of the rudist species diversity appearing in the classical fossil localities from Le Beausset basin. The detailed study of these specimens will permit to update the description of some species as well as contribute to a better characterisation of the sites from a stratigraphical and palaeontological point of view.



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# The micropalaeontological collections of the Museu de Ciències Naturals de Barcelona (MCNB): a tool for learning from the past

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The rich scientific palaeontological collections housed in many public and private institutions are an incredible source of information of past times. The evolution of Earth is understood by direct observation of current dynamic processes and from the study of all the geological and palaeontological elements contained in present and future collections. The natural sciences collections make uncountable contributions to society, not only in terms of reconstructing the Earth history, but also in present and future topics related to agriculture, biological invasions, global climate changes, etc. Each specimen composing the collections can be considered as a potential source of information; hence they should be arranged and conserved for long time preservation. In the reconstruction of past climate crisis, in particular, the analysis of the evolution of marine microfossil communities is of special interest as they can be extremely sensitive to local, regional and global environmental changes. The micropalaeontological collections play a special role in this scenario, not only in the analysis of the impact of these changes in past ecosystems, but also in the understanding of the meaning of the fluctuations of marine biodiversity. As well as other important microfossil groups, foraminifera are used as bioindicators to evaluate the modifications occurred in the marine water column. The larger foraminifers K-strategists, for instance, living under a shallow-water column conditions were extremely delicate and sensitive to palaeoenvironmental changes. The MCNB scientific micropalaeontological collections preserve an extensive register of this type of foraminifera of different palaeogeographical areas. In particular, the museum houses collections of material collected from both sides of the Mediterranean, mainly from the Cretaceous of the Iberian Peninsula and the Middle East. The specimens kept in these collections are witnesses of some key global changes occurred in that period of the Earth history, such as the Cenomanian-Turonian and the Cretaceous-Paleogene crisis. In some particular cases, the register kept is so complete that permit to observe other local or regional changes, such as the intra-Cenomanian biotic crisis observed in the shallow-water platforms as a consequence of sea-level fluctuations.

The scientific micropalaeontological collection of the MCNB can be considered of reference for research community, permitting to develop multidisciplinary studies that contribute to understand the nature of marine ecosystems and its evolution.



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# S31 - Palaeobiodiversity and evolutionary history of vertebrates in Africa

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# Early burst or gradual divergence? – Patterns of body size evolution in fossil and extant Macroscelidea (Afrotheria)

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Macroscelideans or sengis are rapidly moving, monogamous, and insectivorous afrotherians. Extant species exhibit divergence in behavior, morphology, and body size corresponding to the two extant subfamilies, Macroscelidinae and Rhynchocyoninae. It was suggested that the early branching event between both subfamilies accounts for most of the disparity among species rather than later, gradual divergence, thus implying an 'early burst'-like evolution of macroscelideans. However like other afrotherian lineages, extant sengis represent only the relict remains of an ancient pan-African diversity. The fossil record reveals a considerable diversity in terms of body size and foraging modes in macroscelidean evolution. Thus, evolutionary patterns might be more complex than extant disparity suggests. Although most fossils are fragmentary, body size can be approximated even from sparse remains and is a good predictor of a large number of ecological and physiological traits. Here, phylogenetic comparative methods were applied on the body size data of more than 40 macroscelidean species covering all extant and extinct subfamilies in a Bayesian Markov Chain Monte Carlo framework. The results actually confirm an 'early burst'-like evolution of body size. However, the burst is not driven by the Oligocene-Miocene divergence between extant subfamilies alone but also by the Eocene-Oligocene diversification of stem macroscelideans. The simulations additionally uncovered a decrease in disparity rates with a drop after the early Miocene. Yet, there is a significant mid-Miocene shift to a lower body size optimum in the stem line of the Macroscelidinae coupled with a decrease in the evolutionary rate. As microhabitat usage and body size are correlated in extant species, a broad ecological diversity can thus be inferred in early sengi history. Nevertheless, an adaptive radiation is not supported by the combined pattern of lineage and trait diversification. Overall, these findings highlight the importance of fossil evidences for the understanding of evolutionary patterns in extant afrotherians.



S31 // Oral

Speaker

# The origin of hair and whiskers as inferred from palaeoneurology of South African non-mammalian Synapsida

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The evolution of hair in mammals is notoriously difficult to study since keratinous structures do not readily fossilize. In 1931, Watson hypothesized that the presence of numerous small foramina for the trigeminal nerve (CNV) on the snout of Permo-Triassic non-mammalian synapsids (NMS) were the insertion points of whiskers. Since then, this hypothesis has been widely accepted and these foramina are usually considered as important landmarks to infer the evolution of hair. Using CT-scan and virtual 3D palaeoneurology, we reconstructed the osseous canal for the CNV that connects these foramina in a large variety of NMS species (~70). This study shows that the pattern of ramification of the branches of the CNV canal is common to most NMS and can be homologized with that of the actual nerve in modern mammals. However, the ramified anatomy of the CNV canal inside the bone and the resulting presence of foramina on the snout in most NMS are very similar to that in reptiles. This shows that the trigeminal nerve was completely enclosed in a bony canal that limited movement and thus prevented whisking in NMS, which makes Watson's hypothesis unlikely. A more probable hypothesis is that the foramina were for dermic sensory receptors, as in modern reptiles. In contrast, modern mammals have an infraorbital foramen for the infra-orbital branch of the CNV to leave the maxilla, ramify in the soft tissue of the face and innervate the whiskers. This gives this nerve more flexibility and enables it to accommodate whisking movements. Among NMS, only those belonging to the clade Probainognathia (which also comprises mammals) show evidence of a mammal-like infraorbital foramen. This suggests that the snout of probainognathians was equipped to support motile and tactile vibrissae and incidentally suggests that the genetic toolkit to produce hair was also available for the rest of their body to be covered with fur. Coincidentally, the probainognathians also lost the parietal foramen and developed an enlarged cerebellum. Both characters are pleiotropically linked to the maintenance of body hair coverage since they are all controlled by the same homeogene, Msx2, in mice. This gives an overall consistent signal indicating that hair was present in the last common ancestor of probainognathian cynodonts some 246 mya.



<sup>&</sup>lt;sup>°</sup> Speaker

## Deciphering the drivers of Plio-Pleistocene evolution in an African rift valley: a plea for focusing research efforts on paleobiotic interactions

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The Turkana Depression is renowned for its rich fossil record of Miocene to Pleistocene vertebrate evolution, including abundant hominid osteological and behavioral remains. In the northern Turkana graben, the Shungura Formation deposited in the Lower Omo subsidence area and accumulated almost continuously between 3.6 Ma and ca. 1 Ma the currently largest vertebrate record known in eastern Africa (nearly 56,000 specimens). This unique record at local scale of a faunal community evolutionary history and other similar records from other formations of the Turkana Depression have been abundantly used to extrapolate the mechanisms of African vertebrate evolution during the late Neogene, including its main drivers. In this framework, tentative correlations have been established between the Turkana evolutionary record on the one hand, global climate variations and, to a lesser extent, regional tectonic dynamics on the other hand. Climate is generally cited as the main driver of human (and other vertebrate) evolution, but without fully evidencing a direct effect of climate modifications on vertebrates. Yet, some evolutionary histories recorded in the Shungura Formation as well as at a more regional scale suggest that biotic interactions played a significant part in driving biodiversity changes throughout the Plio-Pleistocene. Given the intricacy of such interactions, tracking them down in a fossil record is all but an easy task. The Shungura fossil record constitutes a promising playground for developing a vanguard research on biotic interactions during the Plio-Pleistocene at a local scale, thanks that its chronologically well-constrained sequence and to the on-going efforts to directly elucidate the paleoecology of its major vertebrate taxa.



<sup>&</sup>lt;sup>\*</sup> Speaker

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## Titanosaur life history: insights from *Rapetosaurus krausei* (Maevarano Formation, Madagascar)

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Titanosaurian sauropods diversified across all continents and obtained a peak diversity of more than 50 known species by the end of the Cretaceous. In spite of this cosmopolitan distribution, a limited fossil record has left critical aspects of titanosaur anatomy, phylogeny, and paleobiology poorly understood. *Rapetosaurus krausei* from the Maastrichtian Maevarano Formation of Madagascar is among the most complete titanosaurs yet discovered. A wealth of wellpreserved cranial and postcranial elements has proven pivotal to ongoing revisions of titanosaur anatomy and phylogeny. Skeletal material from many *Rapetosaurus* individuals spanning neonatal to adult ontogenetic stages yields a rich dataset with which to test hypotheses relating to titanosaur growth, development, and life history.

We analyzed *Rapetosaurus* histology using a growth series of forelimb, hind limb, and girdle elements representing different ontogenetic stages, including samples from a hatchling (femur length = 19.5 cm) and the largest *Rapetosaurus* known (femur length = 143 cm). *Rapetosaurus* shares highly vascularized primary fibrolamellar bone, compact primary osteons, and an early occurrence of secondary remodeling with other large-bodied sauropod dinosaurs, including the titanosaurs *Alamosaurus, Lirainosaurus,* and *Phuwiangosaurus*. Interestingly, the largest known *Rapetosaurus* is still actively growing, while some much smaller individuals record a pause in primary osteogenesis.

Several aspects of *Rapetosaurus* bone tissue are distinctive. First, in individuals less than 40% adult size, osteoclastic resorption has eroded vacuous cavities within mid-cortical primary fibrolamellar bone, which are later infilled with irregular osteons that are significantly larger than normal osteons. At similarly small juvenile ontogenetic stages, peripheral growth marks accompany a shift to slower-growing, poorly vascularized lamellar primary bone that together indicate a temporary cessation in bone growth. In individuals larger than 50% adult size, more rapid primary growth resumes, and early ontogeny peripheral growth marks and irregular osteons are replaced by overlapping generations of normal secondary osteons. These unusual signals, particularly when combined with data on osteoderm anatomy, vertebral pathology, sedimentology, and taphonomy, are consistent with an osteological response to chronic resource challenges posed by the Maevarano Formation paleoenvironment.



Speaker

# New perspectives on the homogeneity of the *Tapinocephalus* Assemblage Zone of the Main Karoo Basin, South Africa

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The tetrapod assemblage zones of the Main Karoo Basin are fundamental to biostratigraphic correlation across southern Gondwana during the Guadalupian to the Middle Triassic. Since 1995, eight assemblage zones have been officially recognized, but continued fieldwork over the intervening years has shown that several of these biozones are not homogeneous and that subdivisions can be recognized. Attempts to subdivide the mid-Permian (Guadalupian) *Tapinocephalus* Assemblage Zone (AZ) have been based on clade relative abundances as well as the sequential first appearance of dicynodont genera, but work has been slow compared to some younger biozones. However, understanding the degree of homogeneity within the stratigraphically-thick *Tapinocephalus* AZ is of increasing value, because it represents a period of several millions years preceding the Capitanian mass extinction among tetrapods. Our work has shown that fossils attributed to the *Tapinocephalus* AZ overwhelmingly occur in the upper part of the biozone and that its lower portion is poorly sampled. Over the last three years we have conducted fieldwork to collect the lower part of the *Tapinocephalus* AZ and determined that it is a distinct from the upper part of the biozone, primarily in its constituent dicynodont taxa. This confirms that the *Tapinocephalus* AZ is not homogeneous and that the ecosystem was dynamic, if comparatively stable, during much of the Capitanian.



Speaker

# Fish-eating habits in spinosaurs are shaped by heterochrony and bone microstructure

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*Spinosaurus aegyptiacus* is one of the most enigmatic dinosaurs ever found. The recent description of a neotype specimen provided new insights into the anatomy and ecology of this bizarre giant theropod. Here, we present novel research on the osteohistology and anatomy of *Spinosaurus*. Several postcranial elements belonging to the neotype were sectioned: a neural spine, dorsal ribs, the fibula and the femur. All the sampled elements show increased bone compactness in comparison to other theropod dinosaurs.

Bone compactness analyses were performed to compare ecological adaptations in *Spinosaurus* and related megalosauroids to those in extant taxa. Using a broad dataset of 130 diapsid taxa, including sauropterygians, extant crocodilians, non-avian dinosaurs and extant birds, the compactness of long bones was used as a proxy for ecological inference in extant and extinct taxa. Long bone compactness was quantified using Bone Profiler. Phylogenetic regression tests between compactness against size and gait supports bone density as a good proxy for ecological proxy in Archosauria. Ontogeny has a relevant influence in determining ecological niches, suggesting that only adult individuals should be included in the studies. Paleoecological proferved in other clades, bone compactness preceeds anatomical adaptations to new ecological niches in archosaurs.

Finally, the role of heterochrony in patterning the anatomical characteristics present in spinosaurids was examined in the light of osteohistological data. It has previously been suggested that ichthyosaurs and tanystropheids underwent paedomorphic events through their progressive adaptation to aquatic lifestyles. We performed 2D geometric morphometrics on non-avian theropod skulls using 45 landmarks. We found a peramorphic trend in Megalosauroidea shaping the crocodile-mimic skull morphology adapted for fish-eating, contrary to other clades of tetrapods with secondary adaptations for an aquatic or semiaquatic lifestyle.



Speaker

# A primitive adapid (Mammalia, Primates) in the Lutetian of Namibia and primate dispersals from Asia to Africa

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Continuous field work in the locality of Black Crow led to the recovery of a small primate mandible bearing P/3 to M/3, as well as an isolated P/4. The lower molars show typical adapid characters such as a shelf-like paralophid descending ventrolingually, high and pointed crests, a broad talonid basin posteriorly bordered by a high transverse postcristid. In contrast, its premolars are anteroposteriorly short and simple, P/4 having a differentiated metaconid but only an incipient talonid basin and P/3 being unicuspid. Such primitive traits suggest a close relationship with the Middle Eocene Adapoides from Shanghuang, China, and with Microadapis from Egerkingen in Europe (MP 14, close to the Lutetian-Bartonian boundary). The new material belongs to a new genus clearly different from the latter two. By comparison with the known North African faunas and their stem-lemuriforms, the new species documents a strong intra-African provincialism. Compared with the late Eocene Fayum adapids Aframonius and Afradapis, it appears much smaller and much more primitive, suggesting a relatively long endemic evolution of African adapids, unsuspected until now. An overall comparison with Adapoides and Microadapis is hampered by the fragmentary nature of the three species. However, the morphological differences observed between them suggest that they belong to three distinct lineages. The marked adapid affinities of the new genus prompted us to reappraise Notnamaia from the same locality, a genus which was poorly understood until now. An adapid affinity appears to be the best hypothesis for Notnamaia, the upper molars of which are quite distinct from those of Adapoides and from the only upper molar attributed to Microadapis. This evidence reinforces the distinctness of early African adapids, suggesting an earlier (late Early or early Middle Eocene) dispersal of the group from Eurasia to Africa than hitherto thought possible. Such a scenario provides indirect fuel for the ongoing debate about the dispersal from Asia to Africa of the first African anthropoid, stem-anthropoid or tarsiiform. For the latter as for the earliest strepsirrhine, the first dispersals from Asia to Africa are poorly understood. The new Namibian adapid adds a crucial piece of evidence.



S31 // Oral

<sup>&</sup>lt;sup>'</sup> Speaker

### New data on the evolution of Eocene proboscideans in Sub-Saharian Western Africa

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Africa seems to have played a pivotal role in the evolution of early placental mammals, yet the Sub-Saharian Paleogene fossil record is very limited. Relatively little paleontological work has been carried out in Sub-Saharian Africa. The potential to discover Eocene mammals in Senegal was demonstrated over half a century ago, when a right upper molar was found in the cuttings of a 20 meter deep well in the village of M'Bodione Dadere (North of Kaolack). This fragment of tooth, Lutetian in age, was then attributed to the genus Moeritherium. We re-examined this molar and find that it appears sufficiently distinct from other early proboscideans to be considered a new taxon. It differs from *Eritherium* by being of larger size, having a wrinkled enamel, lacking centrocrista, and showing development of a strong lingual cingulum. Its morphology also differs from Phosphatherium, in that it has a pronounced bunodonty, and from Moeritherium, Phiomia and Palaeomastodon by being of smaller size, having a more bunodont dental pattern, a relative lower crown, retaining a mesostyle, and containing a protocone and hypocone located in more labial positions. We propose the Senegalese molar displays an intermediate morphology between early bunodont incipiently bilophodont taxa (Eritherium and Khamsaconus) and Moeritherium. Such a hypothesis would not only strengthen the evidence that Moeritherium holds a basal position within proboscideans, but could also support the assumption that the Moeritherium 'lineage' originates from the middle Eocene. In parallel to this exciting discovery, recent exploration in the Lutetian deposits from phosphate basins of Togo revealed an untapped fossil resource, including a complete proboscidean lower molar. The Togolese tooth is bunodont and bilophodont, but also has an incipient third lophid and a posterior crescentoid. Its proportions and molar pattern are similar to the Oligocene genus Palaeomastodon, which is one of the earliest elephantiforms. If confirmed, such a result would push back the origin of elephantiforms by about ten million years. The continued exploration of fossil-bearing horizons in Senegal and Togo has the potential to greatly improve our knowledge on the origin and evolution of early proboscideans and associated faunas.



### The carnivore guild of Bolt's Farm, South Africa: Carnivore biodiversity in the Plio-Pleistocene

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The fossil locality of Bolt's Farm is a system of numerous fossil deposits spanning the Plio-Pleistocene. The carnivore guild represented from these loci range from small bodied carnivores to an as yet unidentified giant felid. Here we examine the identified carnivore species from the various fossil deposits to date and discuss biodiversity and possible palaeoecological implications for each deposit. Current research has focused on 12 fossil deposits, 11 of which have identified carnivore material; Aves Cave I, Aves Cave II, Brad Pit A, Brad Pit B, Bridge Cave, Cobra Cave, Femur Dump, Garage Ravine Cave, Milo A, Waypoint and X Cave. Families represented include Mustelidae, Herpestidae, Canidae, Hyaenidae and Felidae. Felidae is further broken down to Machairondontinae, Felis and Panthera. Hyaenidae is comprised of Crocuta, Proteles, Hyaenid and Chasmaporthetes. Canidae has material assigned to Canis and Vulpes. While some deposits have thus far yielded few carnivore fossils, such as Garage Ravine Cave (1), Waypoint (1), Aves Cave II (2), Cobra Cave (2) and Brad Pit B (5). Other deposits have fewer than 100 carnivore remains (Femur Dump (31), Aves Cave I (81), Brad Pit A (53) and X Cave (25)). Carnivores are only identified at Milo B by the presence of a hyaenid coprolite. The Bridge Cave deposit has over 300 carnivore specimens that are dominated by material from large bodied felids. Similarly the material from Femur Dump is dominated by material from Dinofelis barlowi. Aves Cave I has the most diverse set of carnivore taxa to date. Compared to many other fossil deposits within the Cradle of Humankind, the deposits at Bolt's Farm have a higher number of Panthera fossils when compared to other carnivore species. Here we look at the identified remains to date and compare them with the carnivore assemblages of other fossil deposits in the region.



<sup>&</sup>lt;sup>°</sup> Speaker

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# New data on the microvertebrate fauna from the Jurassic-Cretaceous site of Ksar Metlili (Anoual Syncline, Eastern Morocco): significance for African and Gondwanan vertebrate evolution

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The Jurassic-Cretaceous transition is a critical period for continental vertebrate evolution. Some major modern terrestrial vertebrate groups (e.g., lissamphibians, squamates, mammals and birds) and angiosperms emerged at this time, in the key palaeogeographic context of Pangea fragmentation and early evolution of Gondwanan and Laurasian faunas, which is accompanied by an abrupt cooling and a global drop in sea level.

This work aims at improving our very poor knowledge of Gondwanan and especially African faunal palaeobiodiversity and evolution at this time, with the study of the two successive Moroccan microvertebrate faunas of Ksar Metlili (Berriasian, Early Cretaceous?) and Guelb el Ahmar (Bathonian, Middle Jurassic) from the Anoual Syncline. These faunas are among the richest known for the Mesozoic of the whole Gondwana. Morocco is a key region for this issue because of its geographical position on the African shores of the Tethys, well placed to record faunal interchanges between Laurasia and Gondwana. Furthermore, the diverse faunal associations preserved in the Anoual microvertebrate sites provide a better picture of African and Gondwanan palaeoecosystems, including some uncommon species rarely found in macroremains sites.

Here we focus on the Ksar Metlili site, which produced more than 24,500 microvertebrate remains representing 28 species of 8 main groups, from selachians to mammals, that were identified and studied using comparative anatomy, taxonomic and statistical approaches. It includes remarkable taxa: the oldest therian mammals from Gondwana (and one of the richest Mesozoic mammal assemblages), some of the last known non-mammalian cynodonts, a basal ornithopod, a possibly freshwater teleosaurid crocodylomorph, and some of the scarce choristoderan reptiles and albanerpetontid amphibians known from Gondwana. A large scale faunal comparative study of Ksar Metlili with some closely aged sites, such as Guimarota (Kimmeridgian, Late Jurassic, Portugal), evidences noticeable shared taxa with Laurasia, resulting from either trans-Tethyan dispersals and/or a vicariant Pangean inheritage, but few Gondwana affinities. It suggests peculiar palaeobiogeographical relations of North Africa within Gondwana at the Jurassic-Cretaceous transition. Finally, the faunal similarities between Guelb el Ahmar and Ksar Metlili question an Early Cretaceous age for the latter, and instead advocate a more likely Jurassic, and at least a Late Jurassic age.



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# The first Neogene terrestrial fauna from Senegal: a window on Pliocene western Africa history

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The Pliocene of Africa is well-documented and intensively surveyed in the eastern and southern parts of the continent. However, this time period is poorly documented in northern and central Africa and virtually unknown from western Africa. The presence of important Quaternary sand deposits, the lack of exploitable outcrops, and major weathering events make Pliocene fossil discoveries exceptional in western Africa. Recent surveys led by the members of the PaleoSen project discovered new vertebrate fossils in the TÁ'iba phosphate quarry in Senegal. Most of these remains correspond to marine vertebrates retrieved from Lutetian limestone deposits interbedded with phosphate ore. Other remains, however, were found in more recent deposits located between the ore and its sand cover, and constitute an original Pliocene fauna. Here, we describe an unparalleled fossil collection from Senegal that enables us to establish the first Pliocene faunal list of Sub-Saharan West Africa. This locality has yielded few complete remains but at least ten mammalian species were recognized, including proboscideans, primates, bovids, giraffids, suids, and carnivores. The fossiliferous locality is younger than the last weathering event (estimated between 3.4-2.9 Ma) and we propose an age older than Hadar (Ethiopia) and younger than Langbaanweg (South Africa, close to 5Ma) according to biochronological evidence. Even if taxonomic attributions are made difficult by the nature of the remains, numerous similarities are highlighted with Aramis (Ethiopia) and Kanapoi (Kenya), both localities estimated around 4 and 4.4 Ma. The TÁ'iba locality undoubtedly opens a new window on a very important time interval in Africa related to hominine history. The specific richness of the locality, the presence of primates and the abundance of carnivorans are positive indicators for future discoveries.



Speaker

# Biogeographic and climatic implications of Early Pliocene fossil frogs from Langebaanweg, west coast, South Africa

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Fossil frogs from southern African sites have frequently remained unanalyzed due to a dearth in taxonomic expertise and comparative material from the region. This despite the fact that due to their biology, breeding habits, and sensitivity to fluctuations in moisture levels and temperature, frogs are excellent proxies for rainfall patterns over time. The dearth of skeletal comparative material led to an initiative to build up a reference collection for fossil frog bones, using computed tomography (CT) scans of almost all modern southern African frog genera. This has provided new comparative information which has led to the identification of fossil frog taxa from several South African archaeological and palaeontological sites, and has provided important new palaeoenvironmental data on the amount, and seasonality, of rainfall.

At the palaeontological site of Langebaanweg (5.1 Mya), found on the currently arid west coast of South Africa (approximately 100 mm of winter rainfall is received annually), a large number of frog taxa which includes eight frog families (Hyperoliidae, Brevicipitidae, Pyxicephalidae, Pipidae, Heleophrynidae, Bufonidae, Microhylidae and Ptychadenidae), indicates that the current aridity, previously assumed to have begun prior to the Early Pliocene, had not yet occurred. The diversity of the fossil community is put in perspective when one considers that frog species richness on the west coast is low today (1-10 species from four families). Identification of the Langebaanweg frogs is still underway, but the minimum number of species present is 17. There are currently only six frog families in the entire Cape region, and 12 in the whole of South Africa. The presence of two *Ptychadena* taxa, as well as *Kassina*, provide evidence for a summer rainfall regime during the Early Pliocene, a period during which it was previously assumed that the current winter rainfall regime was already in place. It also indicates that the distribution of genera such as *Ptychadena* (Family Ptychadenidae), and *Phrynomantis* (Family Microhylidae), have changed extensively since the Early Pliocene. Significantly, no biogeographic evidence remains of the once rich and diverse frog population which lived on the west coast of South Africa some 5.1 Mya – this issues a note of caution for using current distributions of taxa for past climatic modelling.



Speaker

## A bird's eye view of an evolving landscape at Olduvai Gorge, Tanzania

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Fossil bird data are used here to better understand the paleo environmental context of hominin evolution and behavior at Olduvai Gorge, Tanzania. These fossils come from excavations made by the Olduvai Landscape Paleoanthropology and Archaeology Project (OLAPP), the Geochronology and Archaeology Project (OGAP), and from the original (c. 1970's) Leakey expeditions. The Olduvai birds come from sever al temporally distinct and in cases, geospatially overlapping, paleolandscapes dating from approximately 1.9 to 1.4Ma. Their largely extant taxonomic (genera, some species) composition facilitates the use of modern analogue behavioral and ecological profiles for attributing their ecologies. Taphonomic and quantitative ecological methods and supportive data from other environmental proxies reinforce resulting environmental reconstructions. The oldest deposits (Lower Bed I) are reconstructed as wet with a high lake stand that eventually inundated the landscape. Subsequent lake regressions helped shape the Middle Bed I landscape, producing greater landscape heterogeneity and a more ecologically diverse avifauna. Upper Bed I reflects a shift away from wetland and water taxa towards birds of mudflats and drier habitats. A series of lake fluctuations scoured the landscape and provided greater heterogeneity and niche space for what was a taxonomically and environmentally diverse avifauna in Middle Bed I. A period of aridity later in Bed I resulted in low diversity and few avifaunal remains but a combination of lake transgression and tectonic - induced topographic heterogeneity allowed for the establishment of extensive, vegetated, but possibly immature and/or ephemeral wetlands and a diverse waterfowl and wetland bird community. The landscape of Middle Bed II is more open and potentially drier with matured wetlands, scattered trees, and a greater expansion of grasslands with an ecologically - diverse avifauna indicative of greater landscape heterogeneity (patchiness). Such fine - scale paleoenvironmental reconstructions, as have been made possible through the inclusion of these avifaunal data, can provide greater insight in to the causalities behind major events in hominin evolution and behavior at Olduvai and elsewhere, including patterns of stone tool distributions, technological shifts, competition, and diet.



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### Suidae (Mammalia, Artiodactyla) from Bolt's Farm Palaeokarst System (Plio-Pleistocene) South Africa

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Recent excavations at Aves Cave I (AC), Brad Pit A (BPA), Milo A (MA), Bridge Cave (BC) and Alcelaphine Cave (AL), in the Cradle of Humankind, Gauteng, South Africa, have yielded fossil suid remains which provide biostratigraphic information about the periods of deposition in the Bolt's Farm Palaeokarst System. At Aves Cave I there are Late Pliocene deposits (ca 3-2.7 Ma) which have yielded the extinct suid *Potamochoeroides hypsodon*, including skeletal elements that were poorly represented in previous collections from Bolt's Farm as well as rare remains of *Notochoerus capensis*. At Brad Pit A, Milo A and other deposits, remains of the giant suid *Metridiochoerus andrewsi* have been found which indicate a later phase of endokarst sedimentation (Early Pleistocene, ca 1.8 Ma). The augmented samples from Bolt's Farm invite detailed comparisons with the Suidae from Makapansgat and other African Pliocene localities (Malawi, Namibia) and they permit a review of the taxonomy of *Notochoerus* and *Potamochoeroides*. It is shown that both genera are Suinae, and could by synonyms.

Speaker

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## Stable isotope record implicates aridification in late Guadalupian mass extinction

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The late Capitanian mass extinction (~260 million years ago) represents one of the greatest biotic perturbations of the Phanerozoic and was the earliest mass extinction to affect terrestrial tetrapods and ecosystems. In the past, this extinction has been largely associated with taxonomic loss and ecological restructuring in marine environments but more recently it has also been recognized in terrestrial ecosystems. Though various environmental mechanisms have been proposed for the former, little evidence has yet been presented for the cause of terrestrial extinctions. We determined the stable oxygen and carbon isotope compositions of dentine apatite from twenty-eight specimens of the dicynodont therapsid Diictodon feliceps, to investigate the potential role of climate in driving terrestrial tetrapod extinctions. Studied specimens were recovered from a 270 m stratigraphic interval constraining the peak in tetrapod extinction rates in the uppermost Abrahamskraal Formation in the well-sampled main Karoo Basin of South Africa. Our results demonstrate a positive excursion of  $\delta^{13}$ C values coinciding with the extinction peak that is followed by a return to pre-extinction  $\delta^{13}$ C values, suggesting a local increase in aridity at the time of the extinction. For the same time interval, the  $\delta^{18}$ O values did not statistically demonstrate significant changes, suggesting constant temperature in the South African paleoenvironment. This unusual increase in aridity but not in temperature has been interpreted as the possible result of orogenesis in the Cape Fold Mountain source along the southern margin of Gondwana.



Speaker

## Taphonomy of the Maevarano Formation vertebrate assemblage: life and death in the Late Cretaceous of Madagascar

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The Maastrichtian Maevarano Formation of Madagascar yields an amazing assemblage of terrestrial vertebrates, including spectacularly preserved frogs, turtles, lizards, snakes, crocodyliforms, nonavian dinosaurs, birds, and mammals. Strata that yield these fossils accumulated on an alluvial plain characterized by dryland soils (Masorobe Member) and ephemeral shallow streams that experienced highly variable discharge punctuated by intermittent debris flows (Anembalemba Member). Aspects of vertebrate fossil preservation in the Maevarano Formation reveal the dire circumstances that repeatedly befell the Maevarano ecosystem. Here we focus on taphonomic data recovered from the Anembalemba Member over the past 25 years (350+ localities), and explore key elements of the member's taphonomic history. Whereas the present focus is on taphonomic insights provided by a few key bonebeds, isolated occurrences of solitary bones and single individuals (of variable quality) are plentiful; these occurrences also yield valuable information about this ancient ecosystem. Locality MAD93-18, an exemplar of bonebed taphonomy, is multitaxic (at least six higher taxa are represented), with body sizes ranging from massive titanosaurian sauropods (adult Rapetosaurus) to small birds. Adult and juvenile dinosaurs are preserved alongside amphibious and aquatic forms in three distinct layers (each layer is a unique event of localized mortality and burial), and the remains are clearly time- averaged (fossils exhibit variable states of articulation, association, and weathering). Locality MAD96-01 replays the taphonomic theme of MAD93-18 (albeit only once), but this locality offers additional insights into transport upon burial by mass flow (minimally mere centimeters), and scavenging (intense carcass utilization by the cannibalistic dinosaur Majungasaurus). Locality MAD05-42 again follows the general taphonomic trajectory of Anembalemba bonebeds (multitaxic, time-averaged, burial by debris flow), but this site affords unique clues that point to a particularly lethal killing agent-toxic algal blooms. This reconstruction is consistent with the Maevarano bonebed record because cyanobacterial poisoning is a recurrent phenomenon today (as inferred for MAD93-18), is fast acting (it will rapidly kill animals, including birds, which are notably plentiful in MAD05-42), and it is not selective (consistent with the taxonomic diversity represented in Anembalemba bonebeds).





## Three-dimensionally preserved pterosaur material from the Late Cretaceous of Afro-Arabia provides insight into pterosaur flight

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Pterosaurs were the earliest and largest vertebrates to evolve powered flight. Attempts to understand the evolution of pterosaur flight mechanics are complicated by a lack of extant descendants and rely instead on extant birds and bats for comparison. Birds exhibit internal wing bone structure in the form of struts and ridges that are created in response to the mechanical stresses of flight and thus correlate with flight behavior. Investigation of internal bone structure in pterosaurs requires three-dimensionally preserved specimens, which are rare. Remarkably, two new individuals of large-bodied pterosaurs were recently recovered from the Late Cretaceous (Maastrichtian) of Jordan. These specimens represent two azhdarchid pterosaurs, including the giant species Arambourgiania philadelphiae (ca. 10 m wingspan) and a new, smaller species (ca. 5 m wingspan). Both specimens consist of wing elements preserved in three dimensions with internal bone structure. In this study, we used high-resolution micro-computed tomography scans to reconstruct and compare the internal osteology of the humeri of these two differently sized species. The humerus of Arambourgiania exhibits a series of helical ridges formed along the cortical bone, whereas the smaller species exhibits a denser pattern of hollow struts. Variation in internal structure for these individuals likely reflects responses to mechanical forces applied on the wings of pterosaurs. Preliminary results suggest that the smaller species has internal bone morphology similar to that of flapping birds, whereas the internal morphology of Arambourgiania is most similar to that of gliding birds.



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## Presence of *Namalestes* (Todralestidae?) in the early Priabonian of Egypt

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The placental mammalian family Todralestidae is definitively known from the late Paleocene and early Eocene of Morocco (genus Todralestes), and has more recently been identified at a Paleogene site in Namibia (Black Crow) that is of uncertain age, where the relatively large species Namalestes gheerbranti occurs. Biochronological age estimates for Black Crow range from Bartonian to Ypresian. Here we report on the presence of Namalestes at the relatively well-dated early Priabonian (~37 Ma) BQ-2 site in the Fayum Depression of northern Egypt. The Namalestes collection from BQ-2 includes a maxilla with M1, isolated P4 through M3, and isolated lower p4-m3. Comparison of this material with Namalestes gheerbranti from Black Crow reveals only very minor differences, primarily in the morphology of the M3, with the Fayum specimen having a slightly larger and more hook-like parastyle and more distinct preparacrista. M1-2 of Namalestes from BQ-2 also have more distinct precingula than do the specimens from Black Crow. These slight morphological differences are of debatable significance at the specific level, and the close similarity of Namalestes from BQ-2 and Black Crow suggests that the BQ-2 population represents either Namalestes gheerbranti or a closely related species, thereby providing the first compelling biochronological link between the two sites, which are separated by over 6,500 kilometers. Given other faunal differences between Black Crow and BQ-2, it is unlikely that the two localities are directly contemporaneous, but this new evidence more clearly supports a later middle Eocene (Bartonian) age for Black Crow, rather than the much older Ypresian age that has recently been proposed. If Namalestes is indeed more closely related to Todralestes than to any other known Afro-Arabian genus (such as Chambilestes, placed in the family Chambilestidae), then BQ-2 would provide a new last appearance datum for Todralestidae in Africa, and would indicate that the family persisted in Africa for at least 20 million years, and through most of the Eocene.

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## Reassessment of historical sections from the Paleogene marine margin of the Congo Basin reveals the absence of Danian deposits

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The early Paleogene is critical for understanding global biodiversity patterns in modern ecosystems. During this interval, Southern Hemisphere continents were largely characterized by isolation and faunal endemism following the breakup of Gondwana. Africa has been proposed as an important source area for the origin of several aquatic vertebrate groups but its Paleogene record is poorly sampled, especially from sub-Saharan Africa. To document the early Paleogene marine ecosystems of Central Africa, we revised the stratigraphic context of sedimentary deposits from three fossil-rich vertebrate localities: the Landana section in the Cabinda exclave (Angola), and the Manzadi and Bololo localities (western Democratic Republic of Congo). We provide more refined age constraints for these three localities based on invertebrate and vertebrate faunas, foraminiferal and dinoflagellate cyst assemblages, and carbon isotope records. We find an almost complete absence of Danian-aged rocks in the Landana section, contrary to prevailing interpretations over the last half a century. Refining the age of these Paleocene layers is crucial for analyzing fish evolution in a global framework. The combination of vertebrate fossil records from Manzadi and Landana sections suggests important environmental changes around the K/Pg transition characterized by an important modification of the ichthyofaunal. A small faunal shift may have occurred around the Selandian/Thanetian transition. More dramatic is the distinct decrease in overall diversity that lasts from the Thanetian to the Ypresian. The Lutetian of West Central Africa is characterized by the first appearance of numerous cartilaginous and bony fishes. Our analysis of the ichthyofauna moreover indicates two periods of faunal exchanges: one during the Paleocene, where Central Africa appears to have been a source for the European marine fauna, and another during the Eocene when Europe was the source of the Central Africa fauna. These data indicate that Central Africa has had strong connections with the Tethyian realm.

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## Why the long teeth? Were changes in third molar morphology in Plio-Pleistocene African suids driven by climatic changes or by ecological niche partitioning? A case-study using *Kolpochoerus*

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The Plio-Pleistocene fossil record of African suids documents repeated convergent instances of progressive changes in third molar morphologies (increases in crown length and height). Based on uniformitarianism, those changes were classically interpreted as adaptive responses to herbivory in more and more open landscapes resulting from global climatic changes. Here we provide new dental microwear texture analyses of Kolpochoerus samples from the Shungura and Konso formations from southern Ethiopia and we produce a synthesis of existing morphological and paleoecological (mostly stable carbon isotopes) data. We scanned the shearing enamel facets of the molars using a white-light confocal microscope to reconstruct a high resolution 3D model of the enamel surface. We compared dental microwear textural parameters to a database of extant African and Eurasian suids, encompassing most of the taxinomic, morphological, and dietary diversity. Early specimens of K. limnetes in Shungura and K. cf. majus in Konso display short and low-crowned third molars that are not expected in grass-eating suids. Both stable carbon isotopes and dental microwear textures (low complexities and heterogeneities) indicate a diet dominated by C4 monocots as early as 2.8 Ma in K. limnetes from Shungura, long before the dramatic elongation of the third molars. Dental microwear textural data (low complexities and high heterogeneities) from Konso suggest a mixed feeder herbivorous diet overall similar to the diet of the extant Hylochoerus meinertzhageni. Overall, we observe a strong discordance between the diet and the third molar morphology, as early specimens of K. limnetes and K. cf. majus display conservative short and low crowned third molars even though they consumed high amounts of plant matter. The strong subsequent morphological changes could be related to ecological niche partitioning among suids and other herbivorous mammals. Elongation of third molars in the lineage K. limnetes in Shungura could reflect a shift from a diet of long grass to a diet dominated by small mouthfuls of short grass. Conversely, K. cf. majus, with its shorter third molars, would have consumed more long grass and other plants, possibly in C4 plants-dominated humid environments.

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## A dwarf among giants: *Titanohyrax tantulus* (Hyracoidea, Mammalia) from the Eocene of Chambi, Tunisia and Glib Zegdou, Algeria

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The Hyracoidea was a successful mammalian order in Africa from the early Eocene to the mid-Miocene. Through the Eocene/Oligocene, hyracoids represented the dominant 'ungulate' group in terrestrial ecosystems. Among them, the genus *Titanohyrax* embraces very large species as well as a small one, T. tantulus, only known from the ?early/middle Eocene of Chambi, Tunisia. Recently, the generic affinity of this species has been disputed, implying a latest Eocene origin for Titanohyrax. Testing the competing hypotheses requires new data as most species of Titanohyrax are documented by few specimens. Based on new fossils from Chambi and CT scan analysis of the holotype, we revised T. tantulus. A complete skull from the coeval locality Glib Zegdou, Algeria, is also discussed. This analysis reveals that the holotype bears a part of dP3-4 and M1-2 rather than dP2-M1 as it was proposed. More importantly, derived dental characters, including a small compressed hypocone on P2-M3 and highly molarized P3-4 with a W-shaped ectoloph, are distinctive features of Titanohyracidae. Enamel microstructure also indicates affinities with the titanohyracids Antilohyrax and Afrohyrax. Titanohyrax tantulus and Antilohyrax also share a tall, narrow and vertically oriented supraoccipital and no diastemata between the anterior teeth. Moreover, the lack of postorbital bar, a well-developed metastylid on p3-m3, and broad spatulate lower incisors, that lacked tines or serrations, are diagnostic characters of *Titanohyrax*. As a result, there is no apparent reason to question the generic affinity of T. tantulus. However, the latter differs substantially from the other species of the genus, in harboring a suite of primitive characters: lower crowned cheek teeth, absence of mesostyle on P1- 2, less labially expanded mesostyle and parastyle on P4-M3, more labially positioned paracone and metacone, blunt parastyle and mesostyle, longer preprotocrista and prehypocrista, and presence of a paraconular swelling on molars. Titanohyrax tantulus finally differs from late Eocene titanohyracids (Antilohyrax and Titanohyrax sp.) in having sharp supraorbital ridge and extensive sagittal crest, certainly also primitive cranial characters. To conclude, T. tantulus represents an early offshoot of the titanohyracids; this family thus testifies to the longest fossil record among hyracoids. It only disappeared during the early Miocene, likely due to competition with artiodactyls and perissodactyls.

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\* Speaker

## Investigating the role of competition and biotic interaction on the evolution of African bovids: a geometric morphometric & phylogenetic approach

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Modern bovid species are distributed from equatorial rain forests to arctic tundra, where they are intimately adapted to climatic regimes and vegetational habitats. In Africa, bovids dominate the modern landscape and are prolific in the fossil record, providing important ecological information on the paleoenvironment of human evolution. Niche competition has often been used to explain the range of skull shapes seen in bovids today but its importance in shaping fossil forms has not been fully explored. We here present the preliminary results of a study looking at the evolution of skull shape disparity in Bovidae over the last 18 million years, and its implications for biotic competition and facilitation. The dataset contains 46 cranial landmarks for 78 extant and 17 extinct species. Landmarks were collected digitally using 3D models produced using a combination of CT and Artec 3D surface scanning. This, in conjunction with a newly calibrated phylogeny and a greater insight into the fossil relationships, allows us to examine drivers, rates and modes of phenotypic evolution along with exploring phenotypic disparity in relation to modern and fossil community diversity. Within the constructed morphospace, fossil species are constrained in their morphologies, residing well within the confines of the modern morphologies. This implies a gradual radiation to more extreme morphologies within the group, reflected in the selection of Brownian motion as the best fit evolutionary model. A notable exception to this is the position of *Pelorovis turkanensis*, which sits well beyond the modern Bovini morphospace and represents a shift from the gentle expansion of the morphospace through time. Moreover, phylogenetic clustering is strong at the tribal level, with some tribes seeing an increase in disparity with the inclusion of fossils. Comparisons with randomly drawn communities suggests that modern African bovid communities are more similar (less disparate) than predicted by chance for morphology, but more disparate in terms of body size. This implies a combination of competition and facilitation has affected the evolution of disparity in bovids and that body size may have been more important than skull shape differences in limiting competition at the timescale of community assembly. This work – using 3D techniques to study skull shape in bovids – provides data on the importance of interspecies interactions in the Neogene and African fossil record.



<sup>\*</sup> Speaker

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## Middle-Upper Eocene Archaeoceti whales from the Sahara Desert in Morocco

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The middle-upper Eocene Archaeoceti whale remains come from two different places in the Moroccan Sahara: (1) the sabkha of Gueran, a remote depression in the Sahara Desert located about 125 km southeast of the Atlantic city of Boujdour; and (2) the Atlantic coast area between Puerto Rico and Punta Chica to the southeast of the Ad-Dakhla peninsula. At Gueran, all fossils come from a single meterthick sandstone unit. At least three species of Protocetidae (a small and medium sized protocetid and Pappocetuslugardi) and at least five genera of Basilosauridae (from smallest to largest: Chrysocetus, cf. Dorudon, cf. Masracetus, Platyosphys, and Eocetus) are present. The co-occurrence of protocetid and basilosaurid whales indicates a probable Bartonian age for the locality, because basilosaurids are unknown during the Lutetian, and only a single protocetidis known from very earliest Priabonian. Thus, Gueran is one of the most important sites in the world documenting the cetacean evolutionary transition from footpowered to tail- powered swimming. The fauna from Gueran also includes abundant selachian teeth, few remains of bony fishes, rare fragments of turtle shells, crocodile remains, marine snake vertebrae, seabird remains, and fragments of proboscidian teeth. In the Ad-Dakhla area, fossils are known from stratigraphic sections along 30 km of Atlantic Ocean coastline, from Porto Rico in the north to Garitas in the south. Archaeoceti remains come from three stratigraphic levels labeled A1, B1 and B2. The lower level, A1, which is Bartonian, yielded a few remains of a small protocetid and several cheek teeth of the large protocetid (cf. Pappocetuslugardi). Bonebed B1 has yielded at least five Archaeoceti whale species, from smallest to largest: cf. Saghacetus sp., cf. Stromerius sp., Dorudonatrox, cf. Dorudon sp., and Basilosaurusisis. The only identifiable cetacean found in bonebed B2 is Basilosaurus sp. Dugongid sirenians identified as cf. Eosiren sp. are the most common mammals in bed B2. Abundant and diversified selachians as well as remains of sirenians, rare proboscideans, actinopterygians, turtles, palaeophiid snakes, crocodiles and pelagornithid seabirds are also found in these localities. A late Eocene Priabonian age was assigned to both B1 and B2 bonebeds based on the selachian fauna and the Archaeoceti assemblages.



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# Discoveries in the Cretaceous Kem-Kem plateau (SW Algeria): sedimentology and paleontology

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The Cretaceous deposit of the Kem-Kem plateau outcrop in a vast expanse rocky, semidesertic located on both sides border between Algeria and Morocco. The wealth of fossiliferous Kem-Kem outcrops in Morocco suggests a great paleontological potential in the Algerian Kem- Kem. This was confirmed by the study of fossil material collected during recent field work, conducted two years ago. The prospections allowed the collection of many macroremains attributed to taxa regularly found in the Kem-Kem outcrops including many teeth and fragments of rostra of the selacian *Onchopristis*, isolated teeth of dipnoans, bony remains of the coelacanth *Mawsonia*. Moreover the discovery and excavation of microremains-rich levels documented an astonishing biodiversity made of elasmobranchs, actinopterygians, dipnoans, one amphibian, sauropod and theropod dinosaurs, pterosaurs and finally crocodylomorphs. Moreover, these paleontological data are stratigraphically well constrained and their sedimentologic context was also studied in details.

The aim of our communication is to provide the preliminary results of these discoveries that bring new data on the diversity of the paleofaunas of Kem-Kem Beds, and to present for the first time, as far as the Kem-Kem of the Algerian side are concerned, a sedimentological study that supplements the paleontological information and permits to determine deposit environment.



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### Postcranial anatomy of the gorgonopsian *Gorgonops torvus* from the late Permian of South Africa

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Gorgonopsia is one of the most iconic clades of synapsids (the mammalian stem-lineage) and includes the top predators of the late Permian. Despite this, gorgonopsians are a remarkably understudied group. Although there are a number of recent cranial descriptions bearing on the systematics of the group, very little information is available on gorgonopsian postcranial morphology and paleobiology. Here we present the first thorough comparative investigation of postcranial anatomy in the 'original' gorgonopsian, Gorgonops torvus, based on a nearly- complete skeleton (SAM-PK-K10591) housed at the Iziko South African Museum in Cape Town. Gorgonopsians are characterized by a notoriously conservative anatomical bauplan, but recent studies have shown ecomorphologically important variation in their crania. Here we demonstrate comparable variation in the rest of the skeleton, supported by our comparisons between SAM- PK-K10591 and other gorgonopsian postcranial specimens. Gorgonopsians exhibit substantial variation in the robustness of appendicular bones (including size-independent examples) as well as diverse morphologies of the pectoral and pelvic girdles. The Gorgonops specimen SAM- PK-K10591 exhibits postcranial specializations comparable to more distantly related sabre- toothed taxa such as the extinct metatherian Thylacosmilus (i.e. robust forelimbs and more gracile hind limbs, interpreted as adaptations for a quick pounce towards prey). Additionally, our examination of SAM-PK-K10591 reveals postcranial autapomorphies for Gorgonops (at least among gorgonopsians with known postcrania), including two posterior grooves on the medial side of the ilium. SAM-PK-K10591 also preserves one of the few intact sterna known for gorgonopsians, which is composed of a plate-like manubrium and three unfused body segments.



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### The evolution of endocranial size in Proboscidea

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As the largest and some of the most behaviourally complex terrestrial mammal, the elephant figures among the most emblematic African animals. However, very little is known about the evolutionary origins of the proboscidean brain. Indeed, despite the fact that hundreds extinct genera of Proboscidea are known, the fossil record of proboscidean endocasts is paradoxically very patchy. In order to gather data to better understand the evolution of the proboscidean brain, we undertook a broad scale survey of the literature and collections of endocranial casts internationally. This study highlights that the record of proboscidean endocasts is for the larger part confined to the last ten million years, in taxa mostly belonging to the clade Elephantimorpha. Despite the scarcity of data, our dataset indicates that endocranial volume and body mass evolved rather independently among fossil proboscideans since both very large taxa with comparatively small brain (e.g. Zygolophodon borsoni) and small taxa with comparatively large brains (e.g. Palaeoloxodon falconeri) existed. An analysis using ancestral character state reconstruction suggests that the diagnostic morphological features (enlarged temporal lobe and cerebellum, ventrally positioned olfactory bulbs) and size of the Elephantimorpha endocast evolved once during the Oligocene period. This corresponds to a period of important environmental changes (e.g. global cooling, drought) that may have increased the selective pressure on proboscideans memory and social capabilities, and enhanced their ability to process sensory input to help them cope with increasingly distant water holes and/or larger social groups.



Speaker

## Rare dinosaur, mosasaur, turtle and other vertebrate remains from marine Cretaceous deposits of South Africa

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The Cretaceous outcrops of the False Bay coastline of South Africa are well known for the exceptional preservation of ammonites and other invertebrates. It was surprising therefore when about 30 years ago, two titanosaur caudal vertebrae were recovered from the Lower Santonian aged deposits of KwazuluNatal, South Africa. Since then one other isolated titanosaur vertebra was found. In the hopes of recovering more vertebrate fossils, two fieldtrips were undertaken to the region during 2015 and 2016. Several vertebrate skeletal remains were recovered. The most notable of these was an associated partial skeleton (consisting of part of a skull, a humerus, and 5 vertebrae) of a marine reptile, which appears to be a dermochelyid. This material is interesting since demochelyid turtles are quite scarce from Africa. The first hyoplastron of a chelonioid sea turtle was described from Morocco in 2004, and since then there have been two other finds, one in Angola in 2009, and more recently (2014) from the Late Maastrichtian, Oulad Abdoun Basin of Morocco, a 70cm skull was recovered. The latter represents the best record of a cryptodiran turtle from the Cretaceous of Africa. Our find of a dermochelyid in South Africa supports the hypothesis that the family had a wide geographical distribution in the Cretaceous. Besides, the turtle, we also found an isolated mosasaur vertebra, which adds to the rather scarce remains of mosasaurs from South Africa. In addition to the material mentioned above, several other isolated fossil bones were collected but diagnoses of these elements remains elusive because of their fragmentary nature.



Speaker

### New hominin postcranial remains from the Shungura Formation, Lower Omo Valley (Ethiopia)

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The time period ranging from 2.8 to 1.8Ma in Africa is a key period in human evolution that is marked by the contemporaneity of multiple hominin taxa including *Paranthropus, Homo* and *Australopithecus*. However, despite this taxonomically diversity, little is known about the postcranial anatomy of these hominins and their morphological variation.

Since 2006, renewed paleoanthropological fieldwork on the Shungura formation deposits, (Lower Omo Valley, Southern Ethiopia), by the OGRE (Omo Group Research Expedition), yielded several thousands of vertebrate remains including three isolated hominid limb bones from the locality OMO 323 (unit G8, dated from 2.14 to 2.12 Ma). Here we describe the unassociated remains of a complete second right metatarsal (OMO 323-76-2117), a complete manual proximal phalanx (OMO 323-10003b) and the proximal two-thirds of a left radius (OMO 323-10003a).

Overall, the two upper limb bones display an archaic morphology, showing greater affinities for African apes and early hominines (i.e. *Australopithecus, Paranthropus*) than for modern humans and early *Homo*. The radius exhibits enlarged surface for the zona conoidea, low circumferencia articularis and long neck, which mainly reflect propensity for frequent climbing activities, facilitated by stabilized forearm rotation and powerful flexion at the elbow. The phalanx is robust and displays a moderate degree of longitudinal curvature and accentuated flexor sheath ridges that suggest a frequent use of below-branch behaviors. By contrast, the second metatarsal has a morphological and architectural pattern that is very similar to that of modern humans and early *Homo* (straight shaft, proximal articular arrangement and robusticity, dia physeal angles, head angle and dorsal morphology) providing evidence of a stiff and arched foot compatible with a frequent bipedal locomotion. Unambiguous signs of infection reveal that this aptitude was most probably altered at the time of death of this individual.

Despite the morphofunctional disparity of the new postcranial remains, there is no objective reason for now to consider that they represent two distinct taxa. Because OMO 323 previously yielded a cranium of *Paranthropus boisei*, it is then more parsimonious to consider their potential attribution to this latter taxon.

\* Speaker

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## Late Miocene rhinocerotid assemblage from Samburu Hills and Nakali in Kenya

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The Family Rhinocerotidae diversified in Africa during the Miocene. There are many Miocene fossil localities in present sub-Saharan East Africa. However, few of them are of early late Miocene age. Abundant rhinocerotid fossils have been found in the Namurungule and Nakali Formations in Samburu Hills and the Nakali (ca. 10 Ma), respectively. The taxonomic revision of these specimens, however, had not been undertaken since their initial descriptions. We review the rhinocerotid assemblage of the Namurungule and Nakali Formations.

*Chilotheridium pattersoni, Kenyatherium bishopi, Samburuceros ishidai*, and *Diceros* sp. were found in both formations. In addition, *Brachypotherium* cf. *B. minor* was found from the Namurungule Formation.

*Brachypotherium* is considered to live in a swampy habitat. The Namurungule Formation includes lacustrine deposits that yields *B*. cf. *minor*. Therefore, the habitat of *B*. cf. *B. minor* is concordant with the paleoenvironment of the Namurungule Formation. The cheek teeth of *Diceros* sp. show the characteristics of a browsing diet. Therefore, the discovery of *Diceros* from the Nakali and Namurungule Formations coincides with the paleoenvironment of Nakali (forest habitat) and Samburu Hills (woodland habitat). In contrast, *C. pattersoni* and *S. ishidai* show grazing diet. Probably, they did not share the same niche.

The rhinocerotid assemblage of Samburu Hills and Nakali is composed of Early to Middle Miocene and Modern forms. Early to Middle Miocene form includes *C. pattersoni*, *B.* cf. *minor*, *K. bishopi*, and *S. ishidai*. *C. pattersoni* are a dominant species during the early to middle Miocene. *B. minor* is a middle Miocene species. *K. bishopi* is morphologically similar to the early Miocene taxa, such as *Ougandatherium napakense* from Napak in Uganda and *Bugtirhinus praecosor* from Bugti in Pakistan. *S. ishidai* is closely related to the middle Miocene species, *Victoriaceros kenyensis* from Maboko in Kenya. Thus, *K. bishopi* and *S. ishidai* is at a morphologically primitive grade. The modern form includes *Diceros* sp. which diversified in the late Miocene to Pliocene period. To date, no Early to Middle Miocene form has been discovered from sub-Saharan East Africa after the age of Nakali and Samburu Hills. Therefore, the early Late Miocene would be the period of the beginning of the turnover in sub-Saharan East Africa, although further Middle/Late Miocene materials are needed to discuss this hypothesis.



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## A finite element analysis for the limb loadings in *Thrinaxodon liorhinus* (Therapsida, Cynodontia): postural validation of non-mammaliaform cynodonts

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Therapsida is a lineage consisting of extant mammals and their extinct relatives, the latter of which form a series of transitional fossil groups. Although much is known about the locomotion of extant mammal groups, fundamental questions remain about the postures of the transitional non-mammaliaform therapsids. The fossil forms were severely affected by the Permian-Triassic mass extinction event, resulting in the survival of only a few lineages. One of these lineages, Cynodontia, includes one of the best known non-mammaliaform transitional fossil species, the Early Triassic Thrinaxodon liorhinus. This species has been key for a better understanding of the evolution of therapsids. Fossilized skeletons of Thrinaxodon are abundant in the South African Karoo Basin, which permits for a presumably accurate reconstruction of their limb posture. This research seeks to better understand *Thrinaxodon* limb functional morphology using finite element analysis (FEA) and cross-sectional properties of the humeri and femora of Thrinaxodon to assess structural competency. Specifically, the hypothesis to be tested is that proximal limb segment bone (e.g., humeri and femora) are better adapted structurally to resist loading associated with semi-sprawled postures rather than sprawled or parasagittal postures during gait. FEA is a computational technique to evaluate the mechanical behavior of bodies of complex geometry undergoing loading. Thrinaxodon limb loading corroborates external evidence of semi-sprawled postures for this taxon. Ultimately, observed stresses increase for a given bone as the posture of fossil taxa developed from a sprawled to a parasagittal gait. This suggests that Thrinaxodon retained the reptilian (sprawling) skeletal configuration in the forelimb, and confirms that it had adapted a posture that had begun to resemble parasagittal posture in the hindlimb. The application of FEA in similar future studies of Karoo fossil taxa may shed light on the evolution of additional extinct organisms.

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## Juvenile Spinosaurs (Theropoda: Spinosauridae) from the Middle Cretaceous of Morocco and their ecological implications

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The Spinosauridae is a family of specialised theropod dinosaurs known from the Berriasian to the Cenomanian of Africa, South America, Europe and Asia. The spinosaurs were unique among non-avian dinosaurs in exploiting a piscivorous niche within riverine and coastal habitats. This group also contains the largest theropod currently known. Although fossils of giant spinosaurs are increasingly well-represented in the fossil record, juvenile material has not been explored in depth, nor its ecological implications. Here, we describe the first examples of juvenile *Spinosaurus* material from the Late Cretaceous (Cenomanian) Kem Kem beds of Morocco. The fossils include material from a range of body sizes, suggesting that juveniles exploited the same semiaquatic niche as the adults throughout ontogeny, and that the Cenomanian delta habitats supported an age-inclusive population of *Spinosaurus* that was neither geographically or environmentally separated, though some ecological separation is likely based on the new minimum and known maximum size of *Spinosaurus*. We also identify two distinct cranial morphs of Spinosauridae present within the Kem Kem, potentially supporting the previous recognition of distinct taxa in the assemblage.

Speaker

## New species of *Lystrosaurus* (Lystrosauridae, Dicynodontia) from South Africa, implications for our knowledge of the phylogenetic relationship of the genus and the post Permo-Triassic biotic crisis recovery

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The genus *Lystrosaurus* belongs to Dicynodontia, a large group of herbivorous therapsids, which dominate the terrestrial ecosystems from the middle Permian to the Late Triassic. The end-Permian biotic crisis had a devastating impact on the dicynodont biodiversity. Few dicynodont lineages survived the crisis: the kistecephalians *Myosaurus* and *Kombuisia*, the lystrosaurids *Lystrosaurus* and a third lineage that leads to the kannemeyeriforms. However, *Lystrosaurus* was the only genus to survive the PT (Permian-Triassic) crisis with one species, *L. curvatus*. *L. maccaigi* is only known during the late Permian. A rapid taxonomic diversification and a geographical expansion of the group is recorded during the Early Triassic.

Here, we report on an unpublished skull (provisional collection number 432809) belonging to the collection of the Muséum national d'Histoire naturelle (France). It was collected during the 1970's by Christiane Mendrez in the *Lystrosaurus* Assemblage Zone of the Karoo basin, and is dated of the Early Triassic. We compare to all adequately known and valid *Lystrosaurus* species: four Laurasian species (*L. broomi, L. robustus, L. hedini* and *L. georgi*), four Gondwanan species (*L. mccaigi, L. platyceps, L. oviceps* and *L. declivis*) and two species with a large distribution (*L. curvatus* and *L. murrayi*). Our specimen is attributed to a new species, reinforcing the hypothesis of a rapid diversification of this group, as early as the Early Triassic. 432809 differs from all other species of *Lystrosaurus* by its very short internasal suture and a frontal bone with a sharp V-shaped process inserting in the parietal bone. A phylogenetic analysis including all known species of *Lystrosaurus* (51 characters, 18 taxa) was performed with the parsimony software PAUP 4 (version 4.0a152). The analysis shows that our new species is closely related to the Chinese species (*L. broomi, L. robustus, L. hedini*), whose monophyly is confirmed, and that the Russian form *L. georgi* is closely related to *L. oviceps*, from South Africa. In addition, our results show that the *Kwazulusaurus shakai* is sister-taxon to the genus *Lystrosaurus*, contrary to recent analyses that included it within the genus *Lystrosaurus*.

The close relationship between the new South African specimen and the Chinese species provides new data on the world-wide distribution of *Lystrosaurus* during the Early Triassic, and highlights the gap on the distribution of this genus in the northern of Gondwana and in Europe.



<sup>&</sup>lt;sup>°</sup> Speaker

## The first parapithecine (Primates: Anthropoidea) outside of Egypt: a new species of *Simonsius* from the early Oligocene of Libya

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Parapithecines are an extinct subfamily of stem anthropoid primates known only from the Jebel Qatrani Formation in Egypt. Currently, parapithecines are represented by two monotypic genera: Parapithecus fraasi and Simonsius grangeri. The generic distinction between these taxa has been questioned in the past, but recent analyses have maintained the validity of both genera on the basis of differences in their lower dental formulae and cheek tooth morphology. Here, we report the discovery of a new, relatively small-bodied parapithecine taxon from Zallah Oasis in the Sirt Basin of central Libya. This new taxon documents the first occurrence of parapithecines outside of Egypt. It is currently represented by a right m3 and a left p4, both of which show affinities with established parapithecines. The p4 in the new taxon possesses a buccally and mesially inflated trigonid that is much larger than the reduced talonid, which bears no distinct cusps. This is in contrast to Parapithecus, which retains inflated, cuspidate hypoconids on p3-4 and shows less buccolingual inflation of the lower premolar trigonids. In these respects, the morphology of p4 in the new Libyan parapithecine more closely resembles that of Simonsius, although p4 of Simonsius bears virtually no remnant of the talonid. Relative size comparisons between p4 and m3 show that the new Libyan parapithecine resembles Parapithecus in having p4 much smaller than m3. In contrast, the distal premolars of Simonsius are hypertrophied such that p4 is roughly equivalent in size to m3. The m3 in the new Libyan parapithecine is low-crowned and bunodont, to the extent that the metaconid is the only readily discernible cusp. As in all parapithecines, the paraconid is completely absent. The overall shape of m3 seems to ally the new Libyan parapithecine with Simonsius, as both taxa possess buccolingually broad trigonids and narrow talonids that taper evenly into the hypoconulid lobe. A phylogenetic analysis based on dental characters reconstructs the new Libyan parapithecine as the sister group of Simonsius, with Parapithecus as sister to this clade. The new Libyan parapithecine augments previously reported evidence supporting a modest degree of faunal provincialism across northern Africa during the early Oligocene. The relatively small body size of the new Libyan parapithecine likewise supports the convergent acquisition of body mass larger than ~700 g among multiple clades of early Oligocene African anthropoids.



<sup>&</sup>lt;sup>\*</sup> Speaker

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## The rise of the modern African fish fauna as a consequence of great environmental changes during the last 120Ma

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High level of endemicity and presence of archaic fish are some of the striking features of the African fish fauna. In a preliminary correlative approach to link the diversification events that shape this diversity with the various potential extrinsic controls, I depict the evolution of the African freshwater fish replaced in its palaeoenvironmental context along the Tertiary. The evolution of the African fish fauna is described from the fossil record considering four groups on the basis of the phylogeny, of the modern distribution and of the habitat: each group has probably its diversity driven, at least partially, by similar or close environmental conditions. (I) The Archaics, belong to old depauperate lineages. They were close to extinction at some point during the Tertiary and saw a recent radiation that I link to the advantage of breathing the air in the Neogene contrasted climatic context. (II) The Archaeolimnics are far the more diverse: they belong to primarily freshwater endemic families that diversify after the Western Gondwana dislocation. Geological events appear to constraint greatly their diversity pattern, particularly tectonics and the related topographical modifications of the hydrographical divide. (III) The Invaders are freshwater fish from Eurasia that mostly invade Africa at the plate collision 18Ma ago, and then at the favour of further tectonic events. (IV) The Neolimnics invade the waters from the sea at different times and knew various success such as the cichlids and the latids. Tempo of "conquest events" and "key role" of certain regions are also proposed.



Speaker

## S32 - Palaeobiogeography

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## Pleistocene marine fish biogeography and paleoenvironmental implications in the eastern Mediterranean

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The eastern Mediterranean marine fish faunas today are significantly disturbed due to over- fishing, habitat deterioration, the Lessepsian invasion, and climate change. However, isolating the impact of each parameter is difficult, because pre-anthropogenic impact data are lacking. In this study, we investigate the impact of climate on the fish fauna of an eastern Mediterranean shelf, by identifying the fish otoliths contained in the early-middle Pleistocene marine sediments of northeastern Rhodes Island (Greece). Our findings allow us to revise the paleobiogeographic and stratigraphic distribution of twenty-three taxa, identify similarities and differences with the present-day marine fish fauna in the region, and hypothesize on the oceanographic and climatic conditions that drove marine fish distribution range shifts during that time. The Pleistocene climatic variability is reflected in the fish fauna through multiple periodic and gradual replacements in both the coastal-neritic as well the pelagic assemblages. Overall, the coastal environment is inhabited by small pelagic fish such as anchovies, sardines, and mackerels, as well as gobies and congers. The pelagic domain contains a well-established and diverse mesopelagic fauna, comprising cods and lanternfishes. Furthermore, the episodic invasion of cold-water North Atlantic mesopelagic species is correlated with distinct intervals of climatic deterioration. Finally, the identified fish species are used as paleobathymetric indicators in order to reconstruct the paleoenvironmental evolution of the northeastern coast of Rhodes. Acknowledgement.

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32 // Ora

# Marine connections between the northern Pacific and north Atlantic regions during the Paleocene

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Northern marine faunas, especially those from the northern Atlantic and the Boreal seas, have been suggested to be separated from most of the other oceans during the Mesozoic. In contrast, their Paleogene biogeographical history is relatively poorly known. Recently, the Paleocene aporrhaid and pseudomelatomid gastropods and arcid and astartid bivalves have been recovered from the Paleo-western Pacific margin deposit of Katsuhira Formation, eastern Hokkaido. The aporrhaid gastropods flourished in the Cretaceous and suffered from severe extinction at the K/Pg boundary. The Katsuhira species, Kangilioptera inouei is similar to K. ravni from the Paleocene deposit of western Greenland. From Spitsbergen, the Paleocene aporrhaid has been found. The pseudmelatomid Boreocomitas sp. from the Katsuhira Formation is very similar to Boreocomitas biconica from the middle to upper Eocene Cowlitz Formation in northwestern Oregon, the Greenland Paleocene species, B. sp. and B. brevior from the Paleocene of Denmark. In the northern Pacific, the Paleocene Astarte is very small in size and has been reported from Hokkaido and Sakhalin. These species are similar to A. trigonula from the Paleocene of Denmark. The oldest record of the deep-sea arcid genus Bentharca has been found in the Katsuhira Formation in eastern Hokkaido. Barbatia (Acar) hennigi from Maastrichtian to Danian deposits in Denmark is possibly an ancestor of this genus. Moreover, the Paleocene Conchocele conradii has been found in Paleocene and upper Eocene to lower Oligocene of Spitsbergen. Species of this genus are common in the Eocene and Oligocene of the northern Pacific area, and are common in cold seeps of that age. Based on these criteria, the north Atlantic fauna had some connection with the northern Pacific one.



Speaker

## Using glacial age megatsunami fossil deposits to unveil palaeobiogeographical patterns and processes in volcanic oceanic islands

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The expansion and contraction of geographical range distribution of species (taxon cycles) is a common and well-studied biogeographical process. For terrestrial taxa, both fossil and extant records document poleward shifts, with range expansion of tropical species and range contraction of temperate species. For extant marine species, the geographical range contraction of cold-water taxa to higher latitudes as a result of the current global warming, as well as the range expansion of warm-water species to higher latitudes are also documented. Regarding the fossil record, outcrops on volcanic oceanic islands testify the range expansion of tropical marine species towards higher latitudes during interglacials. However, so far, no studies have shown the expected range expansion of cold-water marine species during glacial episodes. This is probably because such deposits are seldom preserved due to erosion by rising sea levels during the subsequent interglacial episode. Thus, tsunami events occurring during glacial times and transporting large amounts of sediments onshore, away from the erosive action of interglacial high sea levels, are probably the only way to have access to glacial fossil assemblages. Here we document and discuss, for the first time, the palaeobiodiversity of the Tarrafal tsunami deposit (Santiago Island, Cape Verde), attributed to a flank collapse of Fogo volcano ~73 ky ago, which conclusively proves the tropical-ward geographical shift of marine molluscs during the glacial MIS 5a.



32 // Oral

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## The main paleobiogeographic features of early human dispersals in Eurasia

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Paleobiogeography is proposed here as a helpful source of information on limiting environmental factors and the shape and range of the archaic hominin ecological niche. The cluster analysis of Early Pleistocene ircum-Mediterranean mammal faunas confirms a single way of early hominin dispersals into the Eurasian mainland via Near East. Despite of the assumed belonging of early hominins to the carnivore guilds as a commensal scavenger, the biogeography of early hominin dispersal and area of distribution dynamics were different from those of true ubiquitous carnivores, which dispersed over entire continents. The hominin area of distribution on the Eurasian mainland during the Early and beginning of Middle Pleistocene was limited by geographic and climatic factors. The hominin dispersal toward Sundaland (ca. 1.8 Ma) was successful due to the hominin adaptation to arid environments that permitted to overcome the Indo-Burman Ranges, which represented an effective biogeographic obstacle for tropical forest species. The westward hominin dispersal took place later (ca. 1.1-1.4 Ma) and represented an independent paleobiogeographic event that coincided with dispersals of large-sized south-Asian herbivores (Praemegaceros obscurus, Eobison georgicus /tamanensis, Rucervus simplicidens /colberti /verestchagini). Apparently, the progressive climate-induced deforestation of Western Eurasia was one of factors that triggered this dispersal event. By ca. 1.0 million years ago, the area of hominin distribution was limited by the Alpine-Himalayan Mountain belt in Western and Central Eurasia and, presumably, by the Qin Mountains in Eastern Asia. The seasonal drop of temperatures north of the Alpine-Himalayan and Qin mountain ranges could be one of the limiting factors for hominin dispersal. The further hominin dispersal north of the mountain belt during the beginning of Middle Pleistocene is marked by the Movius Line in Western Europe. This new area of hominin distribution acted as a paleozoogeographic wet- climate mammal refugium characterized by the mitigated seasonality due to the Gulf Stream influence.

<sup>°</sup> Speaker

### **Testing Devonian bioregionalisation**

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Devonian bioregionalisation has become poorly constrained since the foundational work of Arthur J. Boucot in the late 1960s. Our study presents the first attempt to review and test the hypotheses of Boucot, the functional standard for Devonian biogeography.

Distributional data from Devonian taxa, including fish, brachiopods, and trilobites, were structured into a polytemporal matrix which marks taxic occurrences both spatially and temporally. The data were then analysed using biotic similarity analysis; the polytemporal matrix structure allowing consideration of both inter and intra area relationships. The phylogeny, revision, and biogeography of the Homalonotidae (Trilobita) provides the second test of the bio regionalisation through comparative bio g eogr aphy. Th is study presents the first phylogeny of the Homalonotidae family and an assessment of their biogeographical significance.

The testing of bioregionalisation is important for biogeographic studies, the identification of natural areas, and palaeorec onstruction. Given that life and Earth have a dependent relationship, the test of Devonian bioregionalisations offers insight into the evolution of both.

Speaker

## Diversification patterns of brachiopods after the end Ordovician mass extinction and its palaeobiogeographic significance

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The Late Ordovician biotic crisis was associated with a brief but intense glaciation episode in earth history. Post-glacial marine transgression created vast habits in epicontinental seas, in which benthic faunas established and diversified, with brachiopods being one of the most abundant and diverse fossil groups. Based on detail data of brachiopod occurrences after the end Ordovician mass extinction, together with newly published information, we analyzed the diversification patterns of brachiopods from the Rhuddanian to the Aeronian (early Silurian) by Network Analysis and Frequency Distribution Analysis. Rhuddanian brachiopod faunas were characterized by low diversity and localized high abundance, except for a relatively high-diversity early Rhuddanian fauna in Avalonia-Baltica and South China. Invariably, these faunas were predominated by re-established holdover and once-cosmopolitan taxa from the Late Ordovician, primarily orthides and strophomenides. By the Aeronian, global brachiopod diversity nearly doubled in comparison with the Rhuddanian, owing to a major diversification of Silurian-type brachiopods in both the paleotropics and high-latitude Gondwana, as well as the concomitant proliferation of endemic and cosmopolitan taxa, in association with a global expansion of epicontinental seas and heterogeneity of specialized local habitats. A drastic turnover of brachiopods from the Ordovician to the Silurian type significantly affected the Paleozoic evolutionary fauna. With the ordinal data of brachiopods in major palaeoplates, we discussed the turnover process. Compared with orthides and strophomenides of typical Ordovician brachiopods globally increased their diversity after the extinction, atrypides and pentamerides of Silurian group displayed a drastic diversification from Rhuddanian to Aeronian only in lower latitude continents, demonstrated the two new orders more preferred warm water environments than the Ordovician groups. Atrypides recovered from the early Rhuddanian, whereas diversification of pentamerides delayed until to Aeronian typically demonstrated by the record of many endemic taxa from South China. The Silurian-type atrypide and pentameride communities thrived mainly in relatively shallow environments (BA2-3) during the Rhuddanian, but expanded and dominated in deeper, mid-shelf and outer-shelf settings (BA3-5) by the Aeronian.



<sup>&</sup>lt;sup>\*</sup> Speaker

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## Eocene shallow-water ostracods from the deep Tasman Sea (IODP Expedition 371)

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Early Eocene to Recent ostracod fauna were discovered in International Ocean Discovery Program (IODP) Sites U1506, U1508, and U1510 from over 1000-meter water depths from the Lord Howe Rise and Reinga Basin, Tasman Sea during IODP Expedition 371 (July 27 to September 26, 2017). Core catcher and additional section samples yielded more than 3500 specimens. Preliminary results show that abundant and diverse shallow-water taxa that are clearly distinct from the modern deep-sea faunal composition were preserved in Eocene sediments at these sites. The shallow-water taxa include ostracods with eye tubercles and species showing affinity with shelf taxa observed in Southern New Zealand and Australian areas. Future investigations will focus on the paleogeographical distribution and major turnovers of ostracod assemblages that might be associated with the tectonic and paleoceanographic evolution of this region.

Speaker

# The role of Iberian insularity in the Cretaceous evolution of charophytes

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Iberia was shaped during the Cretaceous as one of the largest islands of the European Archipelago. In the Lower Cretaceous this island formed an isolated landmass between Gondwana and Laurasia while in the Late Cretaceous it fused with parts of today's France to form the so-called Ibero-Armorican Island. The insularity of Iberia and of other neighbouring islands shaped largely the Cretaceous biogeography of charophytes and probably other groups of land plants, such as conifers. Two main patterns are observed:

*Iberia as an Early Cretaceous speciation factory*. Many charophyte species, especially of the Early Cretaceous family Clavatoraceae have their first record in the Iberian island to migrate later to other parts of the European Archipelago and elsewhere. The Berriasian and the Barremian appear to be more favorable for migration, coinciding with an increase of tectonic subsidence in intraplate basins that enhanced the development of freshwater wetlands in Iberia. Insularity does not seem to result in long-lasting endemisms but rather in a short endemic period close to the origin of each species followed in some cases by an expansion to the European Archipelago, and in rare cases continuing the migration to reach as far as China or South America. Species migrated during periods lasting from less than a charophyte biozone (ca. 2 Ma) up to 5 Ma and are in some cases important biostratigraphic tools for long-distance correlation.

The European Archipelago as a Late Cretaceous refugium. The end of the Cretaceous was a time of change for many plant groups, mainly related to the radiation of angiosperms, but insularity in the European Archipelago played a role in delaying the extinctions of some groups. The Porocharaceae dominated charophyte floras worldwide until the Early Cretaceous when they began to decrease in species richness and abundance. The last species, probably only a few of them, became extinct worldwide by the end of the Maastrichtian, while in the European Archipelago they appear to last until the Danian. Also, the last Clavatoraceae occurred in the Ibero-Armorican Island and possibly in other islands of the European Archipelago until the upper Maastrichtian, while in the other parts of the world this family became extinct generally before the Santonian (early Maastrichtian in China).

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Speaker

## Beyond the Karoo: Patterns of ecological and taxonomic diversity and recovery among vertebrates from the End-Permian mass extinction

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The End-Permian Mass Extinction (EPME) is the largest mass extinction in Earth history, with ~81% species extinction. Our primary understanding of the effects of the EPME on tetrapod communities is based on the well-sampled Karoo Basin of South Africa, which contains a continuous sequence of fossiliferous exposures spanning the extinction. This record shows that ecologically stable assemblages collapsed during the EPME. By the Middle Triassic, diversity and ecological stability increased, but not to pre-EPME levels and regained stability came from novel community structure.

For the last decade, we have conducted fieldwork in the Luangwa Basin of northeastern Zambia. The upper Permian Madumabisa Mudstone Formation and Triassic Ntawere Formation preserve successive tetrapod assemblages that are biostratigraphically correlated via dicynodont and cynodont therapsids to the Cistecephalus, lower Daptocephalus, and Cynognathus assemblage zones (AZ) of the Karoo. Recognition of a new assemblage equivalent to the Daptocephalus AZ means the Luangwa Basin contains more data on upper Permian community evolution than previously understood. For each community, we calculated richness, evenness, and relative abundances for taxa and ecological guilds. We used these data to quantify community stability using the cascading extinctions on graphs (CEG) model, and assess biogeographic patterns using bipartite network and cluster analyses. We found that during the late Permian there was high taxonomic and ecological similarity between vertebrate communities across southern Pangaea, and with similarly high-latitude communities in China. In the aftermath of the EPME, similarity decreased drastically because of heterogeneous recovery of ecosystems as tetrapods re-diversified. Our work shows that the Triassic Ntawere assemblage is much more like assemblages in Brazil and Argentina than it is to the Karoo Cynognathus AZ. Unlike the African strata, South American sequences have been radiometrically dated, calling into question conclusions on the timing and pattern of tetrapod recovery from the EPME based solely on the Karoo.

Important insights into the taxonomic and ecological composition of tetrapod assemblages before and after the EPME, and what they indicate about extinction recovery, have emerged from consideration of this novel system.



<sup>°</sup> Speaker

## Quantifying the palaeogeographical driver of Cretaceous carbonate platforms development using niche modeling

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Platform carbonates are a major component of the Earth System but their extent is difficult to reconstruct back in geological time. Coupled niche modeling and deep-time general circulation models are used to predict their occurrence at the global scale throughout the Cretaceous. The niche model uses the fuzzy logic to predict a susceptibility of occurrence of the platform carbonates as a function of the surrounding environment. The predictive variables considered include sea-surface temperature, sea-surface salinity and net primary productivity as well as a binary bathymetry mask. The first three of these parameters derive from new Cretaceous simulations conducted using a coupled ocean-atmosphere general circulation model (MITgcm) while bathymetry is taken from our paleogeographical reconstructions. Model predictions are validated on the well-documented Aptian stage by comparison with abundant geological data. Simulations are subsequently extended to other Cretaceous time slices.

Climatic simulations reasonably capture Aptian climate. Results of the niche model show overall agreement with Aptian database when an autotrophic affinity is considered for the rudist- dominated platform carbonates. The alternative, heterotrophic nutrition mode does not allow to satisfactorily reproduce the extent reported based on geological data. When changing the continental configuration, the model predicts an increase in the extent of the carbonate platforms in agreement with the geological record, mainly due to the increasing extent of shallow-water environments available to carbonate development.

Results of the simulations identify the Cretaceous long-term rise in sea level as a major driver of the increase in platform carbonate extent throughout the Cretaceous.



Speaker

## A Miocene – Early Pliocene Paratethyan type ostracod fauna from the Denizli Basin (southwestern Anatolia) and its paleogeographic implications

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The Miocene-Pliocene sedimentary succession of the Denizli Basin in southwestern Anatolia (Turkey) displays a unique record of undisturbed stratigraphy and provides an excellent opportunity to study long-term paleoecological changes, using and characterizing a previously poorly investigated Paratethyan-like ostracod fauna. In this study we further focus on the sedimentary successions of the Basin to elucidate the role of the region as a source/sink-area for Paratethyan ostracod biota. The so-called Paratethyan ostracod fauna is characterized by a distinguishable diversity originated from a variety of paleoecological domains inside Paratethyan Basins, a high rate of endemicity and a Pannon Lake origin.

The ostracods studied have been recovered from 106 samples collected from two different outcrop localities of Miocene – Early Pliocene age near Babazanan village close to the provincial captial of Denizli. The lower part of the studied succession (possible Middle Miocene) consists of a Pannonian type microfauna represented by brackish ostracods dominated by candonids associated with few leptocytherids and loxoconchids. Morphological similarities between the studied fauna and ostracods of Pannon Lake origin are remarkable still the migration patterns are questionable. The existence of an unknown intra-Turkish gateway between the Denizli Basin and the Paratethys is not to be excluded, even if there are no clear evidences found yet. An alternative hypothesis would be the assumption of long distance dispersal (LDD) of ostracods via water birds. Avian dispersal proved to be an important dispersal mechanism for introducing aquatic microorganisms into new habitats. Therefore we assume that ostracods might have been transported from the Paratethys (Pannon Lake) to the Denizli Basin, where similar ecological conditions encouraged the spreading of an endemic fauna that is remarkable similar to the one from the Central Paratethys.

The ostracod fauna in the upper part of the section (possible Late Miocene- Early Pliocene) suggests a pronounced change of the pre-existing paleoecological conditions. A shift towards a more freshwater influenced setting is marked by the evolution of an endemic ostracod fauna. This development can be related to the progressive isolation of the Basin and the formation of a terminal lake, coeval with the restoration of shallow lakes in adjacent Basins of the area.

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## New information on the dinosaurs of the Hanson Formation, and patterns of Early Mesozoic vertebrate evolution and paleobiogeography in Antarctica

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The stratigraphic sequence in the central Transantarctic Mountains preserves a unique record of high-latitude vertebrate assemblages that span two major mass extinction events, and includes three early Mesozoic vertebrate faunas. Early Triassic vertebrates have been collected in the lower Fremouw Formation around the Beardmore and Shackleton Glaciers. The Beardmore has also produced an early Middle Triassic assemblage in the upper Fremouw Formation, and an Early Jurassic assemblage from the Hanson Formation on Mt. Kirkpatrick. The Hanson Formation includes the theropod Cryolophosaurus and the massospondylid sauropodomorph Glacialisaurus, which fill major anatomical and temporal gaps in early dinosaur evolution, and reinforce the paraphyly of the classical groups Coelophysoidea and Prosauropoda. Recent field work in the Beardmore Glacier region recovered new dinosaur material from the Hanson Formation, and U-Pb zircon dates of -~194.0 Ma help constrain the site's age. New material of Cryolophosaurus, including a second braincase and two left fibulae, demonstrates the presence of at least two individuals in the quarry, and new character data added from this specimen and CT scan data corroborate a close relationship with Dilophosaurus, in contrast to recent analyses recovering Cryolophosaurus as a basal Tetanuran. A new distal right tibia represents part of the massospondylid Glacialisaurus holotype. In addition, two new species of sauropodomorph were recovered; one of which is represented by a nearly complete skeleton. Several features on the distal femur (an extensor fossa, absence of a medial epicondylar crest, transversely narrow tibiofibular crest) distinguish the new sauropodomorph from Glacialisaurus. Additional characters imply a close relationship to Ignavusaurus from the Early Jurassic of South Africa, whereas the second new species of sauropodomorph is found to share traits with Leonerasaurus from South America. The presence of three distantly related sauropodomorphs in Antarctica supports prevelant dispersal across Pangea during the early Mesozoic, but also suggests that multiple lineages of sauropodomorphs independently adapted to a polar light cycle during this time. Coupled with data from the Fremouw vertebrates, the Hanson vertebrates also suggest that early Mesozoic vertebrate faunas of Antarctica became progressively more dissimilar to other assemblages worldwide, and this rising endemism is consistent with predictions for biotic response to the increasing climatic and physiographic isolation of Antarctica from other Gondwanan landmasses during the early Mesozoic. Additional collection in the central Transantarctic Mountains and the development of comprehensive regional datasets will be essential to assessing how biotic crises in Earth history played out at different scales and across different environments and latitudes.



<sup>\*</sup> Speaker

# The legacy of past environmental changes on diversity of oceanic islands

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Models in island biogeography suggest changes in island characteristics over millions of years to influence immigration–speciation– extinction dynamics. Current day biodiversity patterns on islands thus reflect the characteristic geological ontogeny of volcanic islands (Biol.Rev.; doi: 10.1111/brv.12256). However, climatic oscillations over shorter geological timescales cause sea level fluctuations resulting in massive changes in island area, isolation and connectivity. These changes are orders of magnitude faster than the geological processes of island formation, subsidence and erosion. Using a global data set of 184 islands, we demonstrate a strong legacy of past environmental changes on angiosperm diversity of oceanic islands (Nature; doi:10.1038/nature17443). We find that changes in island characteristics caused by ice-age cycles have left a strong imprint on present diversity, particularly affecting those species that evolved in situ. We conclude that an understanding of past environmental changes in essential to understand patterns of island endemism and its underlying evolutionary dynamics.

Speaker

## Silurian and Devonian trilobites of Japan: 'eye witnesses' to the early geological evolution of the Japanese islands

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Trilobites are widely represented in the Silurian and Devonian strata of Japan, with taxa described from the South Kitakami, Hida Gaien and Kurosegawa Palaeozoic terranes. Here we present a palaeobiogeographical review of nine trilobite groups represented in the Japanese rock succession that have received recent taxonomic revision: Illaenidae, Scutelluidae, Phacopidae, Proetida, Aulacopleurida, Encrinuridae, Cheiruridae, Calymenidae and Lichidae. Silurian illaenids and scutelluids show generic and species links with the Australian segment of the Gondwana palaeocontinent; encrinurids indicate genericlevel links between the three Japanese terranes, as well as with Australia and the South China palaeocontinent; whilst Devonian phacopids, and possibly proetids, suggest generic-level links with the North China palaeocontinent. Devonian lichids suggest generic-level links with Australia. Cheirurids and calymenids show uncertain palaeobiogeographical relationships at present, but are undergoing further appraisal. The markedly different patterns between different groups may in part reflect the fragmentary biostratigraphical record of Japanese trilobites, but also appears to reflect their lithofacies ranges and palaeoecology. Thus, lithofacies appears to exert controls on the widespread distribution patterns of Japanese proetids and phacopids in deep-water clastic lithofacies, which also occur in North China. Japanese scutelluids and illaenids are strongly associated with shallow marine carbonate lithofacies that are similar to those of their occurrences in Australia. These constraints caution against the use of the Japanese trilobite assemblages for palaeobiogeographical assessment without a fuller understanding of their palaeoenvironmental context.



Speaker

## Lucinid bivalve fossils from Miocene hydrocarbon seep sites in the Hawke Bay area of North Island, New Zealand, with remarks on the Miocene hydrocarbon-seep fauna in New Zealand

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Three fossil species of lucinids are recorded from lower to middle Miocene hydrocarbon seep carbonate deposits in eastern North Island, New Zealand. Three species of *Meganodontia*, *Elliptiolucina* and *Lucinoma* are proposed as new species. Of these taxa, *Meganodontia* only occurs in the Ihungia Limestone in the southern East Coast Basin (ECB), a Miocene forearc basin of the Hikurangi convergent margin. Elliptiolucina occurs only in the Bexhaven Limestone in the northern ECB. Based on the depth that living representatives of *Meganodontia* and *Elliptiolucina* are found, the difference in the fossil faunal distribution can be explained, because the seep deposits of the dominantly micritic Bexhaven Limestone formed in deeper water than the seeps in the sandier Ihungia Limestone. Among the lucinids, *Meganodontia* is one of the oldest records of the genus, and its distribution has shrunk from worldwide in the Miocene times to only around Taiwan today. *Elliptiolucina* is the second oldest species in the genus. Since the Miocene the distribution of *Elliptiolucina* has narrowed but its habitat range has increased to both seeps and sandy environments, mainly around the Philippines.



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#### The Jurassic marine reptiles of Mexico

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The fossil record of marine reptiles between the western Tethys and eastern central Pacific, trough the Hispanic Corridor, has been increased in the last years, particularity in Late Jurassic localities of Mexico. The first Mesozoic marine reptiles of in this country were collected in the 19th century, with isolated report or lost materials, but in last years that have changed with new discovered of the localities and new fossils material. Here we showed this new discovered in Mexico and its biogeographical significant. Such Mexican fossils correspond to the four major groups of marine reptiles. Talattosuchian crocodyliforms are well represented in Mexico, and include metriorhynchid species, as Cricosaurus saltillensis, Cricosaurus vignaudi, Torvoneustes mexicanus, and specimens attributable to Dakosaurus, Maledictosuchus, and Geosaurus, as well as an indeterminate primitive Talattosuchian species. The pliosaurids are well represented by specimens of Liopleurodon and abundant indeterminate isolated bones. The Talattosuchian and Pliosauruds found in the western Tethys Sea (Cuba, and Mexico) show strong affinities with the faunas from the eastern Tethys Sea Europa. A recently Jurassic turtle Notoemys tlaxiacoensis described by the south of Mexico complete the patterns for the genus thought of the Hispanic Corridor and support the hypothesis of the diversification of this group occurred on the Corridor. Abundant remains of ichthyosaurs of the Family Ophtalmosauridae are also present in México, as Ophtalmosaurus cf. icenicus, Ophtalmosaurus sp. by the northeast of Mexico, and a new genus for the northwest of Mexico. The association of ichthyosaurs in the Hispanic Corridor has unique and shared element with the eastern Tethys Sea. The taxonomical groups represented in this Mexican fossil association of marine reptiles show particular distribution of each marine reptiles group, but a weak relationship with those American similar fossiliferous.



Speaker

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### Plio-Pleistocene diversity of the tribe Galictini (Mammalia, Carnivora, Mustelidae) across Eurasia. The state of art

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The taxonomic status of the subfamily Galictinae of Mustelidae has been highly debated in the literature with no unanimous agreement yet. In the last twenty years, research has greatly improved our knowledge of these mustelids both from a palaeontological and from a neontological point of view: e.g. new evidence of a greater paleodiversity previously not recognized in literature thanks to recently described new genera Oriensictis and Martellictis; molecular phylogenies showing that "Galictinae" should be better grouped under the subfamily Ictonychinae with the genera Ictonyx, Poecilogale and Vormela. Here we review the most recent studies on the fossil members of the tribe Galictini in the light of their biogeographic dispersion. One of the oldest Eurasian taxon of this tribe is Pannonictis, as the earliest specimens related to this genus may be those from Late Miocene sites of China. During the Pliocene, few records testify to the beginning of the westward expansion of this mustelid (found in: Wölfersheim, Germany and Etulia, Moldova) and also to the appearance in Central Europe of Martellictis (Ivanovce, Slovakia) and of the genus Eirictis in Mongolia (Shamar) and China (Yushe basin). The peak of radiation of these small- to medium-sized mustelids was reached during the Early Pleistocene, when these three genera become important elements of faunas throughout Eurasia, differentiating into numerous species. For instance, from the Chinese localities of Longdan comes E. robusta and from Renzidong, E. variabilis. In Europe, three Pannonictis species have historically been recognized: P. pliocaenica, P. pilgrimi and P. nestii from various localities of Europe. In the second half of the Calabrian, their fossil evidence is very scarce although Galictini are recorded for the first time in the African continent (Tighennif, Algeria) and in the British isles (West Runton). One of the most interesting record is that of the Early to late Middle Pleistocene Sardinian site of Monte Tuttavista, in which appears an early member of the genus Enhydrictis. This peculiar taxon, exclusive (endemic) of Sardinia and Corsica, developed anatomical similarities with members of the subfamily Lutrinae and was probably adapted to an aquatic lifestyle. Lastly, in the Middle Pleistocene of Eastern Asia appears Oriensictis, in Zhoukoudian 1 (China) and in Matsugae cave (West Japan). The variety of the morphologies of the Eurasian Galictini is indeed remarkable, deeply studied but yet not fully understood, especially considering the relation with the habitat they lived in or with the instable climatic context of Plio-Pleistocene times.



<sup>&</sup>lt;sup>°</sup> Speaker

#### Taxology and biogeography of Longfengshan biota

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Macroalgea as the most thriving biotes, worldwide distruibution and morphological stability, in early Neoproterozoic(1000-780Ma), characteristic as Chuaria-Tawuia-Iongfengshania. Longfengshan Biota, as the first macroscopic algal biogroup(Chuaria -Tawuia -longfenshania) in Neoproterozoic, has great signaficance for knowing the biology and its evolution. With the research results of microobservation and morphological statistics analysis of the new samples, we reconstructs the former taxonomy system, revises the generic characters of Chuaria and Longfenshania, and agrees with that the elliptic, oval, glossoic, bangdin, roblike shape fossils and their elongate individuals are all synonyms of Tawuia, which viewpoint from Hofmann. Introducing modern morphological statistics analysing method-Systemic Clustering, we classify five morphology types of Longfengshaniaceae. As the same time, macroalgeas of Longfengshan Biota can be found worldly in the nearshore shallow water basin and lagoon, early Neoproterozoic (Qingbaikou Era,1000-780Ma), when Rodinia Supercontinent is in aggregation. We analyse Longfengshan Biota systematicly, and find out a standard biometrics and bioassemblage of marcroalgea in that time. According to the correlations with credible biota date reported worldly, we make the paleobiogeographic analysis of the marcroalgeas and zoning them into a North China Craton(NCC)-North Luran(NL) Region, character with Chuaria-Tawuia-longfengshania and the same regional changing discipline in each other, and a South China Craton(SCC)-Great India Craton(GIC) Region, characteristic simpl Chuaria-Tawuia, they constitutes a big low latitudes Macroalgae Realm. Comprehensive the results and previous research consequence, we suppose that, in 1000-780Ma, NCC should have more cloes relations with WL, in the centre of the Rodinia, and SCC locates in the western margin, nearby GIC.

Speaker

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### Paleobiogeographic significance of the Janthinid snails on the Japanese Islands based on fossil and modern records

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Marine gastropods in the family Janthinidae are widely distributed around the Japanese archipelago and are a common component of the macroneuston around the world. The members of this family are pelagic and live at the ocean surface by constructing bubble-rafts comprised of mucus-coated air bubbles. The stratigraphic positions and geologic ages of Japanese Janthina fossils are divided into the Late Miocene to Early Pliocene horizon and the Early Pleistocene horizon. The Late Miocene to Early Pliocene (Messinian-Zanclean) horizon is correlated with Blow's N17-N18 boundary (ca. 6-5 Ma), represented by Janthina typica, and assigned to the warm event belonging to the tropical-subtropical realm. The Early Pleistocene (Gelasian) horizon is correlated with Blow's N21 zone (ca. 2 Ma), characterized by Janthina chavani, and is also assigned to the warm event belonging to the subtropical realm. Fossil records of Janthina species in the former horizon are limited on the Pacific Ocean-side of Japan because of incursions of the warm Kuroshio Current at that time. In modern Japanese waters, the Janthinidae is mainly represented by Janthina globosa, J. janthina, J. umbilicata and J. pallida, which are primarily distributed in southwestern Japan and are rare in northeastern Japan. Janthina globosa and J. janthina are found on the Pacific Ocean- and Japan Sea-sides of Japan, and the northern limits of these species are Ishikari Beach and Otsu Beach in Hokkaido, respectively. The remaining species, J. umbilicata and J. pallida, are distributed mainly on the Pacific Ocean-side of the archipelago. Inflow of the warm Tsushima Current transported Janthina species on the Japan Sea-side northward from southern regions have appeared during the Holocene period. The paleobiogeographic significance of fossil and modern Janthinid snails is illustrated in this study and the relationships among their distribution, water currents and sea surface temperatures are discussed.



<sup>'</sup> Speaker

### Report of possible ?*Phyllograptus* at the Ordovician/Silurian strata of the Paraná Basin Northern border, Brazil

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The samples were collected from diamictites and shales with dropstones of the Vila Maria Formation (Late Ordovician/ Early Silurian) from Mato Grosso State, Central Brazil. These are the beds of the Late Ordovician glaciation, an interval when most of the Gondwana is interpreted as being covered by an immense ice sheet. The studied sedimentary rocks represent a transition to a lowstand system tract (LST) followed by a transgressive system tract (TST); the depositional environment is a glacially influenced shallow epicontinental sea. Two samples, fragmented due to field work, were recovered. The specimens are black films, having both a dark coloration. They do not show volume and contrast with the light-colored matrix. Their shapes (3-4 cm) are rounded with several small protrusions on their margins. These protrusions (4 mm) are similar to small hooks, *i.e.*, slightly elongated and curved, tapering at their extremities. These samples are being correlated to the genus ?Phyllograptus Hall, 1858, a type of graptolite that has four thick stipes, arranged (rhabdosome) in an overall oval shape. The protrusions are interpreted as the thecae. No nema or sicula was observed in these specimens. The samples have been analyzed under SEM microscopy, EDS chemical analysis, and Raman spectroscopy. The SEM sample was covered with gold and analyzed under 20 and 30 kV tensions. No BSE and SE images were taken, once no structures could be identified. The EDS analysis showed a higher concentration of Fe, O, and Al at the black film. The other sample, bigger and better preserved, was submitted to the non-destructive Raman spectroscopy technique. The analysis shows the wider G band, and a tall and elongated D band; these features are typical of a well preserved kerogen. Assuming that the carbon is biogenic, no known macro algae of the Ordovician have the structures observed in these specimens. Organic microfossils pertaining to this interval (Late Ordovician/ Early Silurian) are being studied and can bring new information in relation to the age of the strata. No occurrence of graptolithes was previously recorded on these beds, and there are different opinions on the age of these strata.

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Speaker

# S33 - Shell beds through time: implications for palaeoecology, taphonomy and evolution

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### *Aturia* (Nautilida) shell beds in the Upper Eocene Brito Formation of S-Nicaragua: mass mortality and transport into a deep water turbidite fan environment

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A "Nautilus" shell bed, long known to local geologists, crops out in a cliff W of El Remanso Beach (suppl. a, former name: El Sucio, Rivas, S-Nicaragua,  $11^{\circ}13'14.8"$ N;  $85^{\circ}51'6.3"$ W). We measured a 9 m thick sequence of 11 lenticular *Aturia* shell accumulations, comprised in an overall coarsening-thickening upwards turbidite fan sequence of the upper Brito Formation. The sequence starts on the beach with basin-plain distal sand-mudstone turbidities. After a syn-sedimentary deformed interval, a sequence of rapidly thickening, coarse sandy channelized turbitites/grain flows crops out in cliffs (suppl. e), accessible even at high tide. The11 layers contain > 100 visible *Aturia* and occur systematically at the base of individual fining-upwards channel-fill sequences. *Aturia* bed No. 3 (suppl. b) is the most spectacular one, preserved on an overhang as the exposed bottom of a channel fill. A 2 m2 surface yields 33 slightly imbricated *Aturia*, ranging in diameter from 18 to 45 cm. Many specimens show an intact body chamber (suppl.c) and totally lack bio-corrosion. While the outer whorls are intact, many specimens reveal fracturation of the inner, more fragile whorls, and injection of the sand matrix from the broken inner whorls into the chambers is indicated by convex lamination (suppl. g). Collected entire specimens show suture lines and the sometimes preserved outer shells, indicating a monospecific assemblage tentatively assigned to *Aturia peruviana* Olson (suppl. d). Larger Benthic Foarminifera such as *Nummulites* spp., *Operculina* sp. and *Lepidocyclina* sp. of Late Eocene age, and common terrestrial plant remains co-occur with *Aturia*, attesting for a shallow marine origin of the coarse sandy channel fills.

SEM and Cathodoluminescence (suppl. f) analysis of polished and slightly etched shell sections reveal a coarse calcite spar replacement showing pseudomorphosis after the typical stacked platelets of the original aragonite. Shell surfaces are mineralized by black Fe-oxides.

We propose the following scenario for the formation of the *Aturia* beds: Large groups of adult *Aturia* were feeding in an offshore forearc area below wave base, where terrestrial input of plant material and probable coastal upwelling provided a basis for a rich epibenthic food web. Large volumes of coarse sand were mobilized in a shallower shelf area by storms or earthquakes, reached the feeding grounds as high density turbidities or grain flows and dragged the still living *Aturia* downslope into the channels of a turbidite fan system. The inner whorls of many specimens imploded under the high water pressure and the gas-filled chambers became intruded by the flow matrix. The absence of bio-corrosion and overgrowth of shells indicates that the *Aturia* shells were not previously exposed on a substrate, nor to floating. The overall coarsening upwards sequence culminates above the *Aturia*.

To our knowledge, this is the first report of *Aturia* mass-accumulations in a deep water, turbiditic environment.

Speaker

IPC 5

### Why the oysters are often overlooked? The challenging case of Pliocene oysters from Valle Botto area (AT, NW Italy): taxonomy, paleoecology and morphometry

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This preliminary study is aimed at palaeontology of Cenozoic Ostreoidea with a special attention paid to systematic and morphometric analyses of Pliocene oysters from BTP (Tertiary Piedmont Basin, northwestern part of Italy). The most common oyster species is represented by Ostrea edulis Linnaeus 1758, stored at "Museo Paleontologico Territoriale dell'Astigiano" of Asti and at Geological and Paleontological Museum of University of Turin, NW Italy. The samples come from Valle Botto (nature reserve, AT, NW Italy) beloging to the Asti sands, Middle-Upper Pliocene. The deposition environment is referred to the transition from the circalittoral to the infralittoral zone, particularly due to the facies that marks the gradual transition from silty to sandy sediments (Caretto, 1963; Damarco, 1983). In particular at Valle Botto the transition facies marks the boundary between the "SFBC" (fine well calibrated sands) paleocommunities and the "DL" detrital biocenosis, rich in Neopycnodonte genus (Baroncelli, 1997; Zunino, 2008). Some of the studied specimens manifest moderate bioerosion and bioencrustation caused typically by sponges, bryozoans, worms and bivalves (oysters as well); we can observe reticular, channel shaped and punctuate structures, referable to the Entobia and Gastrochaenolites traces. Morphometric analyses included the measurements of shell height (H), shell maximum length (W), hinge length (W1), distance between resilifer area and upper part of the muscle scar (H1), ventral length (W2), distance between lower part of the muscle scar and ventral margin (H2) and opening angle of the muscle scar ( $\alpha$ ). Ratios W/H, W1/H1 and W2/H2 were compared, through a regression analysis, often highlighting a linear correlation among these parameters; we propose using these models in the determination of the uncertain species. Especially on the left valves in comparisons with right valves this proportion is evident, where the ratios are represented by 2nd degree polynomial function.

The second goal, in reference to the previous studies (Miocene oysters from Carpathian Foredeep) and analyses on 3D oyster reef, is characterized by developing a "workflow" for the analysis of the oyster morphospace, based on the morphometric profile, from the 2D oyster model to the 3D model, in order to get a retopologied shape; in this way we can match qualitative data analyses from all oyster samples.



Speaker

## A monotaxic lingulid brachiopod bed provides information on palaeoenvironments in the Upper Devonian Witpoort Formation (Witteberg Group, Cape Supergroup, South Africa)

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A laterally extensive organic rich mudstone horizon in the lower part of the Witpoort Formation, was sampled during road excavations. It preserves numerous lingulid brachiopod shells, distributed in patches over 3.5 km of outcrop. Both bedding-oblique (in-situ) and bedding parallel valves are concentrated in the upper part of the mudstone layer, which has a maximum thickness of 12 metres. Lingulids are associated with transported, fragmentary terrestrial plant remains, which are sparsely distributed throughout the layer. A large sample of bedding parallel valves (n=121) showed a greater degree of variability in width to length ratio than expected for a species of Palaeozoic lingulids. Variability in shell shape and dimension in the sample formed a continuum and we therefore attribute all valves to a single taxon, comparable to Dignomia (Lingula) lepta (Clarke, 1912, emended Emig, 2003, 2006). This degree of variability is congruent with studies of extant taxa, suggesting that width to length ratio is a poor taxonomic character for lingulid brachiopods. Sedimentological analysis indicates an extensive backshore lagoonal lake influenced by washover, tidal and fluvial inputs. A planar beach barrier deposit separates this environment from underlying deposits of a high energy shoreface. Exceptional tolerance to stressful environmental fluctuations and an infaunal mode are characteristic of extant lingulidae. Their abundance here, in the absence of associated Devonian marine shelly taxa, is consistent with reduced salinities. We propose that fluctuating salinity levels in this palaeoenvironment excluded both marine and brackish water shelly invertebrates, allowing lingulids to dominate – thereby resulting in a monotaxic assemblage.



Speaker

# Clypeasteroid echinoid shell beds: sedimentology, taphonomy and paleoecology

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Shell beds consisting of mass occurrences of clypeasteroid echinoids are a common feature of Cenozoic sedimentary successions. Recent detailed studies have been conducted in the field in Sardinia, Catalonia, California and the Southeastern Unites States, augmented by the examination of extensive museum collections as well as a literature survey. These deposits are known to range from the Eocene onwards in age. Detailed field studies encompass the assessment and, if possible, quantification of sedimentary features, depositional biofabrics, accompanying faunal elements, trace fossils, size frequency distributions as well as preservation styles and orientations. In general, these echinoid deposits represent monotypic assemblages, or contain at most only few taxa. Preservation ranges from excellently preserved complete tests often admixed with highly fragmented material which can lead to the presence of an echinoid rudstone with grain- or packstone matrix. The deposits vary in complexity with respect to component densities, preservation patterns, fragmentation rates, and orientation of the echinoids. A wide variation of depositional environments in both siliciclastic and carbonate environments are recorded. These mass occurrences occur within shallow water deposits, with varying water movement, though often representing higher energy conditions. The origin of these shell beds is related to 1) high original densities of sand dollars which are known to occur in recent clypeasteroid populations, 2) increased preservation potential of the multi-plated shells of clypeasteroids which is correlated to the presence of internal supports and interplate skeletal connections, and 3) the concentration of these biogenic components by wave movement as well as by winnowing. The conspicuously wide stratigraphic and geographic occurrence of these mass shell deposits closely follows the evolution and distribution of clypeasteroid taxa and their exploitation of generally, higher energy shallow water environments.



Speaker

#### **Ecological information from transgressive shell beds**

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Transgressive horizons are important markers in basin analysis and sequence stratigraphy. Although transgressive shell beds are rich in palaeontological information, it is very difficult to interpret their condensed information ecologically because they tend to be strongly time- averaged by physical or biological reworking. Only very recent efforts in dating shells of Holocene sediment-starved shelves disentangled the stratigraphic and ecological complexity of transgressive shell beds. Here, we document temporal abundance in abundance of mollusks and their preservation in beds with varying shelliness from sediment cores from the Holocene of different areas of the northern Adriatic Sea. From a geological perspective all the 1.5 m long sediment cores, each covering > 7000 year of ecological history, can be summarized into relatively simplistic lithostratigraphic units, based on sedimentology, taphonomy, and faunal content. Unmixing the stratigraphic record on the basis of dated shells of Corbula gibba, Timoclea ovata, and Gouldia minima, we show that the reconstructed fluctuations in abundance either do not correlate or correlate only to some degree with abundances of these bivalves in the raw stratigraphic record. For example, the raw stratigraphy does not reliably estimate the timing of C. gibba outbreaks in the northern Gulf of Trieste, which are indicative of hypoxic conditions on modern shelves, even when death assemblages do not show signs of condensation. A shell bed with high abundance of G. minima in the southern Gulf of Trieste does not reveal a recent most decline in abundance of this species. Our dating efforts show that benthic assemblages of different areas of the Northern Adriatic shelf can be grouped into similar age bins, but they all are very distinct and preserve strong spatial ecological heterogeneity that would be only poorly recognized with standard palaeontological field practices.



Speaker

### Upper Triassic (lower Carnian) terebellid build-ups from Slovenia

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Lenses with high density of terebellid agglutinated worm tubes in lower Carnian limestone at Lesno Brdo (central Slovenia) are interpreted as biogenic build-ups. This is the first example of such mounds

The massive limestone containing terebellid tubes is exposed in an active quarry of natural stone. Terebellid lenses are embedded in micritic limestone (mudstone, wackestone, packstone and partly washed-out packstone with peloids and bioclasts). Besides terebellid lenses, metres-scale globular masses of sponge-microbialite boundstone are present. Large amount of fragments of dasycladacean algae and common platform-dwelling foraminifers, as well as the lateral transition to bedded dasycladacean dolostone suggest deposition on a shallow marine carbonate platform. Rare levels of mosaic blocky breccia with violet claystone matrix, and lenses of violet and green claystone are presently interpreted as short emersion phases, although no definite proof of vadose conditions has been found. A major palaeokarst surface at the top of the quarry marks the final demise of the platform in the lower Carnian.

Lenses of accumulated worm tubes are irregular in shape, up to several metres long and more than 1.5 m high. Specimens are up to 10 cm long and 9 mm in diameter, slightly curved, lying horizontally or slightly oblique to the former sea floor (position shown by geopetal structures). Tube walls are composed of bioclasts (mollusc and algae fragments, rare ostracods, foraminifers and echinoderms) and peloids from the surrounding matrix. The build-ups originated from the baffling effect of the upper tip of the tubes, which protruded above the sea floor, and the branching feeding tentacles of the animal. Fine-grained sediment deposited between protruding tubes, thus allowing entire population of worms to gain small elevation above the sea floor. The lateral extent of the colony subsequently widened, when the sediment supplied to the surrounding of the mound was slow, or contracted, when sedimentation rate was high.

encountered in the fossil record.

IPC 5

<sup>&</sup>lt;sup>'</sup> Speaker

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### Precambrian shell beds consisting of body fragments of Ediacaran macroorganisms

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In the stratotype section of the Ust-Yudoma formation (southeast of the Siberian platform, Russia), a type of organogenic-detrital rock closely resembling a typical Phanerozoic shell bed is found in layers, attributed to the Ediacaran both paleontologically and according to isotope dating. The rock is a finely cavernous dolomite of light gray color. In places, thin angular plates and curved shells of centimeter dimension make up more than half of its volume by visual observation. The layer of this rock is 1.5 - 2 m in thickness and can be traced along the outcrop for at least 0.5 km. Very rarely there are more or less complete objects that have become a source of debris in the layer. They have the appearance of discs or very low and wide goblets, covered with sharp concentric folds. The fossil was described long ago as Suvorovella aldanica Vologdin et Maslov, 1960. In its general morphology, Suvorovella is very similar to the attachment structure of the frondomorph, Aspidella terranovica Billings, 1872, which is the usual component of most localities of Ediacaran macrofossils. However, in contrast to initially entirely softbodied Aspidella consisting of organic matter, the remains of Suvorovella were solid and mineralized from the very beginning. A microscopic examination showed that fossils are secondary structures and represent incrustations composed of crystalline high-magnesia calcite. Fossil plates consist of two layers, given that the surfaces of the layers facing each other bear the impressions of the organism's body, and the inverted ones are covered with druses of calcite crystals. Apparently, during the fossilization process, the initial substance of Suvorovella was completely dissolved and gave material for incrustations. The acute-angled features of the fragments and no evidence of roundness of the crystals' apexes indicate that the original structures of Suvorovella were also solid. The process of precipitation of the secondary mineral on the fragments and bodies proceeded after the formation of the sediment. An enrichment of the incrustations with calcium in comparison with the dolomite of the host rock indicates the predominance of this element in the composition of the primary substance of the buried organism. Most likely, the outer parts of the Suvorovella dis consisted of calcium carbonate (aragonite?). Thus, the Yudomian finding shows that the Ediacaran organisms were not always completely soft-bodied, but could also form clastic rocks of the Phanerozoic appearance under carbonate sedimentation conditions.



### The first finds of Tridacninae in the Middle Miocene of Eastern Europe

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In the North-West of the Republic of Moldova, on the left bank of the PrutRiver, there is a complicated barrier type organogenic reef zone which is an extension of the Volyno-Podolian area of the Western Ukraine territory. This zone is represented by ridges and massifs that have a stretch along the North-West – South-East line over 90 km with a maximum width of 36 km. The Tridacninae pieces were discovered by the author in 2016 in the limestone quarry in Duruitoarea Veche (Râșcani district, the Republic of Moldova). They are represented by several fragments of a single shell (maximum width: > 1.5 m, wall thickness: 18-25 mm) and other smaller fragments collected at the same stratigraphic levels, which may belong to several other specimens. The structure of the walls is layered. The edges are wavy.

Some fragments of the shells have evident traces of volcanic ash that are a result of volcanic eruptions in the Carpathian mountains. The aggregates of gypsum crystals reflect a stagnant state of water over-saturated in calcium sulphate in the sea basin.

The deposits from which the pieces were collected are represented by reef chalks which correspond to the late Badenian substage in the Central Paratethys, the middle Miocene. From a faunistic point of view, these are well characterized and served as a reference for the reefogenic formations of the regions of Central and South-East Europe.

Associated fauna collected from the same stratigraphic levels of the quarry is represented by numerous specimens of mollusks, coral fragments, worms and their traces. It has been described from similar deposits in the adjacent localities: Şapte Bani, Văratic, Gordinești, Druță.

As regards the territory of Europe, findings of Tridacninae from the Eocene and the Oligocene (species of *Avicularium* and *Byssocardium*) as well as from the late Miocene (species of *Tridacna* and *Hippopus*) are known. The discovery at Duruitoarea Veche is the first from the middle Miocene of Europe and the most eastern within the territory of Europe.

Speaker

33 // Poster

### Time averaging of molluscan assemblages in shell beds: effects of temporally-variable production and mixing

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Oceanographic and evolutionary inferences based on fossil assemblages in shell beds can be obscured by age offsets due to slow sedimentation or mixing. However, estimates of sedimentation can be biased by mixing and/or by temporally-variable production, thus obscuring estimates of temporal resolution of fossil assemblages. To identify the effects of sedimentation, mixing, preservation, and production on age offsets within and between two bivalve species in Holocene shell beds, we simulate the effects of variable production and variable mixing on downcore age distributions, and compare them with downcore changes in postmortem age-frequency distributions (AFDs) observed on the southern California Shelf. We find that (1) within-species age offsets (inter-quartile age range) attain ~50-500 years in Parvilucina and ~2,000-4,000 years in Nuculana and between-species offsets (difference in median age) attain 1,000-2,000 years in the upper 20-25 cm, and (2) with increasing sediment depth, offsets within both species attain 2,000-5,000 years but between-species offsets become minor. Within-species offsets exceeding 2,000 years are in accord with the offsets expected under low sedimentation rate (~0.01 cm/y) and ~20-25 cm-thick, completely-mixed surface layer. However, (1) sediment depths over which 1,000-yr cohorts are distributed exceed 20 cm and (2) thousand-year old shells in the top-core 25 cm demonstrate that they were exhumed from deeper, incompletely-mixed layers. Unmixed production trajectories show that abundance of Nuculana declined were over the past centuries whereas abundance of Parvilucina increased in the 20th century. Out-of-phase production of these two species, coupled with advection of older Nuculana shells to surface, can generate millennial-scale offsets between ages of these two speccies. Estimates of sedimentation rates and the mixed layer thickness can predict within-species temporal resolution to some degree but they do not fully account for incomplete mixing.

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Speaker

## S34 - Testing and developing phylogenetic methods in palaeontology

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### Defining discrete characters using geometric morphometrics: an empirical investigation using macropods

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Morphological data are crucial in evolutionary inference for merging fossils into the tree of life, for calibrating molecular dating, and for overcoming survival biases in inferring biological patterns and processes. Despite the long history of morphological phylogenetics, and important contributions, analyses remain dominated by highly subjective character selection and state definition, which in turn result in highly correlated homoplasy that can mislead phylogeny reconstruction. Geometric morphometrics and multivariate statistical analyses provide an array of tools to study variation in continuous morphological traits, to identify non-phylogenetic correlation among characters and analyse trait distributions. We are applying these methods to a dataset of mandibular and postcranial element 3D surface scans from macropods (kangaroo and their kin). In the case of macropods we find that geometric morphometric methods present similar biases as traditional character coding, whereby ecologically/functionally correlated character complexes can overwhelm phylogenetic signals. However, geometric morphometrics are well suited to objectively delineating character states that are corrected for non-phylogenetic signals, such as from allometry and diet. These innovations are showing strong promise for improving congruence between morphological and molecular phylogenetic inference.



Speaker

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### Is parsimony dead? Bayesian and parsimony phylogenies tested using both empirical and simulated morphological data

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All evolutionary inferences require reliable phylogenies. Morphological data has traditionally been analysed using parsimony methods, whilst likelihood methods are more commonly applied to molecular data. Recent simulation studies have suggested, however, that the Bayesian Mk- model is more accurate for morphology analyses. This is potentially problematic as very different trees can be derived using these methods. Here we simulate data under two distinct models. The first uses a birth-death process to build trees and matrices. The second uses selection of digital organisms in a mutating fitness landscape. In addition to these simulated data, 31 independent empirical datasets were used to compare trees derived from molecular data (using a priori specified models) with trees derived from morphological data through Bayesian and parsimony searches (including both equal and implied weighting). For all comparisons we used both Robinson-Foulds and SPR tree distance metrics. The results of these independent analyses are in conflict: simulation studies suggest that parsimony outperforms Bayesian, whereas empirical data finds higher congruence between molecules and morphology analysed under Bayesian inference. How these results are applied to tests of evolutionary hypotheses depends upon the confidence placed in the realism of simulations versus the reliability of empirical molecular data.



S34 // Oral

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#### The genomic view of diversification

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Evolutionary relationships between species are usually represented as phylogenetic trees. Current methods rely on the paradigm that gene trees are all cast in the same mold, the species phylogeny, with incomplete lineage sorting (ILS) due to random coalescences as the unique locus-specific degree of freedom. This paradigm is materialized in a model called 'multispecies coalescent' (MSC) where gene lineages are enclosed in the rigid tubes of the species tree. However, the presence of gene flow (introgression or hybridization) is now widely recognized between closely related species and even between distant species. Moreover, the ubiquity of genetic exchange across the Tree of Life, suggests that gene flow occurred many times in the evolutionary past and might actually be an important cause of discrepancies between gene histories. To fill this methodological void, we propose a new, plastic framework based on coalescent theory to model the joint evolution of gene and species lineages acknowledging the importance of gene flow and relaxing the hierarchy between the species tree and gene trees. This genomic vision of diversification is close to Wu's genic view of speciation, reconciling phylogenomics with our current knowledge of species diversification.



Speaker

### The effect of discrete morphological character covariation on the accuracy of divergence time estimates in a Bayesian framework

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The appearance of total-evidence approaches to divergence time estimation has promised to refine evolutionary timescales through the inclusion of all available palaeontological data. This includes both fossil and extant cladistic morphological data, which aid in the estimation of evolutionary rates, and therefore timescales, in total-evidence trees. Despite the renewed importance of morphological data for the estimation of timescales there is a reliance on a nÁ'ive model of morphological evolution, the Mk model, which has seen little development in the past two decades. It seems likely that the simplistic assumptions of this model will exert a strong influence on the accuracy of age estimates, given the importance of morphological data in the total-evidence framework.

One strong assumption of the Mk model is that characters evolve completely independently of one another, and that the likelihood of a dataset given a tree is simply the product of the likelihood of each individual character on the same tree. It is easy to see how the assumption of independence can be violated in empirical datasets when considering characters that exist in close proximity to one-another.

Through a simulation framework we demonstrate the effect of varying levels of character covariation on the accuracy of divergence time estimates obtained using the Mk model. We elucidate cases where the influence of character covariation can profoundly impact age estimates, and also cases where character covariation presents less of an issue for the accuracy of total-evidence age estimates.



Speaker

# Comparative cladistics of basal Sauropodomorph interrelationships

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Basal Sauropodomorphs have been thoroughly studied in recent years. Several hypotheses on the interrelationships within this group have been proposed, ranging from a complete paraphyly, where the group represents a grade from Basal Saurischia to Sauropoda, to a monophyletic group. The grade-like hypothesis is the most accepted, although the relationships between the different taxa are not consistent amongst the proposed scenarios. These inconsistencies have been attributed to missing data and unstable (i. e., poorly preserved) taxa. Nevertheless, an extensive comparative cladistic analysis has found that these inconsistencies come from the character coding and character selection, plus the strategies on merging data sets. The characters were then reassessed, recoded, and rescored to produce a new character list and a super-matrix. Partition analyses performed on these new and old data sets have found consistencies in the interrelationships within Basal Sauropodomorpha, and has cast doubt on the validity of several clades and taxa, such as Massospondylidae, *Massospondylus, Yunnanosaurus*, and *Coloradisaurus*. The results of these studies also highlight a different scenario on how quadrupedality evolved, independently originating twice within the group, and provide a better framework to understand the palaeo-biogeography and diversification rate of the first herbivore radiation of dinosaurs.



Speaker

### Impact of errors on cladistic inference: simulationbased comparison between ordered parsimony, unordered parsimony, and three-taxon analysis

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Simulation-based and experimental studies are crucial to produce empirical arguments to solve theoretical and methodological debates in phylogenetics. In this study, we obtain simulation- based results that address two debates: 1) Under which conditions should character states be ordered? 2) How does the performance of 3ta compare with that of parsimony? Here, we build upon our recent work to investigate additional cases, especially the capacity of methods to manage various sources of error and homoplasy, a topic that has almost never been studied. By applying ordered and unordered methods to datasets with iterative addition of errors in the ordering scheme, we show that unordered coding in parsimony is not a more cautious option. A second debate concerns how to handle reversals, especially when they are regarded as possible synapomorphies. By comparing analyses of reversible and irreversible characters, we show empirically that 3ta manages reversals better than parsimony. For Brownian motion data, we highlight that 3ta is also more efficient than parsimony in managing random errors, which might result from taphonomic problems or any homoplasy-generating events that do not follow the dichotomy reversal/convergence, such as lateral gene transfer. We show parsimony to be more efficient with numerous character states (more than four), and 3ta to be more efficient with binary characters, both methods being equally efficient with four states per character. We finally compare methods using two empirical cases of known evolution. Contrary to most recent studies in this field, the method (ITRI, for Inter-Tree Retention Index) that we use to compare experimental results to the true (simulation) tree is based on an asymmetric method that works on rooted trees. This method, which our group proposed in 2013, allows discriminating between resolving power (ability to recover correct clades) from artefactual resolution (recovered clades that are not present in the simulation tree).



<sup>&</sup>lt;sup>'</sup> Speaker

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## Parsimony, not Bayesian analysis, recovers more stratigraphically congruent phylogenetic trees

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Reconstructing evolutionary histories requires accurate phylogenetic trees. Recent simulation studies suggest that probabilistic phylogenetic analyses of morphological data are more accurate than traditional parsimony techniques. Here we use empirical data to compare Bayesian and parsimony phylogenies in terms of their congruence with the distribution of age ranges of the component taxa. Analysis of 167 independent morphological data matrices of fossil tetrapods finds that Bayesian trees exhibit significantly lower stratigraphic congruence than the equivalent parsimony trees. As such, taking stratigraphic data as an independent benchmark indicates that parsimony analyses are more accurate for phylogenetic reconstruction of morphological data. The discrepancy between simulated and empirical studies may result from historic data peaking practises or some complexities of empirical data as yet unaccounted for.



Speaker

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# Bartering accuracy and precision in phylogenetic reconstruction

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The principal aim of phylogenetics is to reconstruct a tree topology that precisely and accurately represents the true evolutionary relationships between taxa of interest. In those many cases where available data do not unambiguously indicate a perfect tree, we must choose between phylogenetic methods that make different trade-offs between precision and accuracy. One way to compare methods is to generate a dataset from a particular tree topology, and see which methods most accurately reconstruct the generative tree from the simulated data. But a focus on accuracy can overlook precision; a completely unresolved tree is entirely accurate, but completely useless. I contend that the best tree is that which is most *informative* with respect to the generative tree; accuracy and precision are complementary aspects of information. Considering precision alongside accuracy has significant implications for best practice. Equally weighted parsimony is only more accurate than implied weighting because it is less precise. Bartering precision for accuracy (by collapsing the nodes with least support) shows that equal weights produces a less accurate tree at any given level of precision, and is thus a poor method of phylogenetic reconstruction. After compensating for implied weighting's inherent preference for precision over accuracy, it can rival the performance of Bayesian approaches – even though the latter are generally considered superior on the basis of accuracy alone.

Speaker

### Inferring net diversification and fossil discovery rates change over time integrating morphological and sequence data

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<u>Background:</u> Integrating both morphological and sequence data to date the tree of life is a coherent approach which can incorporate various sources of information from the fossil record and can model the speciation, extinction, fossilization, and sampling process more realistically. Several studies have shown the advantage of applying such total-evidence dating approach as a superior alternative to node dating. However, the net diversification rate (speciation rate minus extinction rate) and fossil discovery rate (product of fossilization rate and sampling rate) are typically assumed constant over time in empirical studies, potentially resulting in biased divergence time estimation due to severe violation of the reality.

<u>Materials and Methods</u>: The fossilized birth-death model with rates variation over time implemented in the BDSKY package for BEAST2 is used to study two empirical data sets. The mammal data consists of 86 mammal species scored for 4541 morphological characters and 27 genes (36860 nucleotides); while the Hymenoptera data consists of 113 species scored for 353 morphological characters and 6 genes (5096 nucleotides). The net diversification rate and fossil discovery rate are allowed to vary in a piecewise constant manner over time, and this fossilized birth-death process is used as a tree prior in the Bayesian total-evidence dating approach.

<u>Expected Results</u>: The posterior distributions of net diversification rate and fossil discovery rate will be inferred for the two data sets. The diversification pattern is expected to match the species radiation and mess extinction events in history. The fossil discovery rate should reflect the fossil richness and sampling effort in different geological times. Through modelling such rates variation, the divergence time estimates are also expected to be improved, potentially closing the gap between rocks and clocks.



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# S35 - The conservation of palaeontological collections: challenge and perspectives

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### High Resolution 720 panoramic visualization technology of outcrop and its application on the GBDB platform

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The Geobiodiversity Database (GBDB, http://www.geobiodiversity.com/) plays a leading role in the field of global paleontological and stratigraphical legacy data archiving. It has been selected as the official databases by the International Commission on Stratigraphy (ICS), and International Palaeontological Association (IPA), and recently established formal link with the International Association of Sedimentologists (IAS). More than 18,000 global sections and 500,000 fossil occurrences have been digitized into the GBDB platform up to February 2018, which include the "golden spike" sections (Global Stratotype Section and Point, GSSP), as well as hundreds of key sections for regional stratigraphical correlation. Stratigraphic sections are the basis for geological research. However, traditional presentations of sections as text and range charts are not intuitive, lacking the sense of reality and space. The GBDB team is currently utilizing the large pixel panoramic display technique of virtual reality to solve this problem. This panoramic technique is based on image stitching technology. Hundreds or even thousands of images can be stitched together to create full sense of reality which has ability of generating panorama with pixels up to 10 billion level and resolution of millimeter. In comparison of the traditional demonstration methods, such as section description, photo or rangechart, the high-revolution panoramic imaging provides higher level of sense in visualizing reality and space which could give users a much more immersive access experience .Those panoramic images are permanently stored in the GBDB platform to provide free, online service with 720° full-scale, high-precision interactive displays of outcrops. Through the GBDB platform, users can access the published panoramas of outcrops online. They can understand the actual outcrop and the landform characteristics of the surrounding environment through free views of horizontal 360° and vertical 360° perspectives, or zoom in to mm-scale to see the details of lithological changes or sedimentary structures. The GBDB platform also provides additional information of the section, such as stratigraphic descriptions, rangecharts, photos, correlation charts or fossil images, to help users get comprehensive knowledge of the section. Furthermore, combined with accurate GPS locating, users who are unfamiliar with the section, can easily find the position of the section in reality.



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### Digitization of major paleontological collections: the E-RECOLNAT program in the Muséum National d'Histoire Naturelle (Paris) as an example

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The e-RECOLNAT project, funded by the Investissements d'Avenir program of the Agence Nationale de la Recherche (ANR-11-INBS-0004), aims for the digitization of naturalist collections reposited in France. Among them, the MNHN is one of the earliest institutions dedicated to natural history, and one of the most prominent. Its seniority, combined with the political, military, and scientific history of France allowed it to collect specimens of all kind and provenance.

The paleontological collections of the MNHN have been gathered and studied for more tan 280 years, incorporating material from famous collectors (e.g., Lamarck, A. and C. Brongniart, d'Orbigny, Gaudry, Munier-Chalmas, Saporta, Cossmann, Arambourg, Lambert) that made them among the largest and most studied in the world. As such, these collections contain an estimated number of 7500000 lots, of which only 360466 have been digitized including 56269 with a status.

As defined here, e-RECOLNAT aimed to digitize fossils for five years starting with types, figured, cited, and historical lots. The amount of lots implied a selection to prioritize well-inventoried collections. Curators and managers thus submitted applications, requesting entering data, photography, or both for some reference invertebrates, plants, foraminifers, and vertebrates.

Since 2014, a team of four technicians has been digitizing fossil specimens. Data were entered directly into the PALAEO database or using previous data. Pictures were mostly taken using a camera and a lens screwed to a copy stand. Standard specimens have been put on a dark fabric in the fitting anatomical orientation, lighted up, and shaded to capture their anatomy, while thin sections were scanned or photographed with a camera mounted on a trinocular. Once processed through graphics softwares, the pictures have been uploaded on the MNHN public collection database where they are freely available. At the end of March 2018, of the 56269 lots with a status, 32062 have already been illustrated, plus 12284 with none recorded but from historical collections.

These data have been harvested to feed the RECOLNAT database EXPLORE which gathers data from French public natural history collections. By itself, the MNHN houses no less than 94% of the fossil lots in EXPLORE. e-RECOLNAT and its infrastructure give a renewed visibility to the neo- and paleontological collections of the MNHN, improving its referencing, and allowing everyone to access freely data on patrimonial collections.



<sup>&</sup>lt;sup>\*</sup> Speaker

### Conservation issues of pyrite-bearing lignitized woods: stymieing pyrite oxidation by combined bathing and drying processes

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Waterlogged pyritized woods are samples strongly prone to degradation first because of the susceptibility of pyrite to oxidize and second because of their lack of rigidity when waterlogged for prolonged periods. However, these items are essential for palaeobotanists to reconstruct palaeoenvironments and evolutionary history of plants, or to study diagenetic processes. Waterlogged samples of pyritized lignites (fossil woods), newly excavated, were treated according to two protocols. First, drying treatments (fast, slow, depleted in water and/or oxygen) were assessed. Second, bathing in several solvents (water or 1% hydrogen peroxide solution) were realized, with periodical renewal of solution. The aim of this procedure was to converse iron sulphides into soluble iron sulphates, thus removing the source of future degradation once in collection.

To assess the suitability of the treatments, morphological factors were examined and we also performed a monitoring of the composition of the fossil woods by FTIR, PIXE and S-XANES. Results demonstrate that:

- fast drying provokes the breakdown of lignites while no signs of pyrite oxidation develop. Conversely, slow drying provokes a substantial development of sulphates while samples remain mechanically strong;

- moisture is the environmental parameter that dominantly impacts oxidation;

- water does not affect the organic composition of woods contrary to hydrogen peroxide which oxidize reduced sulphur compounds into oxidized sulphur compounds.

A long-term treatment including a water bathing with regular renewal of solution, followed by adequate drying, would be an adequate solution to obtain a sub-stable material, whose composition will be weakly affected by inadequate conditioning.



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### Microenvironments to buffer the detrimental effects of temperature and relative humidity fluctuations in a fossil collection

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Adequate values of environmental parameters are crucial for the long term preservation of fossils in palaeontological collections. In particular, temperature (T) and relative humidity (RH) can affect glued or repaired materials, induce proliferation of mould, breakage due to contraction/expansion, recrystallization or mineral decay, among other detrimental effects. The Palaeontological Collection of Facultad de Ciencias, Universidad de la República at Montevideo, Uruguay has been environmentally monitored since 2009. From April 2015 to March 2017, six data loggers were located in different microenvironments within the collection room to compare the buffering effect of different enclosures: room environment (ENV), movable open rack (C1), cardboard box inside C1 (C2), lidded plastic box inside C1 (C3), drawer in a non sealed cabinet (P) and drawer in a tightly sealed cabinet (G1). Maximum and minimum values of T and RH were gathered on a weekly basis. Statistical analysis (i.e. mean values, standard deviation and Kruskall-Wallis non-parametric variance analysis) were used to compare the measurements obtained in each position/container to those of the ENV. Regarding both parameters, the more extreme values and fluctuation of these were achieved in ENV. With respect to T, all enclosures protected from Tmax variations but no significant differences were found for Tmin. This means that specimens were exposed to lower T inside enclosures. With respect to HR, only C3 and G1 showed significantly lower values of HRmax than ENV values. Additionally, C3 and G1 showed an almost constant difference between maximum and minimum values (with mean values of 50% and 54% respectively) which indicates that specimens were less exposed to fluctuations in HR. An ideal collection environment that ensures the long term preservation of fossils requires a thorough study of the place and conditions where the collection is located (i.e. usage, shared space, local climate, etc.). The results herein obtained show that: any container is better than none at all; that it is safer for specimens to substitute cardboard by plastic containers; and that closed containers/cabinets are better than open ones. These actions are already being taken to minimize the impact of environmental instability in the Palaeontological Collection of the Facultad de Ciencias. In addition, the use of lidded plastic containers protects the specimens from other agents of deterioration such as dust and plagues.



35 // Oral

Speaker

### Testing acidic treatments for use on fossil fish from the Sceltrich beds of Monte San Giorgio, Switzerland, middle Triassic

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Acids are commonly used to treat paleontological specimens embedded in calcareous matrices. However, their effectiveness and side effects remain partially documented. In this work, several acidic treatments were tested for possible application on fossil fish bearing shale from the Sceltrich beds (middle Triassic, Monte San Giorgio, Switzerland). This shale is rich in calcite and organic matter, but very hard and thus difficult to prepare with mechanical tools. Acetic, formic, sulfamic, citric and tartaric acids were tested at different pH values (1.5, 2 and 3). The effectiveness of the treatments was evaluated on pure calcite powder first then on fossil-free matrices. In a third step, small fish fossil fragments of a few millimeters (Late Cretaceous, Aquitaine Basin, Angeac-Charente, France) were treated to estimate possible side effects on the fish fossil itself.

Effectiveness was evaluated with different approaches. Some of them were quantitative (pH increase, weight loss) while others remained purely qualitative (effervescence of carbon dioxide, surface alterations and weakening of the matrix). Experiments on calcite samples and shale fragments qualitatively gave similar results: as expected, the efficiency of the treatments increased with the acidity of the solutions. It also strongly depended on the type of acid that was considered. Formic acid was the most effective at dissolving calcite, followed by acetic and sulphamic acid. Citric and tartaric acids were also effective, but led to undesirable precipitation of whitish components respectively identified by Raman spectroscopy as calcium citrate and calcium tartrate. The use of these two acids was therefore discouraged.

Effervescence occurred during the treatment of the fossil fish scales suggesting some dissolution of calcareous compounds. In the same time, substantial side effects were observed: the most acidic solutions caused fragmentation and surface alterations of the scales while low acidic solutions caused color alterations.

This study demonstrated that both the type of acid and the pH of the solution impact the effectiveness of the treatment. However, none of the 15 tested solutions proved to be ideal on the Sceltrich beds shale.

Acknowledgements : We are grateful to Renaud Vacant (CR2P, MNHN, Paris) and Rudolph Stockar (MCSN, Lugano, Switzerland) for providing the material used in this work.



35 // Ora

### How gypsum growth induced by pyrite oxidation jeopardizes the conservation of fossil specimens: an example from the Xiaheyan entomofauna (Late Carboniferous, China)

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The destruction and damage of fossils in palaeontological collections through pyrite (FeS<sub>2</sub>) oxidation is a major and well-known issue. In this paper we investigate the impact of this reaction on the conservation of Xiaheyan fossil entomofauna (Tupo Formation; Late Carboniferous; Ningxia, China) through three steps. First, we examined and characterized the elemental and mineralogical composition of newly excavated specimens, of museum specimens, and of weathering products at the outcrop (using SEM-EDX, Raman microspectroscopy and XRD). Second, in order to determine the potential reactivity of newly excavated fossils, we performed artificial ageing (AA) experiments, a technique recently applied in palaeontology that can offer valuable insights into long-term conservation of fossils. Finally, we designed and applied a protocol aiming at canalizing the formation of gypsum so as to preserve the fossil integrity, namely crystallisation pits. Our data demonstrate that the depositional environment at Xiaheyan was rich in sulphur and devoid of oxygen, with perhaps oxygen-rich microenvironments, which led respectively to the precipitation of framboidal pyrite and of primary iron oxyhydroxides. The further chemical palaeoweathering led to an extensive oxidation of pyrite in the outcrop, resulting in the precipitation of secondary iron oxyhydroxides, and of jarosite and gypsum, both sulphates. The low abundance of iron oxyhydroxides and the poor diversity of sulphates, compared to analogous localities, indicate a distinct weathering scenario, with a persistence of acidic water and an extensive leaching leading to the maintenance of only insoluble sulphates. Despite the extensive in situ pyrite oxidation, AA experiments demonstrated a remaining weak degradation potential. Gypsum ( $CaSO_4.2H_2O$ ) is the near-exclusive efflorescence to develop within artificially aged fossils, contrary to the most commonly encountered efflorescence on pyritized fossils, namely iron sulphate. This instance can be attributed to the complete mobilization of iron through iron oxyhydroxide precipitation and the availability of calcium ions induced by the dissolution of calcium carbonates present on Xiaheyan outcrops. Unfortunately, the recourse to crystallisation pits failed to prompt gypsum crystallisation. We further suggest preventive storage conditions and prospects for investigation on the gypsum precipitation process at work, notably the role of organic compounds.



Speaker

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# A horse with a side of radon and a thousand fragments of turtle shell

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Hagerman Fossil Beds National Monument/National Park Service (United States)

The Hagerman Fossil Beds in south-central Idaho, USA, were first excavated by the Smithsonian Institution in 1929. Little did those paleontologists know that the nearly three tons of fossils sent back to Washington DC, especially those from the Hagerman Horse Quarry, brought with them potentially dangerous radon progeny. The Smithsonian moved on from Hagerman in 1933, but expeditions by several other institutions followed, and in 1987 this site was established as a National Monument with monitoring, excavations, preparation, and the curation and housing of Hagerman fossils now conducted by the United States National Park Service. Radon emittance from Hagerman's fossils was first recognized in 2003, but only now has its extent and severity been fully documented with proper mitigation procedures, including the building of a new preparation lab and collections space beginning to take place. Hagerman has a radon problem, but it also has a collections space one with an extensive backlog of fossils. This includes over 100 large, jacketed specimens from the Horse Quarry and an estimated 10,000 smaller fossils (e.g., fish, frog, and smaller birds and mammals) that have yet to be properly curated. This backlog, once processed, will require additional museum storage space with a sufficient air venting system and radon mitigation protocol that Hagerman currently lacks. Issues to be discussed include what considerations should be made when collecting, preparing, and housing ? hot ? fossils; the benefits and pitfalls of an ? Easter egg hunt ? collection methodology; why pins and needles are for feet and not rodent teeth, and how a museum can preemptively prepare for the inevitable filling of that last museum tray. While many, these issues are preventable and can often be rectified at minimal cost and with proper planning and management.



Speaker

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# How to make a fossil preparation lab: The case of the Xingyi National Geopark Museum in China

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Fossil preparation, the process of turning a natural object into a scientific specimen by exposing a fossil from its matrix, is essential for paleontological research and museum display. It is very challenging to establish a perfect lab that satisfies all conditions to operate every kind of fossil preparation properly and precisely, due to the budget and space limits of a museum. However, by examining the balance between museum specimens, building infrastructures, and the type of preparation, it is possible to make a good preparation lab suiting the need of a particular museum. The Xingyi National Geopark Museum, a newlyestablished low-budget museum in Guizhou Province of China, had competed its lab over five years by gradually installing 150 items in a given empty space. The museum lab was meant to be dealing with preparing marine reptiles and fishes from nearby Triassic sites. For the first three years, the budget had been invested in the instruments and safety gears for the matrix removal of the limestone and mudstone. Preparators' health and safety equipment was prioritized over any preparation tools; dust masks and an external vacuum cleaner were required for compensating for the lack of proper air ventilation and dust collector, while air abrasive units that were unnecessary for immediate operation were shelved. Molding and casting supplies were purchased later since the matrix removal was the initial step. Besides a few indispensable professional tools such as air scribes and consolidation supplies such as Paraloid B-72, inexpensive domestic products were selected for the general lab equipment such as microscopes and air compressors. Also, a proper arrangement of workstations and traffic flows in the lab reduced the risk of damaging the specimen when a preparator handled it in a limited space.

### S36 - The Devonian: life, environments and time

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Andrew Bush <i>et al.</i> // The Frasnian-Famennian (Late Devonian) extinction event in shallow marine, siliciclastic paleoenvironments of the northern Appalachian Basin, USA
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#### Palynology and microfacies of Middle Devonian leperditian-rich beds from the classical Eifel area (Germany)

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Well exposed Middle Devonian cyclic limestones and mudstones from several quarries in the Hillesheim Syncline (Rhenish Massif, Germany) have been analysed palynologically, sedimentologically and geochemically. In this time interval stable conditions prevailed, but evidence for episodic physical and biotic changes is also present.

Detailed palynological sampling of the Lahr Member (Ahbach Formation, lower Givetian) at the Eich Quarry section provided rich and well to moderately preserved assemblages of terrestrial and marine organic-walled microfossils (OWM) allowing for a bed-by-bed palynofacies study. In addition, rare plant remains have been obtained in particular levels.

The studied succession comprises bioturbated commonly peloidal limestones with stromatoporoids, rugose and tabulate corals, bryozoans, gastropods and brachiopods. Fenestral fabrics, particularly in its lower and upper parts, indicate very shallow water conditions. Leperditian ostracods have also been found repeatedly throughout the section. However, they are more frequent in dark-brown shale layers which also contain abundant terrestrial palynomorphs and plant fragments, especially including remains of non-calcareous macroalgae. These intervals may represent quiet, restricted and possibly eutrophic conditions, associated with terrigenous mud influx, that alternated with times of carbonate mud production.

The distribution pattern, abundance and ratios of miospores and leiosphaerids can be applied for palaeoenvironmental interpretation, as well as biostratigraphic correlation in conjunction with other index fossils. The shaly layers are characterized by thick-walled larger miospores of the genus *Retusotriletes* which dominates over other miospore taxa and commonly occurs in tetrads. Apparently, the parent plant of this miospore taxon niched next to a protected, restricted marginal marine environment. Thus, judging from the distribution of the different associations of palynomorphs (palynofacies), from sedimentology (microfacies) and geochemistry (TOC and carbonate percent), the succession in general can be interpreted as a shallow-marine depositional system, bordering on marginal marine conditions. However, the proportion of terrestrial material in the palynofacies spectrum is high, while marine components (e.g., acritarchs, scolecodonts and chitinozoans) are surprisingly rare. Only prasinophytes such as *Leiosphaeridia* or *Pterosphaeridia* are significant.

<sup>\*</sup> Speaker



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## The Frasnian-Famennian (Late Devonian) extinction event in shallow marine, siliciclastic paleoenvironments of the northern Appalachian Basin, USA

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The Lower and Upper Kellwasser Events together comprise the Frasnian-Famennian mass extinction, one of the "Big 5" extinctions of the Phanerozoic. The Appalachian Foreland Basin preserves a thick package of Upper Devonian sediments in which these events can be examined along a paleoenvironmental transect. In western New York State, the Frasnian-Famennian boundary interval is represented by offshore shales, which transition to shallow marine sandstones to the southeast in northern Pennsylvania. Revised correlations based on biostratigraphy and carbon isotope stratigraphy permit a new examination of these events in shallow-marine paleoenvironments in which brachiopods and other macrofauna are abundant. We have collected fossils bed-by-bed through numerous sections that span one or both Kellwasser Events, which are separated by about 60 m of strata. The Lower Kellwasser corresponds to the Pipe Creek Formation, which in this region consists of several meters of dark gray, silty shale. The Upper Kellwasser corresponds to a dark shale or siltstone bed within the upper Canaseraga Formation, which varies from less than a meter to 2.5 m thick. In at least some localities, small trace and body fossils are present in the Pipe Creek, suggesting a dysoxic environment; geochemical tests for anoxia are currently in progress. Many species of brachiopods go extinct in the Lower Kellwasser Event, including all strophomenids and all atrypids. Large rugose corals also disappear. However, the Upper Kellwasser event only claimed a couple victims, including the last species of atrypid brachiopod, which migrated into the basin after the Lower Kellwasser. Many new species appear soon after the Lower Kellwasser Event, particularly productids, although none do so in the immediate aftermath of the Upper Kellwasser. Thus, the Lower Kellwasser marks the main turnover event in benthic macrofossils in this region.



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#### The Lower Devonian Rhynie Chert plant Horneophyton: its implication for the early evolution of vascular plants

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The exquisite anatomical preservation of the Lower Devonian Rhynie Chert flora has been, and still is, central for understanding the early steps of land plant evolution. Four plants from the Rhynie Chert (Aqlaophyton, Asteroxylon, Horneophyton and Rhynia) occupy key positions in the earliest evolutionary pathways of vascular plants (tracheophytes). During one century, the study of this permineralized flora has provided new insights on the early diversification of land plants, being a constant topic in the Lower Devonian literature. The current evolutionary framework of early land plants suggests that Horneophyton and related plants are part of prevascular lineages of the basalmost polysporangiophytes. In this communication, we report new detailed observations on the Horneophyton vascular strand anatomy. Evidence comes from the historical Hemingway collection of Rhynie Chert thin sections from the Natural History Museum of Lille (France). We show that Horneophyton has a particular type of tracheids characterized by irregular, annular to spiral wall thickenings of putative secondary origin. This is consistent with Kidston and Lang's original description and diagnosis. Most importantly, our phylogenetic analysis accordingly resolves Horneophyton whithin the tracheophytes, but as a sister group of eutracheophytes (i.e., extant vascular plants). Results further show that Horneophyton and allies are an intermediate clade between paratracheophytes (i.e., the former Rhyniaceae) and eutracheophytes. It implies Horneophyton would be the direct precursor of all living tracheophyte biodiversity. The presence in Horneophyton of a previously unrecognized simple type of tracheids adds to the complexity of the early vascular plant plexus and clearly points to a sequential acquisition of the characters of a cell that was crucial for plant terrestrialization.



36 // Ora

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#### Continuity of fossil record and biozonation schemes: an example across the Devonian/Carboniferous boundary

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Most of the marine sections around the world across the Devonian/Carboniferous boundary are characterized by a facies change in connection with the Hangenberg event. In fact, more or less at the beginning of the event, the calcareous sedimentation sharply pass to black shales. Above the shaley interval at place some terrigenous sediments are present ("Hangenberg sandstone" Auct. and equivalents), followed by the restoration of limestone sedimentation. Where the sandstones are not present, limestones occur just above the shale. The contemporaneity of these facies changes can be assumed within a sedimentary basin, but it is unlikely in different palaeogeographic regions, where small differences may occur.

The facies break may also affect the fossil record, preventing a complete, continue conservation and therefore a detailed biostratigraphy. Conodonts are the main tool for correlation in the considered time frame, and are abundant and easy to collect from limestones, but very rare, if not absent at all, in shales and sandstones. Since the deposition of the latter two facies took some time, it result that in most sections a continuous fossil record is missing, and only two "photographs" were registered, one taken at the time of deposition of the last limestone bed before the shales, and the other corresponding to the first bed above. Therefore, even if the deposition of black shales could be geologically considered as synchronous, an "unknown" time interval correspond to the non calcareous sedimentation.

In order to achieve information on that interval, sections without a facies break should be considered, and a global conodont biozonation scheme should be based on those sections, so that errors due to the missing data could be excluded.



Speaker

36 // Oral

#### Astrochronology and chemostratigraphy for the Frasnian–Famennian boundary section (Late Devonian) at Steinbruch Schmidt

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The Late Devonian mass extinction was the second of five global mass extinctions that shaped life on Earth during the Phanerozoic Eon, and occurred at the Frasnian–Famennian boundary (FFB, 372 Ma). Here, we focus on this time interval at the famous Steinbruch Schmidt section in Germany. This section includes the well exposed Kellwasser black shale intervals, the FFB, and a U-Pb dated ash layer. In this study, we sampled an interval of 5.3 m around the FFB, with an average sampling interval of 3 cm, leading to a collection of about 200 samples. On every sample, we measured carbon and oxygen stable isotopes, magnetic susceptibility and micro XRF elemental geochemistry. Magnetic susceptibility (MS) and detritalinput-related elements such as Ti and Al are higher during the Kellwasser, and there is a good correlation between Al, K, Ti, Fe and MS. We selected the MS and Ti signals for spectral analysis, as we expect these proxies to contain the best-preserved astronomical signal. Both proxies give similar results, with important spectral power at frequencies of 0.5, 2, 5.3 and 5.5 and 9.5 cycles/kyr. The peaks are located at similar frequencies but reach different confidence levels in both signals. Subsequently, we applied the average spectral misfit (ASM) method, which assesses the most probable sedimentary rate and searches for the best fit between the frequencies extracted from the Ti and MS spectral analyses and the expected Milankovitch frequencies in the Devonian. Using the ASM results, we transform the signal from the distance domain into the time domain. Furthermore, dating of the ash layer just below the boundary provides an anchor point for this cyclostratigraphic framework. The well-known biostratigraphy of this section, as well as the carbon-isotope stratigraphy, will allow the use of this new time frame at a global scale.



#### **Event stratigraphy accross the Devonian-Carboniferous – New views from the shelf**

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The Devonian-Carboniferous Boundary (DCB) is associated with one of the 'Big Five' extinction events of the Phanerozoic. It was also a time marked by a rapid but short-lasting change in deposition called Hangenberg event. In pelagic sections, where the Hangenberg event was defined below the DCB, the succession displays, in stratigraphic order, an anoxic black shale unit (Hangenberg Black Shale-HBS) recording the main extinction phase, the Hangenberg Shale showing no anoxia, the Hangenberg Sandstone (HSS), and (4) the Stockum Limestone (SL). The HBS is traditionally interpreted as a transgressive pulse followed by a rapid regression (HSS) often regarded as a sequence boundary. In Belgium, the DCB transition is well exposed in shelf settings and the HBS-SL interval corresponds to c. 25 m of mixed carbonatesiliciclastic deposits. In comparison, in classic pelagic sections, the events are condensed in a c. 4 m-thick succession where they appear superimposed to each other. Events are thus best developed and separated in neritic sections and are moreover fossiliferous. The latest Devonian ('Strunian') Comblain-au-Pont Fm recorded a 3rd-order transgression that produced a progressive switch from coastal siliciclastic to proximal mixed deposits with an increase of the carbonate content. Hence the Comblain-au-Pont and lower Hastière fms are regarded as the transgressive system tract. The highstand system tract corresponds to the massive crinoidal rudstones of the middle member of the Hastière Fm. The latter is capped by an erosion surface corresponding to the 3rd-order sequence boundary. The next sequence starts with the upper member of the Hastière Fm, made of thin-bedded crinoidal pack/grainstones. Superimposed to the 3rd-order sequences are well marked orbitally-forced precession cycles of c. 18.6 ka, appearing as regular c. 40 cmthick couplets of limestone and calcareous shale beds. These couplets are interpretedd as climatic cycles deposited during alternations of dry and wet periods. The HBS event is variously developed in thickness and is sometimes not marked on shallow platforms. It is however more likely that the anoxic facies were triggered by a transgressive pulse that did not spread into shallow-water environments where carbonate facies rich in benthic fossils continued to develop. The HSS event, recorded as a sandstone bed in pelagic sections, is variously recorded at the base of the Hastière Fm in S Belgium, either as a sandy siltstone bed in proximal sections, or as a horizon with limestone clasts and reworked fossils in more distal ones. This event was responsible for the final demise of the Late Devonian fauna. The HSS occurs sharply in the stratigraphic record and does not correspond to the long sea-level fall of a 3rd-order sequence boundary, but most probably to a short out-of-sequence event. After this short-lasting regressive phase, normal settings returned with the deposition of the Hastière Fm.



<sup>.</sup> Speaker

#### An interim Devonian bioregionalisation

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Since the 1960s many have enthusiastically countered, amended, or added to hypotheses of global Devonian bioregionalisations. The work of the late A. J. Boucot has served as the functional standard for Devonian bioregionalisations with various authors offering over 100 areas and amendments leading to incomplete and contradictory area classifications. Using the International Code of Area nomenclature (ICAN) as a transparent approach, Devonian bioregionalisations are reviewed and its classifications completed with the addition of three new areas: the Mardoowarra and Eastern Australasia regions, and Western Gondwana realm. This interim regionalisation is the first t o be completed and standardised, made in preparation for future palaeobiogeographic studies and as a prelude to rigorous testing. By standardising the 1969 bioregionalisation of Boucot et al. Devonian biogeography can begin to assess if the proposed bioreg ionalisation is representative of true natural areas.

Speaker

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#### Ammonoids and anoxia from the Belgian Frasnian: the Carrière de Lompret section

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A new rich Belgian Frasnian cephalopod fossil site was discovered in the summer of 2013. In the new pit of the 'Carrière de Lompret', an active quarry located 9 km west of Frasnes, the historical type area of the lower Upper Devonian stage, a recent blast had unexpectedly uncovered a large fault-bounded block of upper Frasnian Neuville and Matagne shales within highly prized middle Frasnian Lion member limestones. Although the presence of cephalopods in this stratigraphic interval has been mentioned in literature for over a century, these have not been studied much in detail yet. The sheer size of the faulted block, making it impossible to quarry it away in one go, favoured large scale in-situ collecting from the summer of 2013 on. With a growing group of citizen and professional paleontologists paying regular visits to the quarry, a huge collection of ammonoid and nautiloid cephalopods from the Lompret quarry was amassed. At the same time, new discoveries were made for many other fossil groups ((crinoids, brachiopods, corals, graptolites, trilobites, ostracods, conodonts, chondrychtians and placoderms). The most intriguing part of the 'Carrière de Lompret' succession is found near the base and within the lower part of the Matagne Formation, where within a sequence of cephalopod rich limestone beds, an abrupt change to darker colored shales and limestones coincides with major changes in the composition of the macrofauna. This change seems to be situated near the base of the upper rhenana conodont zone (preliminary data) and may correlate to the Lower Kellwasser Event. At this point in research, the true nature and context of the observed changes are far from being well understood, and several taxonomical, stratigraphical, sedimentological and geochemical studies are initiated to better document and comprehend them. This interval, the abundance of cephalopods in the section and the possibility to collect bed-by-bed at large scale throughout a considerable stratigraphic interval make from the 'Carrière de Lompret' section the most extraordinary and intriguing Belgian Frasnian cephalopod site.



Speaker

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#### The palaeopsychrosphere in the Devonian

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The interpretation of Palaeozoic marine benthonic ostracods of the Thuringian "Ecotype" or "Megaassemblage" as indicative of a palaeopsychrosphere has been controversial. We review the evidence and conclude that the characteristics and distribution of these ostracods are consistent with the existence of deep, cold, well-oxygenated water masses, formed by high-latitude sinking of surface waters, in the Devonian oceans, comparable with those of the modern ocean that constitute the psychrosphere (waters below the thermocline with temperature < 10 °C). We present a new palaeoceanographic model for the Frasnian-Famennian (Late Devonian) Kellwasser events that resulted in the extinction of 75% of marine ostracod taxa, mostly neritic or pelagic forms, while the deep-water Thuringian Mega-assemblage was relatively unaffected. We offer an explanation for the unlikely preservation of examples of such a deepwater (bathyal to abyssal) ostracod fauna that involves upwelling of deep cold waters on continental margins.

Speaker

#### Diversity of the Lower Devonian icriodontids from the Prague Synform

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The biostratigraphic study of two key sections across the Silurian/Devonian boundary in the Prague Synform provided rich conodont material. The sections (Na Požárech and Praha- Radotín) represent different depositional environment above the Silurian/Devonian boundary which is similarly developed in both sections as so-called Scyphocrinites horizon – light coarse grain crinoidal limestones. The Devonian part of the Na Požárech section is developed in light gray, coarse-grained carbonates and the limestones in the Praha-Radotín section are typically dark gray, micritic with shale intercalcalations. The contrasting depositional environment in both localities was expected to show the differences in composition of conodont faunas.

The abundance of conodonts in both sections is relatively high - several thousands of elements. Apart from the most abundant spathognathodontids, a radiation of icriodontids can be observed. The correlation potential of the most relevant icriodontid taxa and their transitional forms and morphotypes and sedimentary conditions will be discussed in the talk.

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Speaker

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### New data on evolution and palaeobiogeography of Lower Devonian brachiopods from the Rhenish Massif (Germany)

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The ongoing revision of Lower Devonian brachiopods from the Rhenish Massif results in a steady of new implications on brachiopod taxonomy, biostratigraphy, evolutionary dynamics, flow palaeoenvironment and palaeobiogeography. Many classic taxa are revised and partly subdivided into stratigraphically significant new species and subspecies. Evolutionary change is discernible in many genera of different orders, for example in Arduspirifer, Euryspirifer, Paraspirifer, Rhenostropheodonta, Iridistrophia, Platyorthis, Sartenaerirhynchus and Cryptonella. Vertical distribution patterns of brachiopod taxa show the presence of succeeding 'evolutionary faunas'. Faunal turnovers between these are attributed to regional faunal events or crises in the context of short or more extended phases of palaeoenvironmental change possibly triggered by rapid eustatic sea-level fluctuations in combination with varying crustal subsidence and sedimentation rates. Relationships to global events are possible but difficult to substantiate. As an outstanding example, the 'Rhenish Gap' in the upper Lochkovian–Pragian represents an interval of 6–8 m.y. with deltaic to terrestrial conditions and therefore a lack of brachiopod faunas. These processes resulted in shelf-wide or more regional extinction or emigration of substantial parts of a brachiopod fauna and subsequent replacement by a largely new one. New species dispersed across the Rhenish Shelf after they had either evolved by allopatric speciation in small isolated populations with reduced gene pool or immigrated from outside on the Rhenish Shelf. Due to the Rheic Ocean taking affect as barrier to migration, faunal exchange between Rhenish and North Gondwanan shelves was minor in the Lochkovian and increased with its narrowing in Pragian-Emsian time. Based on numerous side-by-side comparisons it is concluded that the studied brachiopod faunas belonged to a discrete Early-Mid Devonian 'Rhenish Province' (including, e.g. Ardennes, Rhenish Massif, SW England, Artois, Poland) with palaeobiogeographic affinities, mainly on the genus level, to a 'North Gondwana Province' (e.g. Ibero-Armorica, Central Bohemia, North Africa), both representing parts of a 'Maghrebo-European Realm'.

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#### Capturing the Kačák Episode (Middle Devonian) in the Palentine Domain (Cantabrian Mountains, NW Spain)

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The Devonian rocks of the Palentine Domain are located in the Pisuerga-Carrion Unit (Iberian Variscan belt). There, three lithological units: La Loma beds (upper part of Polentinos Fm), the Gustalapiedra Fm and the lower part of Cardaño Fm built the Middle Devonian limestones, which mainly represent offshore facies faunas.

The Gustalapiedra Fm. (Lower Eifelian to Middle Givetian) consists of 50-60 m of black shales with scattered lenses of dark mudstones and wackestones; a distinctive 10-15 m thick unit of nodular limestone and ferruginous and bioturbated sandstone developed in the upper half of this formation (Man Member).

Herein, we update records of five selected sections from the Gildar-Montó and Alto Carrión areas: Las Verdes, El Calero, Barranco, Monderrio and Arbejal. All of them belong to the Gustalapiedra Fm and yielded conodonts, dacryoconarids and ammonoids around the Eifelian/Givetian boundary. Besides, we also report an expression of the Kačák Episode within the Man Mb.

House (1985) introduced the Kačák Event, characterised by black and calcareous shale, in which the index *Nowakia otomari* occurs. Walliser (1985) proposed the Otomari Event based on the onset of the *Nw. otomari* lineage. Chlupáč et al. (2000) recognised the entry of the index *Tortodus kockelianus* in the uppermost part of the Choteč Limestone (below the Kačák Mb) in the Bohemian Massif. García-Alcalde et al. (1990) demonstrated that this event was not instantaneous, but represents a polyphased dioxic/anoxic event-interval. In order to avoid confusion, Walliser (2000) proposed a subdivision of the Kačák Episode into two Late Eifelian Events; later, Walliser & Bultynck (2011) and Suttner et al. (2017) demonstrated their existences in the south-eastern Morocco and Carnic Alps, respectively.

The Palentian fossil record from the five sections aforementioned suggests that the Kačák Episode is placed at the top of the Man Mb *Icriodus struvei, Ic. amabilis, Polygnathus costatus, Po. oblongus, Po. angusticostatus, Pinacites jugleri, Subanarcestes macrocephalus* and others ammonoids end at, or prior to, the event level, while *Po. hemiansatus, Ic. obliquimarginatus* and *Agoniatites costulatus* enter above the level. *Po. eiflius, Po. amphora, Cabrieroceras* and *Nw. otomari* start within the interval and extend beyond it.

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#### Upper Givetian (Middle Devonian) Conodont sequences from the Spanish Central Pyrenees and the Montagne Noire (France) and their biostratigraphic correlation

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The Givetian/Frasnian (=Middle/Upper Devonian) boundary was set within Bed 42 in the Col du Puech de la Suque, CPS-E section, Montagne Noire (France). The biostratigraphical criterion was the entry of an early morph of the conodont "Ancyrodella rotundiloba". Subsequent evolutionary studies on the genus Ancyrodella and other genera recorded in the Montagne Noire have provided a worldwide-applied Frasnian biostratigraphical subdivision, the well-known Montagne Noire Zones (MN zones) recently upgraded to Frasnian Zones (FZ). However, the underlain conodont sequence has not received the same attention and the correlation potential for the Givetian conodont faunas has not yet reached its full potential.

In the nearby Spanish Central Pyrenees, several sections demonstrate one of the Givetian finest biostratigraphical sequences worldwide, which is critical for the intended threefold subdivision of the Givetian Stage; this Pyrenean sequence spans the Givetian/Frasnian boundary as well. The main goal of this report is to compare the Upper Givetian conodont sequences between these two regions and establish first correlations.

A preliminary joint re-sampling was carried out in the upper Givetian strata of the CPS-E section. The lowest exposed bed (35) yielded *Klapperina disparilis*, *Polygnathus dubius* and *Pol. dengleri*. This association doesn't start below the Upper *disparilis* Zone. The next biostratigraphical index, *Skelethognathus norrisi* enters in Bed 37, and the *norrisi* Zone extends to the top of Bed 42a. This upper Givetian sequence in the Montagne Noire can be precisely correlated with several sections in the Pyrenees: Beds 51 (or above) to 59 in the Compte Section; Beds 34 (or above) to 36A in the Villech section and from the middle part of Bed 218 (or above) to the lower 122 cm of Bed 221 in the La Guardia D'A` res section. The Pyrenean conodont biodiversity appears to be greater for this interval and could help to increase the correlation potential of the French sequences in the stratotype boundary section. Next sampling in younger strata of the near CPS-F section and its comparison with the Spanish succession has a promising potential for integrating the French data into the most detailed global Upper Givetian correlation net, adding an extra value to the Montagne Noire conodont sequences.

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#### Small-sized brachiopods from the Upper Frasnian (Devonian) of central Hunan, China

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Abundant small-sized brachiopods of the uppermost Frasnian (probably the Palmatolepis linguiformis Conodont Zone) from South China are recently reported. These brachiopods range in size from less than 1 mm to approx. 7 mm and are composed of, in the order of abundance, the spiriferides (Thomasaria ? baii, Thomasaria ? liangi, Xiangia liaoi, and Spiriferida gen. and sp. indet.), the terebratulide Qidongia tani, the athyridide Athyris supervittata Tien and Athyris ? sp., the rhynchonellide Levipugnax ? liui, the spiriferinide Cyrtinaella ? houi, the pentameride Gypidula xui, and the orthide Aulacella ? sp., associated with abundant atrypid juveniles (mostly lowatrypa pseudobodini), Productella sp., and Hypothyridina sp. This fauna represents the last and significant brachiopod flourishing episode in the Frasnian before the Frasnian–Famennian Event in South China. Survivorship curves and size-frequency distributions of 10 fossil species populations have been depicted based on abundant small-sized brachiopod specimens of various growth stages of two samples (C1-0 of Jiangjiaqiao and S-Y-4 of Shetianqiao sections) from Hunan Province of southern China. None of the size-frequency distributions of the C1-0 fauna are of normal bell shaped distribution pattern; only those of Thomasaria ? baii, Thomasaria ? liangi, Xiangia liaoi, Cyrtinaella ? houi and Gypidula xui somewhat resemble a bell shaped distribution, whereas Qidongia tani, Athyris supervittata and Levipuqnax ? liui display a distinct right-skewed pattern. The survivorship curves of various populations are of a concave type of various degrees, which was probably related with their living on the muddy substrate. The differences in size-frequency distributions and survivorship curves of various species are probably a result of their different adaptation to the muddy environments. For example, differences in shell shape might be related to their adaptational differences to both muddy substrate and feeding efficiency. Study of lowatrypa pseudobodini and Hunanotoechia tieni shows that size- frequency distributions and survivorship curves of brachiopod populations can be affected by sampling methods to various degrees in case of fewer specimens by hand-picking. Bulk sampling is recommended for population analysis, in combination with hand-picking in some cases for more actual survivorship curves.



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#### Emsian (Lower Devonian) conodonts from the Lufengshan section (Guangxi, South China)

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The Lufengshan section (Guangxi, South China) is one of the best representative sections of the Xiangzhou facies (benthic facies), from which a few Emsian conodont studies have been accomplished in the past. Herein we present conodonts from the Upper Member of the Ertang Formation at the Lufengshan section. The conodont fauna is characterized by a distinctly low diversity with only six species reported, and is assigned to the *nothoperbonus* Zone. '*Ozarkodina'*? *chenae* sp. nov., '*O.*'? *wuxuanensis* sp. nov., and *Polygnathus praeinversus* sp. nov. are newly described species at this secction. A comparison of the contemporaneous conodont faunas between the Lufengshan, Liujing and Daliantang sections indicates that the conodont biodiversity during the time of the *nothoperbonus* Zone in South China is mainly bathymetrically controlled. Moreover, *P. praeinversus*, which was previously thought to be transitional between *P. inversus* and *P. serotinus*, is interpreted to represent an intermediate form between *P. nothoperbonus* and *P. inversus* on the basis of stratigraphical and morphological analyses. The outline of the basal cavity of *Polygnathus* : the basal cavity in the middle part of the platform starts to invert on the inner side at first, whereas the flat or slightly elevated outer flank of basal cavity is laterally extended to form a shelf-like protuberance on the outer side of the pit.



Speaker

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#### The first palynological assemblage from the Famennian of Scotland and its significance for understanding early tetrapod age relationships

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For over 75 years it has been the consensus that the upper part of the Old Red Sandstone in Scotland is early Carboniferous in age. This had a number of implications such as the ranges of typical Devonian fish (Bothriolepis and Holopytychius) continuing into the Tournaisian and hence survived the End Devonian Mass Extinction. In addition, the inceptions of the important early tetrapods from the Scottish Borders are all late Tournaisian and, as such, distinctly separated in time from the well-known Famennian faunas from East Greenland. For the first time a palynological assemblage has been found in the Scottish Upper Old Red Sandstone which contains diverse and well preserved spores. These include Retispora lepidophyta, Rugospora radiata, Vallatisporites pusillites, Diducites versabilis and the bifurcate tipped spores Ancyrospora, Hystricosporites and Nikitinsporites. All these forms became extinct at the Devonian-Carboniferous boundary. In addition, Tergobulasporites immensus and Retispora macroreticulata are present. Both these taxa become extinct at about the base of the latest Famennian. Both Indotriradites explanatus and Verrucosisporites nitidus are absent, taxa which have inceptions higher in the latest Famennian. This shows that the spore assemblage is from the LL spore zone and early latest Famennian in age. Stratigraphically it is below a supermature calcrete that represents a sustained episode of aridity. This and other new spore assemblages from the Tournaisian Ballagan Formation show that the end of the Old Red Sandstone approximates to the Devonian- Carboniferous boundary. The dead-clade walking records of Holoptychius and Bothriolepis are entirely Devonian in age and the supposed late Tournaisian early tetrapods are spread in time through the entire Tournaisian stage. This effectively fills the lower part of Romer's Gap and brings the Greenland and Scottish tetrapods into a closer age relationship. This demonstrates the crucial role of stratigraphic palynology in resolving problems in vertebrate palaeontology.



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Speaker

#### Palaeoenvironments and sequence analysis of the Early-Middle Devonian Bokkeveld Group of South Africa

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The Bokkeveld Group is an Early-Middle Devonian (Emsian-Givetian) succession of the Cape Supergroup of South Africa. In outcrop the succession is presented as five-to-six along- tectonic-strike continuous upward coarsening successions comprising lower shales and upper quartz wackes and quartz arenites. Previous palaeoenvironmental studies of the Bokkeveld Group suggest that these upward coarsening successions are cyclothems, representative of a series of allocyclic controlled progradational storm-and-wave dominated or mixed wave-and-tide influenced deltaic depositional systems. These studies suggest uniformity among cyclothems, each comprising shelf-prodelta, distributary mouth bar, tidal flat, interdistributary bay and beach-shoreface (comprising washover, estuarine and tidal inlet and channel environments) environments. Proximal-most delta-plain environments are noticeably missing, inferred to have been transgressively eroded with the initiation of successive cyclothems. Revaluation of the sedimentology, palaeontology and sequence stratigraphy of the Bokkeveld Group in the Clanwilliam Subbasin suggests that sedimentation variably occurred within several palaeoenvironments that may be related to three distinct siliciclastic depositional systems. These are: storm-and-wave dominated shallow marine, transgressive barrier-island lagoon and wave-influenced deltaic depositional systems. Storm-andwave dominated shallow marine depositional systems are most ubiquitous in the Bokkeveld Group whilst transgressive barrier-island lagoon and wave-influenced deltaic depositional systems are restricted to the Tra-Tra-Boplaas interval. At this interval they are interpreted to represent a coastal-plain incised valley-fill system. Sequence analysis of the Bokkeveld Group suggests the presence of at least four 2nd order, six 3rd order and twenty 4th order T-R sequences and have allowed for the creation of a relative sea-level curve for the Clanwilliam Sub-basin. These data suggest five major transgressive events occurred within the Clanwilliam Sub-basin during sedimentation of the Bokkeveld Group. With respect to relative age constraints from palaeontological data a single major transgression occurred during the late Emsian, two during the Eifelian, one near the Eifelian-Givetian boundary and one during the Givetian. The timing of these transgressions are similar to 3rd order global eustatic rises for the Devonian, suggesting eustacy as a control on local T-R cyclicity.



<sup>&</sup>lt;sup>°</sup> Speaker

# The Rise and Fall of the Malvinokaffric Realm in South Africa

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The Malvinokaffric Realm is a palaeobiogeographic realm that persi sted at high subpolar-to-polar southern palaeolatitudes from the Early-to-Middle Devonian (Emsian-Eifelian) and was restricted to southwestern Gondwana covering parts of modern day South Africa, Antarctica, Argentina, Bolivia, Brazil and the Falkland Islands with possible extensions into Guinea-Bissau, Ghana and Senegal. Characteristically, conulariids, tentaculitiids and hyolithiids are abundant; reef b uilding bryozoans and corals are rare whilst stromatoporoid sponges, conodonts, goniatite ammonoids, graptolites and certain brachiopods (atrypids, gypidulid pen tamerids and rhynchonellids) are absent. Endemic to the Realm are s everal brachiopods, certain phacopdid trilobites and other invertebrate taxa. Closure of the Malvinokaffric Realm occurred during the end-Eifelian and is recognised on the basis of admixture and replacement with warm-water associated Old World Realm fauna. The appearance of Old World Realm brachiopods in South America and South Africa is thought to mark the closure of the Malvinokaffric Realm. The appearance of these brachiopods in Bolivia and Brazil seems to coincide with a global warming trend and transgre ssion corresponding with the Kačák Event. Until recent the cause for the demise of the Realm in South Africa was unknown. In South Africa, Malvinokaffric fossils are present in the Rietvlei/Baviaanskloof Formations (Table Mountain Group) and the overlying Bokkeveld Group (Gydo to Waboomberg Formations). Fossil fish from the ove rlying Klipbokkop/Adolphspoort F ormations suggest a Givetian age whilst Old World brachiopods and are present in the Karoopoort and Wagendrift F ormations (Witt eberg Group). This suggests that the Eifelian-Givetian boundary is located near the Waboomberg-Wupperthal contact and replacement by Old World fauna occurred with transgression of the Klipbokkop Formation. Biostratigraphic and sequence stratigraphic research suggests that relative sea-level controlled the distribution of the Malvinokaffric fauna in South Africa. Here, the fauna are contained within three 2nd order T-R sequences with transgressive surfaces in the Rietvlei, Tra-Tra and Waboomberg For mations. Closure of the Malvinokaffric Realm coincides with a protracted regressive phase in the Wupperthal Formation prior to transgression of the Klipbokkop Formation. Smaller 3rd order T-R cyclicity further suggests a step-wise decline of the Malvinokaffric fauna leading up to the end-Eifelian.

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# The Late Devonian mass extinction: new geochemical and geochronological insights

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The Late Devonian marked a time of numerous successive environmental perturbations and biotic crises, including one of the 'Big Five' mass extinctions of the Phanerozoic. The Frasnian-Famennian (FF) boundary Kellwasser crises (~372 Ma) represents the largest and best known of these crises, but numerous smaller scale events (e.g. the Late Famennian Annulata Event: ~363 Ma) also occurred during the 20 million year-long Late Devonian. However, despite representing a time of substantial floral and faunal turnover, there remains little consensus as to the cause of these events, either individually or collectively. Extreme continental weathering and subsequent stimulation of primary productivity and marine anoxia has been proposed as a major driver of the Kellwasser crises and other Late Devonian events, but large-scale volcanism and one or more meteorite impacts have also been implicated. In this study, we present new geochemical and geochronological data from the well-studied Late Devonian records of Steinbruch Schmidt (Germany) and Kowala Quarry (Poland). Our new U-Pb date for a bentonite layer at Steinbruch Schmidt of 372.36±0.053 Ma, from which a precise age of the FF boundary of 371.88±0.12 Ma is inferred, confirms previous age estimates for this boundary. However, this age does not match the timing of any known Late Devonian meteorite impact or currently dated volcanics from the Viluy Traps Large Igneous Province. We also present a long-term osmium-isotope (Os(i)) record from Kowala Quarry, including the first stratigraphic coverage of the two Kellwasser crises. The Os(i) values from the FF boundary and Lower Famennian are consistent with those from multiple North American records, suggesting that the record at Kowala documents global osmium-isotope trends. Shifts to very radiogenic Os(i) values are documented at the base of the Kellwasser horizons, potentially supporting globally enhanced weathering rates at the onset of those two crises. A less pronounced shift to radiogenic values is also observed across Annulata event strata at Kowala, perhaps indicating that similar processes impacted the marine realm during that event, possibly in tandem with a late pulse of Viluy Trap volcanism. These results reaffirm the complexity of the repeated Late Devonian crises, whilst supporting previous hypotheses that these events were coincident with times of enhanced global weathering rates, which potentially stimulated the recorded widespread marine anoxia.



Speaker

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#### Selectivity of the Lower Kellwasser mass extinction (Late Devonian) in the Appalachian Basin, U.S.A.

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Mass extinctions are often associated with multiple environmental perturbations. For example, the Upper and Lower Kellwasser Events (the two pulses of the Frasnian-Famennian mass extinction in the Late Devonian) coincide with both global cooling and ocean anoxia/dysoxia. Assessing the selectivity of extinction-which types of organisms survived versus died-can help constrain which environmental changes were most important as kill mechanisms. Here, we examine selectivity with respect to several factors during the Lower Kellwasser Event. A thick package of siliciclastic sediments was deposited in the Appalachian Foreland Basin during the Late Devonian. Thanks to recent stratigraphic revisions, the Kellwasser Events can be traced along a paleoenvironmental gradient that shallows from west to east in New York and northern Pennsylvania. Previous studies have shown that brachiopod species composition varies significantly along this gradient, and that the Lower Kellwasser Event was more severe of the two extinctions. The Wiscoy Formation was targeted for this study as it immediately predates the first extinction pulse. We collected bulk samples from numerous localities along the paleoenvironmental gradient and identified ~8,000 brachiopod fossils from 22 genera and over 27 species. Non-metric multidimensional scaling was used to quantify variation among species in environmental preference; variation in extinction intensity among habitats could indicate that anoxia was a kill mechanism, because oxygen levels likely varied with depth. Brachiopod orders varied in latitudinal distribution in the Devonian, so variation in extinction intensity among orders could implicate cooling as a kill mechanism. We also tested the effects of abundance, paleoenvironmental range, and body size on probability of extinction. Multiple logistic regression strongly supported global cooling as a major kill mechanism-species belonging to orders prevalent at low latitudes had higher probability of extinction than those belonging to orders common at high latitudes. In contrast, paleoenvironmental preference was not a major predictor of extinction in these data.



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#### Biogeographic provinciality of brachiopod faunas and its relationship to Frasnian-Famennian mass extinction

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The Late Devonian brachiopods are known from various blocks in North America, Europe, Siberia, Kazakhstan, North and South China, Turkey, Iran, Pamir and western and eastern Australia, with 979 occurrences assigned to 150 genera (from 63 families) in the Frasnian, and 1189 occurrences assigned to 174 genus (from 68 families) in the Famennian. Palaeobiogeographical analysis by hierarchical Cluster analysis and Non-metric Multidimensional Scaling superimposed by Minimum Spanning Tree reveal regional biogeographical variation from Frasnian to Famennian during which global endemism and provincialism were obscured by wide-ranging lineages and cosmopolitan species. The Euramerica and Cathysia subgroups in tropical region and brachiopod associations in northern margin of Gondwana (roughly correspond to the "Old World Realm") are recognized in the Frasnian, with also links between Siberian and northern North America (Alaska) brachiopod faunas are identified. In the Famennian, brachiopod faunal endemism increased in western Northern America, North and South China, accompanied with faunal links from Europe via North Africa into eastern North America (named as the "Afro-Appalachian links" by House (1973)). The pre-extinction cosmopolitan faunas are broadly adapted lineages which survived with more probability, as have been investigated in the end-Ordovician or end-Permian extinctions. However, interchange of the cosmopolitan lineages appears to have been restricted after the Frasnian-Famennian extinction, suggested by the existence of separate provinces in the Famennian. Many new taxa originated respectively in the North American and Cathysian provinces in the post-extinction faunas. This biogeographic differences were attributed directly to loss of ecological habitats at the end-Frasnian, with which both widespread, broadly adapted lineages and ecological specialists were largely destroyed. Immediately after the extinction, migration or rapid recovery for even ecological generalists was restricted as disjunct geographical distribution prevent faunal disperse or invasion into the vacant ecospace. This is probably related to lower stand of global sea-level that ultimately exposed barriers to faunal exchange, therefore produce increased regional biogeographic differences. Future work are still necessary to improve our understanding of the biogeographic dynamics in more details for both regional examples and global dataset.



Speaker

## Conodont succession of the regional Yangshuo Stage (Late Famennian, Devonian) and possible Annulata and Dashberg events at the Tieshan section in Guilin, South China

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The regional Yangshuo Stage, named from the Yangshuo County in northeastern Guangxi, represents the second last Devonian stage in China, and is approximately equivalent to the late Famennian. Its base is defined by the first occurrence of conodont *Palmatolepis rugosa trachytera*, and the top by the FO of foraminifer *Eoendothyra regularis*. The stratotype section for the Yangshuo Stage is near Tieshan in Guilin City, where it comprises ~236 m of shallow- water intraclastic, oolitic wacketo grain-stones with minor intercalations of black, organic-rich calcareous mudstones that were accumulated on an isolated carbonate platform during late Famennian. A total of 118 conodont samples were collected at intervals between 0.25 m and 18 m within the Yonghsien Formation at Tieshan, among which eighty-one samples yield conodonts and thirty-seven were barren. Representative of genera Palmatolepis, Polygnathus, Pseudopolygnathus, Bispathodus, Icriodus, Spathognathodus have been collected from the succession, and the fauna enables the establishment of four conodont biozones, including the Pa. r. trachytera, Pa. postera, lower Pa. g. expansa and middle Pa. g. expansa zones in ascending order, providing a high-resolution correlation with other equivalent sections in the Palaeotethys. Based on a detailed analysis of conodont biostratigraphy and sedimentary facies, two intervals involving sudden intercalations of black, organic-rich mudstone within the very shallow-water shoal carbonate sediments were recognized in the upper part of the Pa. r. trachytera zone and the top of the lower Pa. g. expansa zone, respectively. These two major lithological changes represent sedimentary responses to sea-level rise and marine dysoxic events, probably paired with unsteady eutrophic conditions in the South China marginal sea, and can be correlated with the global Annulata and Dashberg events.



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Speaker

#### 3D Taphonomic analysis using microCT of an ophiuroid-stylophoran assemblage from the Lower Devonian Bokkeveld Group, South Africa

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A well-preserved echinoderm dominated benthic assemblage at Karbonaatjies Kraal, Western Cape, South Africa, provides a unique taphonomic window into Early Devonian marine ecosystems. The site is located in southwestern Gondwana within the Lower Devonian (Emsian) Voorstehoek Formation, Ceres Subgroup of the Bokkeveld Group. Palaeontological and sedimentological features suggest deposition of siliciclastics within a shallow marine, storminfluenced, offshore transition zone. The fossiliferous mudstones and siltstones yield a highly endemic biota dominated by brachiopods, mollusks, trilobites, and echinoderms of the cool-cold water Malvinokaffric Realm. We describe the occurrence of a 5 cm thick obrution bed with a dense assemblage of intact ophiuroids and stylophorans. The taphonomy of echinoderm assemblages within the Voorstehoek Fm has received little attention as previous studies focused primarily on systematic palaeontology and biostratigraphy. Taphonomic analysis of the Karbonaatjies obrution bed was conducted using microCT scans of a section of the bed that were stitched together to generate a 3D virtual model. This method revealed over 700 articulated protasterid ophiuroids closely associated with 150 stylophorans. The majority of ophiuroids and stylophorans display low levels of disarticulation and post-mortem disturbance indicating rapid and deep burial. Ophiuroids with upturned arm tips occur throughout the bed indicative of failed escape attempts. Individuals with missing arm tips, along with the presence of abundant disarticulated arm fragments, also suggest a pattern of arm autotomy in response to storm disturbances. The combination of well-preserved echinoderms and highly degraded shell hash indicates that rapidly buried communities were living on or within skeletal debris that had accumulated during intervals of sediment starvation. Ophiuroids and stylophorans exhibited a gregarious mode of life as inferred from these deposits and it seems likely that both groups shared a similar mode of life and feeding strategy. Similar co-occurrences have been reported from Middle Ordovician to Lower Devonian deposits. However, the detailed study of the Karbonaatjies ophiuroid-stylophoran assemblage using powerful microCT techniques has the potential to reveal new and important insights into these unique ecologic interactions.



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<sup>&</sup>lt;sup>'</sup> Speaker

#### First record of charophytes in the Devonian of Turkey (Central Taurides)

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In the frame of two Turkish-German cooperation projects aiming at the Devonian of the Eastern and Central Taurides, the Akkuyu Section in the Central Taurides was studied in considerable detail. The sequence is of Givetian age reaching the Givetian/Frasnian boundary interval according to different fossil groups (foraminifers, palynomorphs, brachiopods, conodonts, charophytes). The rich content of benthic fauna (e.g., corals, bryozoans, crinoids and many brachiopods) shows that the respective sequence has been deposited in a shallow-marine coastal environment at the northern Gondwana margin. This is also indicated by the lithofacies of mainly carbonates with some intervals of shales and cross-bedded sand-/siltstones. Coastal habitats are also represented in the underlying Eceli Section by interto supratidal microbial mats, beach deposits and desiccation cracks.

In the upper part of the Akkuyu Section charophytes have been detected in the residues of two conodont samples. They are present as calcified utricles and some are rather well preserved. Additionally, charophytes have been recognised in two thin-sections, also from the upper part of the section. The charophyte flora is represented by two species, assigned to the genera *Sycidium* Sandberger 1849 and *Pinnoputamen* Wang & Lu 1980, determined as *Sycidium volborthi magnum* Li & Zhou 1982 and *Pinnoputamen erikfluegeli* (Langer) nov. comb.

Charophytes – both fossil and modern – are mainly representatives of fresh or brackish water habitats, whereas e.g., conodonts, crinoids and brachiopods are exclusively marine and have been mostly reported from open marine environments. But transport of charophytes from coastal or fluvial areas into marine settings may be considered as a plausible explanation; their tolerance to marine conditions is discussed.

The palaeobiogeographic distribution of both genera shows frequent occurrence on both supercontinents, Gondwana and Laurussia. According to palaeogeographic maps, most charophyte localities are situated in areas of epicontinental seas. For longtime, *Sycidium volborthi magnum* has been recorded only from the Eifelian of the Guangxi Province (Southern China). It is now also known from this part of the world and a longer range is shown by the Akkuyu specimens. The latter is in accordance with recent finds in the German Rheinisches Schiefergebirge which are assigned to the lower Frasnian. The charophytes of the Akkuyu Section are the first known from the Devonian of Turkey.



<sup>&</sup>lt;sup>©</sup> Speaker

## The Annual meeting of the Subcommission on Devonian Stratigraphy SDS/IUGS - The Pragian/Emsian issue

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During the 2017 SDS meeting In Valencia it was agreed to hold the next annual meeting in Paris in conjunction with the 5th IPC. The main item on the agenda will be the redefinition of the Pragian/Emsian boundary. In 2008 the Devonian subcommission reached an agreement regarding the redefinition of the base of the Emsian. The following statement has resulted from the discussion: The current base EmsianGSSP (kitabicus boundary) is located at a very low position, within the traditional Pragian Stage (= the Praha Formation) and it is not the same or even close to the base of the Emsian in traditional German or western European usage (Ulmen Gruppe). After this problem with the kitabicus boundary GSSP definition was recognised the SDS agreed to: 1) Search for a new boundary for the base of the Emsian, which would be located in the Zinzilban Gorge, at a position close to the entry of the excavatus group and specially, the entry of a particular taxon within the excavatus group; this taxon bears semi-crossed ridges on the tongue and it has been cited at about 114 m above the GSSP in Zinzilban. 2) To keep the kitabicus boundary as a reference marker that could be a used for future subdivision of the Pragian (i.e. the Zinzilbanian and after the basal Emsian boundary is moved up). However, the repeated conodont sampling (in 2008 and 2015) failed to provide new data to progress with the definition of a new boundary. Because a new campaign and repeated sampling is unlikely to provide conodont faunas at an appropriate level the question arises of: What to do next? However, the potential of the kitabicus boundary for future subdivision of the Pragian stage is very high, but this can only happen once the new base of the Emsian is formalized.



**S36 // Ora**l

Speaker

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## The Pragian/Emsian boundary in the Prague Synform: possibilities and constraints for the boundary stratotype

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The Pragian/Emsian boundaryin the Prague Synform: possibilities and constraints for the boundary stratotypeLadislav Slavík Institute of Geology of the Czech Academy of Sciences, Rozvojová 269, 16500 Praha 6, Czech Republic The need of redefinition of the basal Emsian boundary has been largely accepted at the meetings of the International Subcommission on Devonian Stratigraphy in the last couple of years. The problem of the position of the prospective lower Emsian boundary also affects the duration of the Pragian and Emsian Stages. Difficulties with scarcity of polygnathids (conodonts) in the critical interval in the upper parts of the Zinzilban section in Kitab Reserve, Uzbekistan, i.e. well above the position of the GSSP, was revealed during the last SDS sampling campaign of 2015. The lack of conodont material represents a serious constraint for the future redefinition of the boundary in this area. Data from other sections of different regions are now strongly needed for further discussion on the position and location of the new international stratotype of the basal Emsian boundary. The purpose of the presentation is to demonstrate both the possibilities and constraints for the boundary stratotype in the Prague Synform. In this area, the Pragian Stage has been originally proposed to correspond to the entire succession of the lithologically and biostratigraphically constricted Praha Formation. The correlation is based on extensive faunal datasets but also on high-resolution petrophysical correlation methods: magnetic susceptibility (MS), gamma-ray spectrommetry (GRS), isotope geochemistry and orbital time scale. The highest precision in the relative dating of Palaeozoic marine carbonate successions is, however, achieved using conodont biostratigraphy. The sedimentation rate can also be deduced from a comparison of the integrity of conodont lineages between sections in areas with different environments. However, since Pragian conodont faunas show a high degree of provincialism, no universally applicable biostratigraphic scheme is available for the Pragian. This is a major issue regarding the future redefinition of the base of the Emsian and subsequent prospective subdivision of Lower Devonian stages.



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#### Conodont sequences spanning the Pragian/Emsian transition (Lower Devonian) in NE Spain (Pyrenees and Iberian Chains) and its relevance for the redefinition of the base of the Emsian

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The Emsian GSSP is defined at the base of Bed 9/5 in the Zinzilban Gorge section, Kitab National Park, Uzbekistan with the entry of the conodont *Polygnathus kitabicus*. After thorough analysis and discussions of this level, the International Subcommission on Devonian Stratigraphy has voted for its redefinition; accordingly, the new boundary shall be placed in a level that closely correlates to the original base of the Emsian in the SE Eifel Hills (Germany) and the conodont sequence shall contain the evolution from *P. excavatus* to *P. excavatus* 114.

Our main goal is to present the conodont sequences from two critical areas in Spain (Central Pyrenees- SCP and the Iberian Chains -IC) and analyse them in the context of the Emsian redefinition.

The SPC conodont record spans from the *pireneae* Zone (lower Pragian) through the *nothoperbonus* Zone (lower Emsian) and is mainly composed of *Polygnathus* and *Icriodus*, allowing a mutual biostratigraphical control of these two genera and, consequently, a correlation with neritic and pelagic sequences. The oldest *Polygnathus* from the SCP is *P. pireneae;* it is followed by a continuous sequence of entries comprising the indexes *P. kitabicus, P. ex. excavatus, P. excavatus* 114, *P. gronbergi* and *P. nothoperbonus*. Many other taxa as *P. sokolovi* and *P. pannonicus* occur within the sequence. In the same sections, *Icriodus curvicauda* appears within the *pireneae* Zone. It is followed by the entry of *I. celtibericus* in the upper part of the Zone and below the income of *P. kitabicus*. Several new species of *Icriodus* span from the *kitabicus* Zone through the *nothoperbonus* Zone. *I. bilatericrescens, I. sigmoidalis* and *I. gracilis* are first recorded from the Middle *excavatus* Zone.

The IC relevant records start in the lower part of Santa Cruz Fm. with *I. curvicauda;* in the upper parts *Acrospirifer* aff. *primaevus* occurs and above it *I. celtibericus* enters. The lower part of the Mariposas Fm. yielded *P. ex. excavatus* and *P. ex.* 114. Higher, *Arduspirifer prolatestriatus* and *Filispirifer fallax* are recorded. The successive entries of *I. sigmoidalis, I. gracilis* and *I. bilatericrescens* are also important records for the discussion on the base of the Emsian.

In brief, the Spanish conodont record is important for contributing to the ongoing discussions and correlations on the intended redefinition of the base of the Emsian.

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\* Speaker

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#### New insights on the *Pedavis* (Conodonta) apparatus

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Klapper and Philip (1971) set up the genus *Pedavis* for a kind of conodont skeletal apparatus classified as a Type 4 skeletal apparatus, composed of three elements, a platform element (I), a pyramidal element, described as a modified saggitodontan element (S1), and a conical element (M2), described as a striate (later changed to costate) conical element.

Subsequent studies demonstrated that several costate elements may be included in the apparatus, increasing the number of elements to six, as in other related taxa like members of the Family Icriodontidae. However, as no intact apparatus has been discovered yet, reconstructions are not convincing.

The main goals of this report are to globally analyze collections containing skeletal elements of the *Pedavis* apparatus and to propose a classification that accommodates our observations.

We have studied 190 samples with *Pedavis* apparatus from sections in Spain, North America and the Czech Republic. The large collections we have examined allowed recognition of, at least, seven kinds of elements, grouped into five types, that consistently occur together with the platform element.

The platform element is "bird-foot" shaped with four processes. It is accompanied by a pyramidal element that can be either costate or smooth. The rest of the elements have all longitudinal costate. The conical elements are the most varied and we have grouped them into two large categories, simple and complex conical elements. Flared elements have a conical or pyramidal shape with a flared base. Denticulate elements are mostly geniculated with one or more posterior spurs. Angulate elements are pyramidal with angulate intersections and a flared start-like base. Our reconstruction brings the kinds of elements up from the three elements in the original reconstruction to, at least, eight.



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# Restudy of the conodont genus *Palmatolepis* at the Lali section, South China

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The conodont genus *Palmatolepis* is representative of the Late Devonian offshore conodont fauna and has a world-wide distribution. The use of species of *Palmatolepis* for biostratigraphic subdivision is due to the high specific diversity and many palmatolepids are index species of conodont zones. Even so the study of conodont genus *Palmatolepis* still faces three major problems.

Firstly, identification standards of palmatolepids are not uniform among different conodont researchers, Ziegler and Sandberg (1994) even cited that "**there are two schools of identifying Late Devonian conodont taxa**". Those uniform identification standards directly led to the difficulty with global correlation of Late Devonian conodont biostratigraphy. The correlation of "Late Devonian standard conodont zonation" and "The Frasnian Zoneation (Montagne Norie Zoneation)" still encounters much difficulty.

Secondly, many long-ranged and important species have a very complex diagnosis and morphology, such as "Pa. proversa ", "Pa. rhenana ", "Pa. winchelli ", "Pa. jamieae ", "Pa. bogartensis ", "Pa. triangularis ", "Pa. minuta minuta " "Pa. perlobata " and "Pa. superlobata ". To provide a better biostratigraphic meaning of each taxon, those species need to be revised.

Lastly, the old phylogenic studies provides very useful knowledge for the evolving pedigree of genus *Palmatolepis*, but the number of new species has increased considerably since 1990, with no review or database of all species. Reliable identifications require a complete overview of all taxa in the genus to solve this near chaos.

Therefore, to solve those problems, we recollected the Lali section in South China and restudied the conodont biostratigraphy which was first studied by Ji and Ziegler (1993). The Lali section is composed of the famous Wuzhishan Formation, which is characterized by an off-shore nodular limestone facies and abundant conodonts. Here, more than 27000 Pa elements, mostly *Palmatolepis*, were picked from 157 samples. The Lali section ranges from the Frasnian *transitans* Zone (FZ 4) to early Tournaisian *duplicata* Zone, and completely recorded the entire evolutionary history of conodont genus *Palmatolepis*.

Here, following the species list of Late Devonian *Palmatolepis* (Becker and Hartenfels, 2016), we present a complete review for all Late Devonian palmatolepids from Lali and the literature.

Most importantly, the identification of every taxon of *Palmatolepis* is restricted to the holotype, no matter the early forms or the late forms. Only those specimens which are identical to the holotype can be treated under a same species or subspecies.

For Frasnian palmatolepids, 40 species were found (including six new species. We recognize nine evolutionary stocks, *transitans* -Stock, *gutta* -Stock, FF-Stock, FE-Stock, *hassi* -Stock, *jamieae* - Stock, *nasuta-Stock*, *salibaevi*-Stock and *winchelli* -Stock. In addition 15 species are believed to be junior synonyms, 4 species are believed to be *nomen dubium*, and there are 19 species which are not found at the Lali section tied with certain evolutionary stocks.

For Famennian palmatolepids, 95 species and subspecies were found at the Lali section including 18 new species and subspecies. We recognized nine evolutionary stocks: *ultima*-stock, *lobicornis* -stock, *superlobata* -stock, *sandbergi*-stock, *minuta* -stock, *glabra* -stock, *delicuta* -stock, *clarki* - stock, *rhomboidea* -stock, *gracilis* -stock and *perlobata*-stock. In addition, 11 species are believed to be junior synonyms, 13 are believed to be *nomen dubium*, there were 15 species not found at Lali section tied with certain evolutionary stocks.

<sup>\*</sup> Speaker

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#### Devonian vertebrates from Andrée Land, Spitsbergen: diversity and palaeoenvironments

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The Lower and Middle Devonian of the Andrée Land (Svalbard) represent part of the Old Red Sandstone successions comprising freshwater to marginal marine sediments well known for their rich early vertebrate record. In this work, we present new species of thelodonts and acanthodians from the Wood Bay and Grey Hook formations of the Andrée Land, together with *in-situ* trace and rare earth element compositions, analysed in an attempt to retrieve geochemical information about the early depositional environments. The REE concentrations appeared to be relatively uniform within the scales of each studied taxon, and REE profiles, together with the presence and absence of the Eu and Ce anomalies, showed evident differences among localities and separate taxa. The description of *Woodfjordia collisa* gen. et sp. nov., *T alivalia svalbardia* sp.nov., *Canonia* cf. *grossi, Amaltheolepis montiwatsonia* sp.nov., *Amaltheolepis winsnesi* and *Amaltheolepis austfjordia* sp. nov., provide comparison with similar Early-Middle Devonian vertebrate faunas from other regions of the Northern Hemisphere.



Speaker

## The early diversification of the Ammonoidea: taxonomic richness of the Devonian faunas from Morocco

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Ammonoids are one of the most abundant and prolific Phanerozoic marine fossil invertebrate groups and have a remarkable evolutionary history of more than 350 million years. These externally shelled cephalopods appeared in the Early Devonian (Emsian) and they became diverse in the context of the Devonian Nekton Revolution. The end of the Devonian (Frasnian/Famennian crisis) also marks the first major bottleneck in the evolutionary history of ammonoids. To better understand the establishment of these biotic events and their potential abiotic triggers, the present work focuses on the analysis of the biodiversity fluctuations characterizing the evolution of ammonoids during the Devonian period. We focus our investigations on the taxonomic component of the biodiversity (taxonomic richness, composition, and similarities) of the ammonoid faunas from Morocco (North Africa), considering two temporal scales (14 substages and 67 ammonoid biozones), and two taxonomic ranks (genus and species). The different analyzes performed for this study are based on a database built from the most recent publications, to have a homogeneous and as accurate taxonomy and biostratigraphy as possible. This dataset contains 1810 occurrences of ammonoids distributed from the Emsian to the Famennian in 64 distinct localities. These occurrences include 444 species, 146 genera, 45 families, and 19 superfamilies. Because the fossil record is imperfect and biased, the fluctuations in taxonomic richness have been analyzed using incidence data (presence) with different indices and methods (ex. sampled raw diversity, normalized diversity, Myr and cross-border rates, poly-cohorts, uniform time bins and re-sampling) to best account for these imperfections. The results show large variations in taxonomic richness, associated to particularly high values in the upper Eifelian, middle Givetian, and uppermost Famennian, as well as very low values in the lower Eifelian, Frasnian, and lower-middle Famennian. The two major preliminary results are as follows: 1) some of these biodiversity fluctuations may be related to known Devonian extinction events, and seem strongly influenced by climate variations and anoxic events; 2) both temporal scales of analysis (substage vs. biozone) show some contrasted patterns indicating that the interpretation of the potential abiotic triggers of these biodiversity changes depends on the temporal resolution of the record.



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## Exceptional preservation of spores from the Lower Devonian Hunsrück Shale, Rheinisches Schiefergebirge, Germany

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The Lower Devonian Hunsrück Shale is renowned world-wide for the exceptional preservation of fossils including soft part preservation due to pyrite precipitation. This allows a rare insight into exceptional and diverse marine biota, which have been preserved under oxygendeficient conditions. Although macroscopic plant remains are very rare, land plant spores have variously been reported and identified. Their preservation, however, is rather constrained by intense tectonism, deep sediment burial together with high thermal maturation and widespread pyrite precipitation. Thus, palynological residues consist mainly of totally opaque carbonaceous clasts. Only in some instances preservation is sufficient for detailed description and reliable identification of spores by SEM techniques.

The Lower Devonian sequence of the Hunsrück includes a complete transition from orthoquartzites (Taunus-Quarzit) to black shales (the classical "Hunsrückschiefer") by the gradual replacement of quartzite. The Postersdepicts a rather diverse assemblage of exceptionally well preserved spores, which were isolated from a sample from the southern Hunsrück. At this site, thin sand/silt layers are intercalated between dominant black shales. Since marine phytoplankton (prasinophytes, acritarchs) is completely missing in the assemblage, it is suggested, that the land plant spores have been drifted to the offshore site by freshwater outflow, which caused salinity stratification and consequently oxygen-deficient bottom water conditions. As indicated by the intercalated sand/silt layers bottom waters may have been flushed by oxygenated currents which modulated reducing conditions and, thus, prevented pyrite precipitation.

A vitrinite reflectance of 5.3 Rmax (equivalent to meta-anthracite) has been determined for randomly occurring organic clasts. This has been confirmed by Raman spectroscopy on individual spores and a consistent maximum thermal overprint of 274 Co +/36 calibrated. Despite this high maturity details of surface morphology can be resolved by SEM, which may not be seen in transmitted light. This has to be accounted for in any future revision of the taxonomy of Lower Devonian spores and could even shed new light on early land plant diversity.



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#### Plant remains from the Devonian of San Juan, Argentina

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Throughout the Devonian occurred the most important stages of plant propagation on land and their subsequent evolution, yet the extent of this process is far from being completely understood, mainly by the scarcity of the register. The fossiliferous localities of the Devonian of Precordillera, in Argentina, have provided sterile or poorly preserved remains of fossil plants and, very rarely, palynomorphs. Associations of low diversity have been described, composed of primitive vascular plants and herbaceous lycophytes. Here we present new samples from the Punta Negra Formation, collected from the Precordillera of San Juan province. Punta Negra Formation lays over the marine sediments of the Lower Devonian Talacasto Formation with a transitional limit and reaches 1000 m thick. The lower limit of the Punta Negra Formation is diachronic, being older in the southern localities. Plants come from four localities. Sandstones from the Río San Juan locality yielded a compression of stem with petiolate, divided microphylls, assignable to Haskinsia Grierson and Banks 1983. It is noteworthy that this is the first record of a lycopsid with preserved leaves from this unit. Southern, nearby Puesto Bachongo fossil remains were found comparable with the bryophyte Sporogonites Halle 1916. These samples consist in an ovoid-globose capsule which shows longitudinal costae in the middle sector, which resembles Sporogonites excellens Frenguelli 1951. Sterile lycophyte stems were found in both localities. Plant debris, consisting in smooth and ridged sterile axes, putative sporangia and isotomous bifurcated stems, was also found. The association is in general consistent with the previously described for the unit, and the discovery of better preserved taxa allow us a more detailed comparison to elucidate the age of the deposits. Sporogonites was found in the Lower Devonian of Argentina, Australia, Belgium, and Brazil, and younger strata from Spain. The lycophyte Haskinsia, on the other hand, was widespread in the Middle Devonian, with a species also found in Sierra de la Ventana (Buenos Aires Province, Argentina). The presence of both taxa is coherent with the age given to Punta Negra Formation and the diachronic nature of its base, could help in the stratigraphic correlation between localities. Lastly, the finding of these new material encourages us to continue the research in this large unit, which could lead to a better understanding of the expansion of the early land plants.



<sup>&</sup>lt;sup>'</sup> Speaker

#### Biodiversity and palaeobiogeographical affinities of Middle Devonian trilobites from Algeria

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Trilobites are widespread in Middle Devonian deposits of north Gondwana. Some of them were collected from the Saoura Valley (Ougarta Basin, Algeria), in the 'Chefar el Ahmar' Formation. Phacopidae dominate clearly the trilobite assemblages, with *Austerops, Morocops, Chotecops,* and *Phacops* as main genera. Comparisons are made with closely allied species, and occurrences have been analysed in terms of their intra- and interspecific variability and biodi- versity. The occurrence of *Struveaspis maroccanica* provides an early Eifelian age, which is also confirmed by the presence of trilobites *Thysanopeltis* and *Koneprusites*, and ostracods *Bairdiocypris devonica* and *Bufina ?subovalis*.

In contrast with the Early Devonian, which is characterized by a diversified fauna that includes numerous common genera between North Africa and Europe, the previously reported Middle Devonian fauna from Algeria is composed of only one new phacopid sub-species, *Struveaspis maroccanica ougartensis*. The scarcity of trilobites after the late Emsian could be linked to the development of more open environments, as this is suggested by the goniatite-bearing carbonate facies. However, as observed in Morocco, the remains are in fact relatively abundant and well-preserved. At both generic and specific levels, the Algerian faunule may be regarded as relatively diversified without marked original features and closely related to Moroccan taxa, due to the presence of *Struveaspis maroccanica* and *Thysanopeltis* aff. *speciosa*.

New samples corroborate the occurrence of Phacopida, Proetida or Corynexochida in Northern Africa. Although the diversity of genera and species preserved in the Ouarourout II section (A4) appears to be better than in the Ouarourout I section, additional fieldwork is required to obtain a more representative picture on Devonian trilobite biodiversity and community structure. Two types of assemblages were recognized from the early Eifelian: A4-biota relatively diversified, dominated by *Chotecops hoseri;* and other biotas characterized by a low diversity and dominated by one or two taxa barely represented.

Finally, at a global scale, the lower Eifelian fauna of the Saoura Valley is more or less comparable to the one recovered from the upper Emsian, which is characterized by a relatively moderate diversity and evenness with barely dominant taxa. The lower Eifelian fauna is slightly less diverse than the upper Emsian one, and characterized by slightly higher dominance and lower evenness.



<sup>&</sup>lt;sup>°</sup> Speaker

## Exceptional Lower Devonian Milankovitch cycles recording from the Hudson Valley and corresponding magnetic susceptibility record, New York State (USA)

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Uncertainties on the radiometric ages of Devonian stage boundaries are currently in the order of several millions of years. A cyclostratigraphic approach is a foremost way forward to improve the Devonian geological time scale. In order to do so, we need good continuous records on the one hand and reliable paleoclimatic proxies on the other hand. The NY Route 199 section, from New York State near Kingston in the Hudson Valley, is a road cut outcrop, which exposes most of the Schoharie Formation. It corresponds to the upper portion of the Emsian Stage (upper Lower Devonian, ~400 to ~394 Ma), with an essentially continuous deposition. The lithology consists of a mixed siliciclastic-carbonate succession with overall increasing carbonate upsection, showing various degrees of bioturbation (primarily Zoophycos, Planolites and Chondrites); colors range from beige white, to brown or dark grey. The quality of most of the outcrop is so remarkable that the color variations by themselves permit recognition of Milankovitch cycles, with prominent bundles of light and dark beds. One type of cycle expression is represented by a succession of about six darker beds nested between lighter beds, which is interpreted as six precession cycles in one short eccentricity cycle (precession in the Devonian was ~17 kyr). Samples were collected every 2 cm through 38 m of the section for magnetic susceptibility measurements. Hysteresis measurements (every 50 cm) provide a high field susceptibility of about ~5.10-8 m<sup>3</sup>/kg and most of the hysteresis loops are straight lines, indicating only small contribution of ferromagnetic grains. The correlation between the high field susceptibility and the overall magnetic susceptibility is high (r = 0.91), while the correlation between the ferromagnetic susceptibility and the magnetic susceptibility is distinctly lower (r = 0.17). Thus, the ferromagnetic minerals have a low impact on the total magnetic susceptibility; its variability is mostly driven by paramagnetic clay minerals. Importantly, despite being remagnetized (throughout the Appalachians, these Paleozoic rock sequences are all remagnetized during the Variscan-Alleghenian orogeny), the magnetic susceptibility reflects depositional information. Typically, lighter beds correspond to lower magnetic susceptibility values; darker beds have higher values. Milankovitch cycles are visible on the outcrop and in the magnetic susceptibility record, allowing a precise floating time framework to be constructed for this interval.



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<sup>&</sup>lt;sup>\*</sup> Speaker

#### Early Devonian ostracods of the Russian Arctic Region

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This study assembles data relating to the distribution of the ostracod faunas in the Early Devonian of the Russian Arctic Region and demonstrates their biostratigraphical and palaeobiogeographical value. In the early Devonian strata of the Russian Arctic, ostracods are an important component of the fossil assemblages. The examined material comes from numerous localities sampled for ostracods during the geological survey in Novaya Zemlya, Severnaya Zemlya, and Kotel'ny Island in 1960–1970th. Noteworthy is that the collections of the Emsian non-leperditicopid ostracods from the reference outcrop section in Novaya Zemlya have been examined for the first time. A transgressive sedimentary sequence from protected-marine near-shore habitats to open-marine environments is recorded for the Early Devonian in the area studied. The marine environment and carbonate sedimentation persisted within both the Kotel'ny paleobasin and the Novaya Zemlya paleobasin in the late Lochkovian - Emsian time. The ostracod assemblages from Novaya Zemlya and Kotel'ny Island have relatively high species diversity during the entire Early Devonian, unlike those from Severnaya Zemlya, where the impoverished monotaxonic leperditicopid assemblages are recorded at some levels. The kloedenelloid, metacopid, and podocopid ostracods appeared to be the most stable element in the ostracod fauna in these regions. Although it is not a typical Thuringian ecotype, the ostracod fauna including "spinous" species of genera Bairdiocypris and Bashkirina, as well as Bairdia and specific Scaphina seems to indicate a relative deep open shelf environment for the Early Devonian assemblages from Novaya Zemlya and Kotel'ny Island. Generally, the Early Devonian ostracod faunas of Arctic Eurasia appear to have close affinities both at genus and species levels. Many of the taxa identified are widespread in the Novaya Zemlya - Urals region, Taimyr, Sever- naya Zemlya, Kotel'ny Island, as well as in the North-East of Russia, and Salair and Kuznetsk basins (southern West Siberia). Several ostracod species show high potential for local as well as long-distance biostratigraphic correlations across the Russian Arctic Region in the Early Devonian.



Speaker

#### A case of preservational bias on Devonian chitinphosphatic fossils from Brazil

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One of the least studied fossil faunas of the Brazilian Devonian is found between the Givetian-Famennian of the western border of the ParnÁıba Basin, in the State of Tocantins, Brazil. Besides the sedimentary successions are poorly known, the descriptions of organisms in these rocks are rare with Echinodermata fauna as preponderant. However, new field trips reveal the presence of siltite fossiliferous layers with Conularids (Conularia quichua) and Discinids (Gigadiscina sp.). These layers are related to the Highstand System Tract (HST) deposited after the Maximum Flooding Surface. In general, conularids preserve finely ornamentate phosphatic periderm and occurs as isolated and incomplete fossils. The specimens are mainly sub-horizontal to the bed and generally compressed perpendicular to their long axis, showing two adjacent side faces side by side in the stratification plane, but exhibit little or no distortion of the periderm parallel to that axis. In contrast, specimens inclined at moderate or high angles to the bed are inflated, with their cross section being rhombic, and may exhibit a slight compaction parallel to their long axis. The discinids are folded without fragmentation. The fossiliferous concentrations are deposited under low energy conditions (HST), which reinforces that episodic events led to this concentration. The observed conularids are typical of the low energy environment and surface bathymetry and reveal taphonomic features that suggest a position outside of life but not related to long bioclastic transport. In addition, there is no coefficient preservation of fossils with calcium carbonate shells, denoting possible diagenetic control in this accumulation. Preservation of chitin phosphatic organisms at sporadic concentrations of HST environments probably reflects more acid conditions. Thus, the fossil faunas of the Brazilian Devonian studied from the western border of the Parnáiba Basin are possibly an example of accumulation of diagenetically controlled fossils where the diversity of ecosystems must be underestimated once this bias affects paleoecological studies.



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#### Paleogeographic differences in temperature, waterdepth and conodont biofacies during the Late Devonian

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The Famennian (Upper Devonian) started and ended with two of the seven largest crises of the Phanerozoic, the Kellwasser and the Hangenberg respectively. In between, global environmental trends have been identified, involving cooling and eustatic regression. Tropical and subtropical marine faunas were cosmopolitan. Overall, this suggests that the Famennian was marked by long-term environmental changes occurring in a relatively homogeneous manner. This was tested by a detailed investigation of two continuous outcrops, one in the Montagne Noire (France) and the other in Saxo-Thuringia (Germany). Both were located in the (sub)tropical area during this period, and belonged to two former microcontinents bracketed between the closing Rheic Ocean and Gondwana. At a high resolution and in the same rock samples, sedimentary facies, oxygen isotopes, and the composition in conodont genera (biofacies) were estimated. Sedimentary facies provided an estimate of water-depth and oxygen isotopes were used as paleotemperature proxy. Conodont biofacies were analyzed using a principal component analysis, allowing the expression of the variations in the two outcrops on the same axes, and a quantitative comparison with the other proxies. Sea-level and temperature variations were different between the two areas. Saxo-Thuringia displayed stable deep and warm conditions throughout. In contrast, the environment was shallower and cooler in the second part of the record of the Montagne Noire, congruent with the global change evidenced elsewhere. The location of Saxo-Thuringia, close to the first point of closure of the Rheic Ocean, might have favored active tectonics, causing a local departure from the eustatic trend, and have limited water masses exchanges with the open ocean, favoring the persistence of warm conditions. Offshore taxa with persisted later at high abundance in the Saxo-Thuringian record. The two conodont biofacies records were otherwise very similar. This suggests that other factors mitigated the water-depth forcing on these conodont assemblages.

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#### Environmental changes during Famennian low-order biocrises - stable isotope data from European successions

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The middle to uppermost Famennian comprises repeated successions of low-order bioevents, the so-called *Annulata*, Dasberg and Epinette/Etroeungt (Ep/Et) events or crises. They are characterized by extinctions, originations, and radiations of selected faunal groups. These intervals coincide with transgressive/regressive pulses and the deposition of black shales and/or organic-rich limestones elsewhere.

Our study focusses on stable isotope geochemistry ( $\delta^{18}O_{phosph}$ ,  $\delta^{13}C_{carb}$ ) from paleogeographically different pelagic limestone sections in Europe in order to reconstruct environmental changes during these biocrises.

The suggested level of the Annulata Event in the Pseudopolygnathus granulosus (= Upper trachytera) Zone at Geuser (Franconia, Germany) is characterized by a weak positive peak in  $\delta^{13}C_{carb}$  with values of up to 2.6. At Beringhauser Tunnel (Rhenish Massif, Germany), the  $\delta^{13}C_{carb}$  values are generally low, and partly influenced by diagenesis, as reflected by negative values. However, highest values of more than 2.5, were measured in the Lower Annulata Limestone. Results at Geuser and Křtiny (Moravian Karst, Czech Republic) indicate a minor but distinct  $\delta^{13}C_{carb}$  excursion during the Ep Event in the Bispathodus aculeatus aculeatus (= Middle expansa) Zone, with isotope ratios ~ 2.8 . The  $\delta^{13}C_{carb}$  values remain relatively high in strata equivalent to the Et Event in the B. ultimus ultimus (= Upper expansa) Zone. At Col de Tribes (Montagne Noire, France) and Křtiny,  $\delta^{13}C_{carb}$  values are also slightly higher in strata equivalent to the Et Event values are also slightly higher in strata equivalent to the Et Event values are also slightly higher in strata equivalent to the Et Event in the B.

While the temperature variations at Beringhauser Tunnel are minor, with  $\delta^{18}O_{phosph}$  values from coeval conodonts between 17.5 and 18.0 below, above and around the *Annulata* events,  $\delta^{18}O_{phosph}$  values from Geuser vary between 16.7 and 18.9. Highest values at Geuser are reported from the *Annulata* and Ep/Et events, while the lowest values, and thus the warmest sea water temperatures, are recorded from the *Polygnathus styriacus* (= Lower *postera*) and *B. stabilis stabilis* (= Lower *expansa*) zones.

Although environmental changes and their impact on faunas during the studied crises are minor in magnitude when compared to the major biocrises in the late Frasnian (Kellwasser events) and at the Devonian-Carboniferous boundary (Hangenberg Event), this study could provide insights into the causes of repeated successions of low-order bioevents during the Famennian.

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# Preliminary Famennian data of the "Ravin de la Fontaine de Santé" section (Montagne Noire, southern France)

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The Montagne Noire represents one of the classical regions for studying Upper Devonian strata in Europe. Therefore, it was no coincidence that three Global Sections and Points (GSSP's) have been ratified by the IUGS in this area, including the Middle/Upper Devonian (Col de Puech de la Suque), Frasnian/Famennian (Coumiac), and Devonian/Carboniferous (La Serre trench E') boundaries.

As the southeastern margin of the Massif Central, the Montagne Noire represents the most southern and external part of this structural unit within the Variscan Orogenic Belt (Aretz et al. 2016). In accordance with Engel (1981), sedimentary successions of the Montagne Noire belong to nappes, which were delivered from the north. Different non-metamorphic (par)autochthonous units can be distinguished: Faugères Nappe, Mont Peyroux Nappe (including the detached Pic de Bissous Block), and olistolithic "Cabrières Klippen" in the east as well as Pardailhan and Minervois nappes in the west. In contrast to the well-studied eastern units, successions of the Minervois Nappe are poorly investigated, so far, although they offer tremendous research potential.

The Fontaine de Santé section crops out approximately 500 m to the northeast of Caunes Minervois, within a small episodically water-bearing valley south of the road to the Rocamat marble quarry. Boyer et al. (1968) first described the succession. Whilst Tucker (1974) and Bourrouilh (1981) revised the sedimentology, Crilat (1983) as well as Bourrouilh et al. (1998) published sparse conodont data. The latter includes a first, but incomplete biostratigraphy. Due to the current outcrop conditions, our re-investigated succession was split in two parts. We measured both sections (A and B) bed-by-bed. Until now, 32 of 87 possible conodont layers were sampled. Section A posses a thickness of ca. 6.25 m and consists of grey to reddish-grey flaserkalk, which is overlain at the top 1.5 m by reddish micritic flaserkalk ("griotte facies"). The main Section B, ca. 15 m in thickness, contains the entire sequence from "griotte facies" to "vraie griotte" and "supragriotte". In contrast to Section A, orange clay seams occur within the "griotte facies". Whereas the "vraie griotte" consists of red micritic nodular limestones, the "supragriotte" is developed as red to grey micritic flaserkalk. First conodont data suggests that Section B ranges from the *Palmatolepis termini / Pa. glabra prima* zones to the *Pa. marginifera utahensis* Zone.



Speaker

# Influence of dolomitization on the trace fossil assemblages from the Plavinas RS deposits, Devonian, Latvia

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The deposits of the Frasnian Plavinas Regional Stage (RS) are widespread in the East European Platform. In Latvia the succession is dominated by dolomite with interlayers of dolomitic marl, clay, sandstone, and siltstone. In eastern Latvia the dolomites change into limestones with similar structures and assemblages of fossils.

In the western part of the Main Devonian Field, following ichnogenera are discovered in the Plavinas RS: Bergaueria, Bifungites, Chondrites, Diplocraterion, Gyolites, Lockeia, Phycodes, Planolites, Psammichnites, Rhizocorallium, Skolithos, Spirophycus, Thalassinoides (Meškis, 2013).

The diversity of ichnofossils in studied outcrops of the Plavinas Regional Stage in the territory of Latvia is insignificant; it represents only six ichnogenera out of all trace fossil material. Detectable ichnofossils in the deposits of the Plavinas Formation are quite rare. They have not been found in the Dārzciems and the Ape quarries, and the only bioturbation has been observed in some dolomite layers in the Sikspārni Caves and the Vizla outcrops. It is likely that such low diversity of detectable ichnofossils is due to their poor preservation due to pervasive dolomitisation of the studied deposits. It is possible that the differences in the ichnofossil assemblages reflect a more active hydrodynamic regime during the beginning of the Plavinas time. There could be different reasons for that, including a higher velocity of tidal currents or stronger storms.

Glossifungites ichnofacies represented mostly by the *Thalassinoides* burrows dominate in the deposits of the PJavinas Regional Stage. The assemblage characteristic of the *Skolithos* ichnofacies was found in deposits of the lower part of the regional stage Pskov Beds, formed in a shallow basin with the relatively active hydrodynamic regime.

The composition of the ichnofossil assemblages and the degree of preservation of separate ichnotaxa in predominantly clastic deposits, limestone, dolomitised limestone, and dolomite was compared in this study. It has been discovered that the features important for the identification of ichnofossils undergo significant modifications or even are lost under the influence of the dolomitisation processes. Thus it is possible that the data on ichnofossils in the studied dolomites only partly represent their initial composition and diversity.



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# Sedimentary environment of carbonate rocks and fossil assemblages from the Plavinas Formation, central part of the Baltic Devonian basin: comparison of the Riežupe outcrop and Randāti Cliff

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Sedimentary rocks of the Upper Devonian, Frasnian, Plavinas Formation in Latvia are represented by dolomites, dolomitic marls and clayey dolomites, as well as partly dolomitized limestones. By lithology, cyclicity, and fossil assemblages the Plavinas Formation is divided in four members – Koknese, Sēlija, Atzele, and Ape (Brangulis *et al.* **//** 1998).

Carbonate rocks from the Riežupe outcrops (western Latvia) and Randāti cliffs (eastern Latvia) were studied in macro-samples, by XRD and TOC analysis. The XRD analysis were performed in *PANalytical X'Pert PRO*. TOC analysis were done in *Multiphase Carbon Determinator RC*612 at 550°C.

The carbonate deposits in both exposures bear evidence of their sedimentation in shallow-water normal-salinity basin. These deposits are rich in stromatoporoid, brachiopod, and gastropod fossils. In several parts of their succession laminite structures, desiccation cracks and tepee structures are present, evidencing shallowing of the basin. Complete dolomitization of the studied carbonate deposits greatly obliterated structures and textures, and it hinders the sedimentological and palaeontological interpretations.

XRD analysis show that in the Randāti cliffs dolomite is highly dominant and accompanied by quartz and a little amount of orthoclase (silt to sand grains). Secondary calcite is present in most of the layers. In Riežupe outcrops XRD analysis shows similar situation, except for lack of the calcite peaks. Only illite is present in the clay admixture of dolomites, and its peak is higher in dolomites from western Latvia. Similarity of mineral composition confirms the evidence of little variability of sedimentary environment in the studied area of the Baltic Devonian basin.

TOC analysis results shows that the primary production of organic compounds were not high in both studied objects. There are also no signs of anoxic conditions, so the organic substances oxidized and dissolved. That leads to conclusion that these carbonates were sedimented in oxic bottom water conditions – low to moderate organic productivity (oligotrophic) conditions.

The diversity of ichnofossils under the influence of the process of dolomitization are very low and determination of taxonomic status of ichnogenera is problematic. During the investigations of the properties of ichnofossils, both carbonate dissolution and XRD analysis were conducted, in order to look for correlations between different impurities in various dolomites of the Plavinas Formation, both from Riežupe outcrop and Randāti cliffs, but no correlations have been found. The authors are thankful to Dr. Michael Wagreich, Geodynamics and Sedimentology Department, University of Vienna (Austria) for help with the XRD and TOC analysis.

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# Conodont biostratigraphy and geochemistry of pelagic Devonian-Carboniferous boundary successions at Trolp (Graz Paleozoic) and Grüne Schneid (Carnic Alps)

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Uppermost Famennian and lower Tournaisian pelagic successions at Trolp (Graz Paleozoic, Austria) and Grüne Schneid (Carnic Alps, Austria/Italy) were re-investigated and correlated using high-resolution conodont biostratigraphy, stable isotope geochemistry, and element geochemistry (ICP-MS, ED-XRF). Both sections consist of continuous limestone successions deposited during the Hangenberg Crisis at the Devonian-Carboniferous boundary (DCB), which is globally characterized by black shales, sandstones or stratigraphic gaps caused by a first glaciation pulse at the end of the Devonian.

The conodont studies focus on the early *Protognathodus* and the *Siphonodella* (*Eosiphonodella*) faunas, the index taxa used for the DCB conodont zonation. The base of the Tournaisian could be precisely fixed with Si. sulcata and/or Pr. kühni within condensed successions. The level between the praesulcata (Lower *praesulcata*), *kockeli* (Upper *praesulcata*) and *sulcata/kühni* (*sulcata*) zones, which can be well recognized by their zonal index fossils, yields a rich Protognathodus fauna, and its faunal evolution could be well documented both at Trolp and Grüne Schneid. While the siphonodellids are generally rare at Grüne Schneid, this fauna occurs relatively abundant at Trolp even in association with the *Protognathodus* fauna.

Oxygen isotope data of conodont apatite ( $\delta^{18}O_{phosph}$ ) from Grüne Schneid suggest increasing water temperatures just before the Hangenberg Crisis, and high temperatures persisted in the *costatus-kockeli* Interregnum (initial Hangenberg Crisis) and during the first occurrence of *Pr. kockeli*. This level is characterized by the onset of a positive carbon isotope excursion ( $\delta^{13}C_{carb}$ ,  $\delta^{13}C_{org}$ ) measured both at Trolp and Grüne Schneid. A temperature decrease occurred after the costatus-kockeli Interregnum which is approximately coeval with the first occurrence of *Pr. kühni* or slightly before. Paleoredox proxies U/Th and Ni/Co indicate prevailing oxic conditions in both sections. At Grüne Schneid, higher enrichment factors (normalized to PAAS) of Zn (EF = 6), Cu (EF = 7) and Pb (EF = 11) reveal enhanced paleoproductivity before the onset of the Hangenberg Crisis (praesulcata Zone) as well as after the biocrisis (*bransoni* Zone). A sharp increase in Al, Si, Ti, Rb concentrations at the base of the *kockeli* Zone at Grüne Schneid is probably a reflection of reduced carbonate productivity related to the Hangenberg Crisis.

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#### New data on latest Famennian microbialites and early Tournaisian bryozoans of the Moravian Karst Palaeozoic (Czech Republic)

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The Devonian-Carboniferous boundary (DCB) successions of the Moravian Karst Palaeozoic (eastern Bohemian Massif, Rhenohercynian Zone) are important for stratigraphy due to a co-occurrence of conodonts and foraminifers, and readily recognized event phases of the endDevonian Hangenberg Crisis. This contribution provides new palaeontological, sedimentological and geochemical (LA-ICP-MS) data from Lesńı lom and Mokrá quarries (NE vicinity of Brno, Czech Republic).

Carbonate petrography and REE geochemistry revealed microbial and authigenic origin of a laminated limestone, which is correlative with the lower interval of the end-Famennian Hangenberg Crisis. Shale-normalized (PAAS) REE patterns of the laminite are similar to those of modern seawater and Devonian microbialites from the Canning Basin reflecting the dominance of authigenic carbonate phases. Elevated U and Mo enrichments and their covariation patterns reflect the episodic establishment of suboxic to euxinic bottom condition during deposition of the laminite. Negative Ce and positive Eu anomalies, low Y/Ho ratios, and very low Al/(Al + Fe + Mn) ratios suggest an influence of diluted high-temperature hydrothermal fluids perhaps related to latest Devonian rift magmatism in the eastern part of the Rhenohercynian Zone. The authigenic and microbial laminite, followed by siltstones, ooidal limestones and lower Tournaisian micritic limestones with common autochtonous microbialites in the aftermath of the Hangenberg mass extinction, represent a typical sequence of anachronistic facies.

Lower Tournaisian micritic succession above the Hangenberg Crisis interval yielded new bryozoan fauna in the *Siphonodella sulcata* and *Si. quadruplicata* conodont zones. Bryozoans occur in intercalated oolitic-intraclastic or skeletal calciturbidite beds with abundant thrombolites. The association is characterized by a low taxonomic diversity represented by species belonging to the orders *Cystoporata* and *Cryptostomata*. Four species were found in the studied thin sections: *Nikiforovella* sp., *Saffordotaxis* sp., *?Streblotrypella* sp., and *Eridopora moravica* nov. sp. Cystoporates are quantitatively dominant in this taxonomically poor bryozoan assemblage (76% of total bryozoan fragments) and are represented by the cosmopolitan genus *Eridopora*. From the palaeobiogeographic point of view, the studied bryozoan association indicates links between the eastern and western parts of the northern Palaeotethyan, Siberian and Panthalassan realms.



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#### Hunting for Eifelian (Middle Devonian) conodonts in the Pedreira da Engenharia Formation (Ossa-Morena Zone, Portugal)

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Middle Devonian strata from the Ossa-Morena Zone are scarce and not well-known; however they are very important for palaegeographic and geodynamics reconstructions of southwestern Europe.

One locality where Middle Devonian rocks crop out is the Pedreira da Engenharia, Portugal, which is located within the northwestern part of the Ossa-Morena Zone. There, in 1972 van den Boogaard reported Eifelian conodonts from the lower part of the quarry, which currently is underwater and, thus, not accessible. Above the water, a steeply wall exposes about 20 m of a Middle Devonian calciturbidites sequence that has yielded a few, but important, conodonts.

Our purpose is to document the conodont sequence from Pedreira da Engenharia and to assign a precise age for the carbonate succession.

Due to the ragged wall, it was necessary to climb down (and back up) with secured ropes, harnesses and a lifeline.

The 20 m thick section is composed of marly limestone and limestone interbedded with lutittes; in the lower third, marly limestone are dominant, while limestones are the main component of the upper two thirds. They belong to the Pedreira da Engenharia Fm.

13 conodont samples were taken. The lower sample (CAB-E 1), about 3 ms above the base of the section, yielded *Polygnathus costatus*, the index of the lower Eifelian *costatus* Zone. The next important yield stems from sample CAB-E 11, from about 2 ms below the top of the section. This sample contains *Tortodus kockelianus kockelianus*, the index of the upper Eifelian *kockelianus* Zone. Sample CAB-E 12, 0.5 m above sample 11, yielded *T. ko. australis*. This taxon starts in the underlain *australis* Zone, but ranges higher into the *kockelianus* Zone; therefore, this occurrence would belong to the upper part of its range.

The conodont record is indicative of Eifelian age and might tentatively suggests the assignation of this section to an interval spanning from the *costatus* through the *kockelianus* zones. A similar range was described for the Odivelas Limestone calciturbidites which crop out in the same domain of the Ossa-Morena Zone. These samples and others from the same section are stil under examination.

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#### Givetian (Middle Devonian) Conodonts from the Iberian Chains (Spain)

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The Middle Devonian Series in the Iberian Chains is partly known and it has been reconstructed from fragmentary outcrops of limited extension, mainly cropping in the south-eastern part of this Mountain Range, the so-called Axial Depression of the Río Cámaras (ADCR). Therefore, any weighted data regarding accurate age, stratigraphical position and correspondence within the current scheme is of enormous value.

This fragmentary and isolated character of upper Eifelian and lower Givetian outcrops makes that one of the current scientific challenges in the DARC is the identification and characterization of the Eifelian/Givetian transition.

Near Moyuela village, we have studied a short, isolated, and overturned section containing *Polygnathus* and *Icriodus* of early Givetian age. Consequently, the goal of this report is to document the conodont succession from this section and discuss is integration within the general stratigraphical scheme for the DARC.

The section is 9 m thick and is composed of thin limestone beds, nodular limestone and shale. Colours are in general dark, from brown to dark grey and black. 11 samples from the limestone and five from the nodular beds were etched for conodonts.

The lowest record from the first nodular layer, above the 1 m thick basal brown shales, yielded the biostratigraphical marker for the base of the Givetian, *Polygnathus hemiansatus*. The cooccurring conodonts *Icriodus obliquimarginatus*, *Ic. struvei*, *Po. pseudofoliatus*, *Po. linguiformis klapperi*, *Po. angusticostatus* and *Po. angustipennatus* correlates this level with the base of the Givetian or just slightly higher. The entry of *Ic. lindensis* in the next Bed supports the basal Givetian, *hemiansatus* Zone. A few beds above, the record of *Ic. excavatus* identifies the *rhenanus/varcus* Zone and the beginning of the Middle Givetian. The entries of *Ic. brevis* and *Ic. eslaensis* in the upper part of the section are consistent with a Middle Givetian age.

Consequently, the studied fragmentary section near Moyuela spans from the base of the Givetian into the lower Middle Givetian and represents the first clear datum for identification of the base of the Givetian.

The section can partially be correlated in age with the 1.3 m thick limestone level of the Barreras Fm, placed 32 m above the base of this formation. However, the lithological features are different.

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# Signatures of tidal processes and the Middle-late Devonian vertebrate assemblages from the epeiric Baltic paleobasin

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Recently the hypothesis was proposed postulating that the presence of strongly modulated tides may have been a significant driver in the vertebrate sea-to-land transition during the Devonian (Byrne et al. 2018). The results of the analysis of resulting semi-diurnal tide and springneap range have shown strong correlation between the location of both large range (> 4m) tides and remarkable fossil sites and findings, e.g. around Laurussia during the Emsian. Lithostratigraphic succession of the Middle-Upper Devonian of the Eastern Baltic, represented by siliciclastic and carbonate deposits of the wide shallow epeiric sea, is wellestablished. An integrated study including facies analysis and sequence stratigraphic approach, biostratigraphical and taphonomical analysis enables to trace signatures of tidal processes and indicators of the climate change, thus providing better understanding of the evolution of the Devonian basins of the Baltic area. Tide amplitude from 2-4 m (mesotidal regime) to more than 4 m (macrotidal regime) is suggested for the Eifelian deposits (Tovmasjana, 2013), and signatures of the tidal processes have been found in many fossiliferous sites of the Givetian-Famennian siliciclastic deposits in the territory of the Baltic Devonian Basin. Such indicators of tidal processes as mud and mica drapes on the cross-beds, graded lamination, wavy and lenticular lamination, tidal bundles, reactivation surfaces, and climbing ripplelamination on cross-beds have been found in various stratigraphic units in Latvia, Estonia and NW Russia, starting with the Givetian Burtnieki, Gauja, and Lode formations, and traced up to the uppermost Famennian Ketleri Formation. Almost all these stratigraphic units are characterised by abundant vertebrate remains, sometimes accompanied by the plant and trace fossils. Joint sedimentological and palaeontological studies provide possibilities for better understanding of the sedimentary environment of the shallow-marine, marginal-marine and sea-land transitional sandstone bodies and palaeoenvironment of the Devonian vertebrates.



# Palaeoenvironments and relative sea-level shifts during the Devonian of South Africa

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The Devonian record of South Africa comprises siliciclastic rocks of the Rietvlei and Baviaanskloof Formations (Nardouw Subgroup: Table Mountain Group), Bokkeveld Group, Weltevrede Subgroup and Witpoort Formation (Witteberg Group) and the Msikaba Formation. Relative age-dating of this portion of stratigraphy, from palaeontological data and comparison with global eustatic trends, suggest that it comprises Pragian/Emsian-to-Fammenian time, whilst palaeomagnetic and palaeoclimatic indicators place South Africa at high subpolar-to-polar southern palaeolatitudes. The Devonian palaeontological record of South Africa has yielded many exciting discoveries that have proved pivotal in understanding of plant, vertebrate and invertebrate evolution as well as global palaeobiogeography and palaeoecology at these palaeolatitudes. Given the global importance of this relatively complete succession, the South African Devonian record provides an excellent opportunity to understand palaeoenvironmental change and relative sea-level shifts at high southern palaeolatitudes which is poorly known. This research presents a review and interpretation of the palaeoenvironmental record of the South African Devonian from an extensive dataset comprising some 85 measured and described lithostratigraphic profiles and in excess of 200 research articles, government reports, theses and dissertations. These data suggest that Devonian palaeoenvironments of South Africa accumulated in a south-and-eastward deepening depobasin under storm-and-wave dominated conditions variably within shallow marine-offshore, barrier-island lagoon and deltaic siliciclastic depositional systems. Sequence analysis of the succession suggests that two-to-three major 2nd order deepening events occurred during the Pragian-Emsian, three during the Eifelian, one during the Givetian, two during the Frasnian and a possible two during the Fammenian. All 2nd order deepening events are bound by transgressive ravinement surfaces that overlie protracted forced regressive falling stage systems tract deposits. The chronostratigraphic placement of these deepening events shows some correlation with major 3rd order global transgressive events, suggesting that global eustacy may have been an overriding allocyclic control in the Cape Basin. 3rd order transgressive-regressive (T-R) cyclicity suggest 15-18 smaller relative sea-level shifts comprising ~60-70 4th order T-R events.



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#### Upper Devonian-lower Carboniferous brachiopods: contribution to the stratigraphy of Armenia

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Upper Devonian sedimentary sequences are encountered mainly in the southern part of Central Armenia within the South-Armenian block of Gondwanan origin. They were accumulated on a platform located at the northern margin of the Gondwana continent. They are made of shallow marine deposits of mixed carbonate/siliciclastic origin. The Upper Devonian-lower Carboniferous sequences are highly fossiliferous and ca. 1,500 meters thick. The present study focuses on the Upper Devonian-lower Carboniferous part of a section that crops out at the locality Sevakavan, in order to establish the biochronostratigraphic frame of these thick sequences and to find out the Devonian-Carboniferous boundary based on its rich brachiopod fauna. The stratigraphic distribution of the brachiopods identified so far led us to recognize the presence of five successive biozones of the regional biozonation introduced by Rzhonsnitskaya & Mamedov (2000). These include the upper Famennian "Paurogastroderhynchus nalivkini" and "Spinocarinifera nigra– Sphenospira julii" zones and the Lower Carboniferous "Unispirifer praeulbanensis–Rhytiophora curtirostris", "Unispirifer tornacensis–Rhipidomella michelini", and "Spirifer baiani–Marginata burlingtonensis" zones.

Field observations and microfacies studies allow to recognize three lithostratigraphic units: (1) a lower unit comprising grey quartzites, dark shales and limestones referred to the Uppermost Famennian Gortum and Arshakiakhpur formations, (2) a middle unit comprising sandy limestones assigned to the Lower Tournaisian Gerankalasy Formation, and (3) an upper unit composed of more massive limestones assigned to the Upper Tournaisian Armarsh Formation. Sedimentation occurred in a very shallow marine environment as suggested by the presence of dasycladacean algae and bryozoans.

Rzhonsnitskaya, M.A. & A.B. Mamedov. 2000. Devonian stage boundaries in the southern Transcaucasus. Courier Forschungs-Institut Senckenberg, 225: 329-333.



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#### Initial reef growth in the Hönne Valley (Hagen-Balve Reef complex, Rhenish Massif)

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In the Givetian and Frasnian, reefal growth was very common on the southern shelf of the Old Red Continent. Many small to large biostromes and bioherms can be found all over Europe, which mostly evolved during the Middle Devonian. Some reefs had optimal conditions, which enabled them to keep up with fast subsidence. The Hagen-Balve Reef complex is located at the northeastern limb of the Remscheid-Altena Anticline, which extends W-SE for about 30 km. It contains a well-bedded succession of platform limestone of more than 1000 meters thickness. Weakly calcareous sandstones and siltstones characterize the underlying Oberhonsel Formation, which is interpreted as a succession of pro-deltaic sediments deposited on the distal inner shelf. With a sharp boundary, the siliciclastics are overlain by dark, coarsegrained crinoid debris. This first bed of the Hagen-Balve Formation yields various reefal organisms, such as tabulates (Platyaxum, Thamnopora), rugose corals (large-sized, solitary Mesophyllum), cyanobacteria (Girvanella), broken bivalves, brachiopods, ostracods, and calcispheres. The subsequent sequence consists mainly of dark, nearly black limestones, with sporadic marl and siltstone intercalations. Single beds contain a high amount of Corg. Crinoid debris occur in nearly every bed, but became more fine-grained upwards. The reefal fauna contains mostly tabulate corals, such as Alveolites, Thamnopora, Pachyfavosites, and Platyaxum; solitary rugose corals and a few stromatoporoids have been observed as well. Stringocephalus, the Givetian index brachiopod, enables a rough dating, but occurs only rarely. Most organisms are broken and suggest storm deposition. Sampling for conodonts was of modest success. The assemblage of Bipennatus bipennatus, rare Polygnatus linguiformis klapperi and various coniform genera (Belodella, Nepanderodus, Dvorakia) is typical for a shallow platform but not zonally diagnostic within the lower/middle Givetian. Residues exhibit large amounts of heteractinid sponge spicules, in most samples pyrite, in some samples mica, and in almost every sample, scolecodonts. The faunal composition changes markedly towards the top of the section. Micritic bafflestones, formed by phaceloid colonies of Dendrostella replace the crinoid rudstone facies. Tabulates (Alveolites, Aulopora, Thamnopora and Pachyfavosites) are frequent and suggest a true biostrome.

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#### Revised classification and diversification of Devonian ambocoelioid brachiopods in South China

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The superfamily Ambocoelioidea is an important group of the Brachiopoda, both globally and in South China. In the Devonian, this group is also most diverse compared with that in other periods. Based on features of cardinal process and cruralium, three types of cardinalia are recognized, including *Ambocoelia* - type, *Emanuella* -type and *Rhyncospirifer* -type. The *Rhynchospirifer* -type cardinalia is a distinct character that distinguishes them from the rest of the Ambocoeliidae; therefore the Rhynchospiriferinae is reelevated to the family rank. *Guangxiispirifer* of the previous Ambocoeliinae is reassigned to the Rhynchospiriferidae while *Ambothyris, Choperella, Crurispina, Diazoma, Emanuella, Ilmenia, Ilmospirifer, Ladjia, Moravilla* and *Zhonghuacoelia* of the previous Rhynchospiriferinae are transferred to the Ambocoeliinae).

Three earliest ambocoelioids in South China are *Ambothyris, Amboglossa* and *Prolazutkinia* in the upper Emsian; their emergences were likely associated with the global Upper Zlichov Event. The upper Emsian occurrences of *Amboglossa* and *Prolazutkinia* are their FADs globally. These two genera probably gave rise to the Rhynchospiriferidae and the Lazutkiniidae, respectively. After an initial gradual increase in generic richness, the Ambocoelioidea reached the highest diversity in the late Eifelian and Early Givetian in South China. From then on, the diversity gradually decreased till the end of the Devonian, and was least affected by the Frasnian-Famennian Event.

The Ambocoelioidea is a strongly facies-controlled group. Their temporal and spatial distributions show a close relationship with sea level changes. Ambocoeliids and rhynchospiriferids were adapted to different environments. The former inhabited deeper and partly dysoxic environments, therefore showed greater capabilities to migrate and survive extinctions. On the other hand, the rhynchospiriferids dwelled in a reef-related, high energy, and oxic environments, which were probably more sensitive to environmental changes; they also showed high diversity and endemism and more easily experienced rapid and regional extinctions.



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# S37 - The onset of the Great Ordovician Biodiversification (GOBE): fossils, radiations and Lagerstätten - IGCP 653 session

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#### An application of Birth-Death Models to phylogenies to determine the timing of the Ordovician radiation

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To determine environmental causes for clade diversification requires a precise relationship between environmental history and clade origin. This relationship presents a challenge for Earth scientists because variability in fossil preservation can obscure when species of a clade first appeared and began to diversify. We use birth-death branching models to determine the time of origin and diversification of the strophomenoid brachiopods, a diverse and abundant clade that originated during the Ordovician radiation. We estimated the timing of strophomenoid diversification with two models: a morphological clock model that assumes a constant rate of character evolution, and a Bayesian model that allows rates of character evolution and probabilities of fossil preservation to vary through time. When applied to our phylogeny of strophomenoid brachiopods the morphological clock model suggests an origin and diversification of this clade in the late Cambrian. The Bayesian model suggests the strophomenoids arose in the Early Ordovician (Floian), and then increased rapidly in the Daipingian. The Floian origin is consistent with other studies that show diversification across a number of disparate clades at approximately the same time and lends support to the Bayesian model. Any environmental cause for the diversification must have similar timing. Temperature is one variable that has been interpreted to play a major role in driving the Ordovician radiation. Based on several environmental proxies, temperature is inferred to have decreased during the Ordovician, although the overall trajectory and rate of change are poorly constrained. Most inferences of dramatic temperature change come from the Late Ordovician, up to twenty million years after the Early to Middle Ordovician burst of diversification documented here. Certainly temperature change may have helped reduce rates of background diversification through the Ordovician, but other causes (environmental and biological) must be sought for this Early to Middle Ordovician burst of diversification. Models of diversification applied to phylogenies that allow evolutionary rates and sampling probabilities to vary over time are needed for many of the major Ordovician clades in order to understand the phylogenetic structure of the Ordovician radiation and to help constrain its potential causes.



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# The Tremadocian age of the *E. symmetrica* Zone revealed by chitinozoans from the Lauzon N section, Québec, Canada

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Until recently, the chitinozoan E. symmetrica was considered an indisputable marker for the Floian Stage of the Lower Ordovician. In eastern Canada, at the G locality, rue du Fleuve section, Lévis, Quebec, Canada E. symmetrica occurs, above a rusty conglomerate, in the lower strata of the Lévis Formation (Achab, 1979). In the same area at the N Section at Lauzon, strata below the conglomerate contain Lagenochitina species, similar to those, from the Cow Head Group in Newfoundland, named L. maxima by Williams et al. (1999). Above the conglomerate the chitinozoan assemblage is different but similar to that of the G locality that contains E. symmetrica. The Tremadocian age of the N Section was firmly established by Maletz (1997) who recognized, below the conglomerate, a graptolite fauna correlated with the A. victoriae Zone of Newfoundland, corroborating the similarity between the two L. maxima microfaunas. Above the conglomerate, a poor fauna of the graptolite A. murrayi Zone is reported. In the uppermost level, A. murrayi is associated with the first specimens of the graptolite T. approximatus, the FAD of which indicates the Floian. During the last decade, E. symmetrica was documented from several upper Tremadocian successions, namely from Estonia, England, Morocco and South China. In South China, Wang et al. (2013) recognized L. destombesi in an interval spanning the tenellus - victoriae graptolite zones, and E. symmetrica in the strata of the murrayi graptolite Zone. They also noted that, contrary to what has been reported in Gondwana and Laurentia, E. symmetrica does not extend into the Floian. More recently, Liang et al. (2017) questioned the presence of L. destombesi in South China. They also confirmed that E. symmetrica is confined to the Tremadocian. These unexpected occurrences of E. symmetrica in Tremadocian rocks have led several authors to suggest that the E. symmetrica zone extends below the Floian into the Tremadocian. However, when considering the chitinozoan data from Lévis and Lauzon, an alternative hypothesis can be considered: At Lauzon, E. symmetrica occurs above the conglomerate in levels of the murrayi Zone. At the G locality, at Lévis, the strata above the conglomerate containing E. symmetrica can therefore be assigned to the murrayi Zone and not, as previously believed, to the approximatus Zone. In conclusion, E. symmetrica can be considered as an indicator of the Tremadocian murrayi Zone, and, as is the case in South China it does not extend into the Floian.

Speaker

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## The pattern of changes in Ordovician radiolarian diversity in the context of the clade's Early Paleozoic diversification

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Based on the study of an exhaustive database of mid Cambrian to Silurian radiolarian occurrences the pattern of changes in radiolarian biodiversity is explored with quantitative methods to find out trends in taxonomic richness, and to test possible biases on these patterns. The data were compiled based on the literature after having selected those studies only that provide independent chronostratigraphic calibrations; thus, for most analysed radiolarian assemblages their age resolution is at the stage level. The dataset analyzed in this study only contains incidence data (i.e. presence/absence), because abundance data are rarely available or not consistent among radiolarian studies. Species described under open nomenclature (e.g. "sp. A") or with species level uncertainty (e.g. "cf.") were accounted for. The choice of the analyzed stratigraphic bins was a compromise guided by the resolution required to address our research questions, the available data, and the maximal precision which data can be assigned to a given stratigraphic interval of the Lower Paleozoic. Taxonomic assignments of species were revised with respect to the original publication and species names were harmonized in order to eliminate possible taxonomic biases. Changes in radiolarian diversity dynamics were estimated with different methods, including binbased, boundary-based, time-based and resampling indices. The Cambrian–Ordovician and Silurian intervals are two contrasted periods. The Cambrian- Ordovician is characterized by short-lived taxa with two diversity peaks in the Tremadocian and the Darriwilian that may reflect sampling bias and/or chronostratigraphic bias. Few are the radiolarian data for the Dapingian stage and none exists so far for the Hirnantian. The Silurian is characterized by long-lived taxa with two robust high diversity values in the Telychian and Gorstian. Thus, the major result highlighted by the various biodiversity indices is a clear, important and protracted Silurian diversification peaking in the Telychian and following the Hirnantian glaciation. Overall, a bias of focus cannot be discarded; the biodiversity curves produced in this study reflect the current knowledge of Lower Palaeozoic radiolarians and highlight the need for additional taxonomic and biostratigraphic studies to evaluate these biodiversity patterns.



#### Evolution of Ordovician marine biodiversity based on data from South China and the CONOP Technique

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With the steady accumulation of stratigraphical and paleontological data, as well as the continuous development of computer science, quantitative stratigraphic study based on big data has become an important trend in paleobiology. Quantitative stratigraphy originated in the 1960s, and has been widely used in solving problems in regional and global stratigraphical correlation. Several main methods have been widely adopted, including Graphic Correlation, CONOP (constrained optimization), UA (unitary association), RASC (ranking and scaling) and HA (horizon annealing). Among them, CONOP represents an automated technique that can conflate all sections in a multidimensional space at a time. It is especially suitable for automatic stratigraphical correlation of large data sets and subsequent paleobiodiversity analyses.

Ordovician marine strata are well developed in South China, with abundant and diverse marine fossil groups. The rocks and fossils have been intensively studied for nearly a century, and a huge number of research material has been accumulated in the literature. Therefore, the South China region seems the best place for the evolutionary study of the Ordovician marine life.

The Geobiodiversity Database (GBDB, http://www.geobiodiversity.com/) is an integrated platform for the integration, management and sharing of stratigraphical and paleontological legacy data. After 11 years' development, the GBDB team has digitized a massive amount of stratigraphical and paleontological data from all over the world. Comprehensive information from over 1600 Ordovician sections in South China have been compiled into the GBDB up to April 2018, which provides an important basis for the present study. All those Ordovician sections were searched and verified through the GBDB platform. Lowerquality sections with few fossils or less sampling effort, as well as those taxonomic names in open nomenclature have been omitted from the data set. All the taxonomic assignments were revised under a uniform standard of identification. The final data set was output as CONOP-format files from the GBDB platform and then run repeatedly with the parallel computing version of CONOP designed by the GBDB team. The final composite sequence, which contains all the major marine fossil group in the Ordovician oceans, was acquired and then used for the reconstruction of the Ordovician high-resolution marine biodiversity curve at the species level. This provides important insights for us to explore the dynamics of the evolution of Ordovician marine life in South China.

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# Katian (Upper Ordovician) conodonts from the Upper Yangtze Platform, South ChinaImplications for understanding conodont diversifications in the Ordovician

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The Katian succession of the Pagoda and Linhsiang formations are described and sampled from three sections on the Upper Yangtze Platform. A collection of 2384 conodont elements has been recovered from 34 samples. The elements are assigned to 24 species (including 6 sp. indet.) representing 18 genera along with 2 genus et species indeterminata. The fauna is dominated by *Hamarodus, Amorphognathus, Scabbardella, Dapsilodus, Ansella, Panderodus* and *Protopanderodus*. It is a typical representative of the South China Province that shares a large number of species with the Atlantic Realm. Two interval zones, *Hamarodus brevirameus* zone and *Protopanderodus insculptus* zone are recognized based on the presence of each nominate species. Compared with bio-diversities of the Early and Middle Ordovician previously counted, the early Katian following the Floian, Mid-Darriwilian and late Darriwilian to early Sandbian, probably is the fourth key stage for the Ordovician conodont radiation during the Great Ordovician Biodiversification Event on the Upper Yangtze Platform, South China.



Speaker

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## Middle Berounian (*ca.* Sandbian 2-Katian 1) trilobite, brachiopod and echinoderm assemblages from the southern Central Iberian Zone, Spain

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Middle Berounian rocks are very fossiliferous and rather well exposed in central Portugal, overlying an unconformity related to the Sardic tectonic phase, followed by the widespread deposition of an oolitic ironstone (the Favaçal bed) which has been correlated with the Zdice- Nučice horizon at the base of the Vinice Formation, Bohemia. In the Spanish prolongation of the Central Iberian Zone (CIZ), middle Berounian rocks also recorded a basal ironstone horizon and may reach a great thickness locally ('intermediate shales' of the Villuercas and Calatrava regions). This horizon is sparsely fossiliferous, yielding chitinozoans and a few barely identifiable trilobites and brachiopods. However, further SE in the Eastern Sierra Morena, two sections of the Cantera Shales have been studied, providing us a relatively abundant and diverse record of trilobites, brachiopods and echinoderms, with many interesting taxa previously only reported from Portugal. The first locality is placed at La Palomera site (Viso del Marqués, Ciudad Real), and the second in El Cantuesal (NW of La Carolina, Jaén). The assemblages comprise sixteen different trilobites (genera Cekovia, Vysocania, Hispaniaspis?, Dalmanitina, Phacopidina, Actinopeltis, Prionocheilus, Colpocoryphe, Iberocoryphe, Radnoria, Nobiliasaphus, Deanaspis and "Panderia"), eleven brachiopods (genera Gelidorthis, Reuschella, Svobodaina, Aegiromena, Triplesia, Dactylogonia, Drabovia, Rostricellula, and some Harknessellidae, Strophomenidae and Rafinesquininae indet.) and eleven echinoderms (genera Macrocystella, Homocystites, Heliocrinites, Rhombifera, Haplosphaeronites, Bohemiaecystis, Anatifopsis, Dendrocystites, Mespilocystites, Ortsaecrinus and Visocrinus). Of particular interest is the first Spanish record of some trilobite species (Cekovia loredensis, Vysocania iberica, Phacopidina armoricana, Actinopeltis tejoensis, Radnoria guyi) and the outstanding diversity of echinoderms recorded from two different beds at La Palomera section, including glyptocystitid, rhombiferan and diploporan cystoids, crinoids, stylophorans, plus single solutan and coronoid. The studied assemblages confirm a middle Berounian age, supporting the lithostratigraphic data. The Spanish association is highly correlated with middle Berounian assemblages described from the Portuguese CIZ and the Armorican Massif, strengthening the Ibero-Armorican biogeographical endemical signature, represented by several species exclusively known from this subdomain.

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#### The Late Cambrian (Furongian) gap: real or apparent

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Two major, extended diversifications punctuated the evolution of marine life during the Early Palaeozoic. The interregnum, however, between the Cambrian Explosion and the Great Ordovician Biodiversification Event is exemplified by the Furongian Gap when there was a marked drop in biodiversity. It is unclear whether the gap is apparent, due to sampling failure, or real associated with unique and fluctuating environments, a distinctive palaeogeography and extreme climates during the late Cambrian. Indications suggest that there has been little attention paid to this interval compared with those below and above, while some of the classical areas for Cambrian research, such as Bohemia, have poor coverage through the Furongian. Moreover, on the basis of information available in databases and the literature, together with the ghost ranges of many higher taxa through the Furongian, suggest that the diversity of this stage has been significantly under estimated. Emphasis, to date, has been placed on the widespread, deeper-water dark shale facies of the interval, with generally low diversity faunas, but shallow-water communities have been neglected.



Speaker

#### Exceptionally preserved Late Ordovician 'starfish beds' from the Tafilalt area, Morocco: Implications for the Great Ordovician Biodiversification Event

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The Upper Ordovician series of the Tafilalt area (eastern Anti-Atlas, Morocco) have yielded several echinoderm *Lagerstätten* (or 'starfish beds'), providing a relatively continuous record of successive, nearshore, cool water, echinoderm-dominated assemblages from the early Sandbian to the Hirnantian. During this time interval, the diversity of the majority of the Tafilalt echinoderm assemblages shows relatively little change, with the persistence of the same dominating groups such as crinoids, coronates, diploporitans, edrioasteroids, eocrinoids, glyptocystitid rhombiferans, solutans and stylophorans. However, these assemblages represent one of the earliest episodes where ophiuroids and asteroids also become a significant, and in some cases dominant, part of the some of the assemblages. This includes some of the earliest preserved examples of dense aggregations of brittle stars, the echinoderm meadows often observed today in deep water/cool water habits. Unlike assemblages of comparable age such as Lady Burn Starfish Beds, Scotland, these examples are likely to be autochthonous. Closer examination of the generic and specific content of the three main asteroids and assemblages reveal that distinct assemblages first dominated by protasterid ophiuroids and asteroids and represent the rapid diversification of the these groups during the Great Ordovician Biodiversification Event.



Speaker

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#### A primitive starfish ancestor from Morocco reveals the origin of crown group Echinodermata

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Somasteroids are widely regarded as ancestors of Asterozoa, the group of echinoderms that includes brittle stars and starfish. The phylogenetic position of somasteroids makes them critical for understanding the early evolution of crown group Echinodermata. However, the origin of asterozoans, the assembly of their distinctive body organization and their relationships with other Cambrian and Ordovician echinoderms remain problematic due to the difficulties of comparing the calcitic endoskeleton of the disparate groups. Here we describe the new somasteroid Cantabrigiaster fezouataensis. A primitive asterozoan from the Fezouata Lagerstätte, Morocco with a unique endoskeletal arm organization that reveals the ancestral morphology of this major clade. Cantabrigiaster differs from all other known asterozoans in the absence of adambulacral ossicles defining the arm margins, evoking parallels with nonasterozoan echinoderms. Developmentally informed bayesian and parsimony based phylogenetic analyses, which reflect the homology of the biserial ambulacral ossicles in Palaeozoic echinoderms indicate that it is the earliest diverging stem-group asterozoan revealing the ancestral morphology of this major clade. Our results clarify the affinities of problematic asterozoans. Somasteroids are resolved as a paraphyletic grade within stem and crown group Asterozoa, whereas stenuroids are paraphyletic within stem-group Ophiuroidea. Cantabrigiaster illuminates the relationship between Ordovician crown group Echinodermata and its Cambrian stem lineage.

Speaker

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# Palaeobiogeographic implications of exceptionally preserved Late Ordovician echinoderm assemblages from the Tafilalt area, Morocco

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In recent years, the Upper Ordovician series of the Tafilalt area (eastern Anti-Atlas, Morocco) have yielded several echinoderm Lagerstätten (or 'starfish beds') providing a relatively continuous record of successive, nearshore, echinoderm-dominated assemblages from the early Sandbian to the Hirnantian. During this time interval, the composition of the Tafilalt echinoderm assemblages shows little change, with the persistence of the same dominating groups: edrioasteroids, eocrinoids, glyptocystitid rhombiferans, ophiuroids, solutans and stylophorans. Asteroids, coronates, crinoids and diploporitans are also present, though generally as minor components of these assemblages. From a palaeobiogeographic point of view, the Tafilalt assemblages share many similarities with Sandbian to early Katian faunas described in other high-latitude (peri)Gondwanan regions of the Mediterranean Province (e.g. Armorican Massif, Bohemia, Spain). During the late Katian time interval, typical 'cool-adapted' Mediterranean echinoderm assemblages are suddenly replaced, in most peri-Gondwanan areas (e.g. Algeria, Aragón, Armorican Massif, Cantabria, Carnic Alps, Corbières, Montagne Noire, Portugal, Sardinia), by more 'temperate' faunas, migrating southward from lower palaeolatitudes, and dominated by coronates, crinoids, and both caryocystitid and hemicosmitid rhombiferans. No such dramatic faunal turnover ('Boda Event') is documented in the Tafilalt area during the late Katian time interval, probably because of its palaeogeographic position at higher palaeolatitudes.



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Speaker

#### New occurrences of the Early Ordovician Fezouata Biota (Morocco): predicted and found

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The Early Ordovician Fezouata Shale, in the Central Anti-Atlas of Morocco, is the only known Ordovician Konservat-lagerstätte yielding abundant and diverse, fully marine assemblages, comparable in preservation to the numerous ones occurring in Cambrian Series 2 and 3. The Fezouata Biota represents a unique mixture of post-Cambrian organisms (e.g. asterozoans, cirripeds, crinoids, eurypterids, graptolites, ostracods), along with soft-bodied to lightly sclerotised taxa, typical of the Cambrian Explosion (e.g. anomalocaridids, demosponges, lobopodians, marrellomorphs, naraoiids, palaeoscolecids). It thus illustrates a key evolutionary transition during the onset of the Great Ordovician Biodiversification Event. In recent years, both the biostratigraphic distribution and the palaeoenvironmental context of the Fezouata Lagerstätte have been clarified. In the Ternata plain (N. of Zagora), exceptional preservation appears to be restricted to two stratigraphic intervals (i.e. within the late Tremadocian A. murrayi Biozone and the middle Floian ?B. jacksoni Biozone), and also to a narrow range of palaeoenvironmental conditions (i.e. distalmost, storm-influenced zone of the lower shoreface). Based on the northward prograding trend evidenced for Lower Ordovician deposits in the Zagora area, investigations for new occurrences of the Fezouata Biota were carried out recently. As expected, new levels with exceptional preservation were found both in slightly older deposits (late Tremadocian) occurring in a palaeogeographically more proximal setting (about 20 km southward), and in younger deposits (late Floian) in a more distal context (about 70 km northward). These preliminary results confirm the close link between exceptional preservation and associated environmental conditions, and the predictive role that the recognition of sedimentary constraints can play for new paleontological discoveries. In the Central Anti-Atlas, the occurrence of diachronous Lagerstätten offers an unique opportunity to describe several successive exceptionally preserved assemblages spanning the late Tremadocian-late Floian time interval.



Speaker

#### Palaeoecology of Floian and Dapingian (Ordovician) chitinozoans in South China

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Chitinozoans are widespread microfossils in the Ordovician to Devonian strata. Although they have been well studied and widely adopted in biostratigraphy, their environmental preferences are rarely discussed. Here we explore biofacies distribution of Floian and Dapingian chitinozoans in six coeval stratigraphic units, based on data from 13 sections in South China. The study is focused on selected biostratigraphic index species: Bursachitina maotaiensis, B. qianbeiensis, Conochitina decipiens and Sagenachitina dapingensis. The assembled data show that B. maotaiensis and B. qianbeiensis occur throughout the distribution area of the Meitan Formation with abundant specimens and well-constrained stratigraphic ranges. The two species can also be observed in the lower Hongshiya Formation and lower Dawan Formation in some sections, but with incomplete ranges and less abundant specimens. It appears that the two species preferred inner shelf environments and could spread to near-shore and shallow outer shelf settings according to the latest sedimentary belt divisions. Conochitina decipiens and Sagenachitina dapingensis occupied wider biotopes in South China. Both of them are recorded in the Meitan and Dawan formations at all localities included. C. decipiens has not been observed in the near-shore Hongshiya Formation or deeper environments as exemplified by the typical Zitai Formation on the Yangtze Platform margin and the Ningkuo Formation in the slope area. S. dapingensis expanded its environmental range even to the Jiangnan slope, but no occurrence has been reported in the Hongshiya and Datangkou sections, which represent the most near-shore settings. The palaeoecological distribution of C. decipiens and S. dapingensis shows that these species were not adapted to near-shore high energy environments. The reported distribution pattern sets the limits where the four species can reliably be used for regional biostratigraphy. For instance, the endemic B. maotaiensis and B. qianbeiensis are good markers for the upper Floian, but their narrow environmental preferences should be taken into account. S. dapingensis proves to be a good marker for the Dapingian in South China, except in the near-shore areas. The globally distributed C. decipiens also has biostratigraphic significance in most areas of the Yangtze Platform. We conclude that well-documented environmental preferences of index species help to provide more reliable and practical biostratigraphic correlations.



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### Exceptionally preserved soft parts in eocrinoid echinoderms from the Fezouata Shale (Lower Ordovician, Morocco)

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The Early Ordovician Fezouata Biota (late Tremadocian—middle Floian, southern Morocco) provides a unique opportunity to document a key evolutionary transition and the onset of the Great Ordovician Biodiversification Event in high palaeolatitude settings. The Fezouata *Lagerstätte* has yielded abundant and diverse fully marine assemblages, comprising both 'classical' shelly taxa and non-biomineralized to lightly sclerotized organisms. Along with arthropods, echinoderms represent one of the two major components of the Fezouata Biota. Eocrinoids are a paraphyletic group of basal blastozoans, known from Cambrian Series 2 to the Late Silurian. They are one of the two most abundant and diverse groups of echinoderms occurring in the Fezouata Shale. Storm-generated accumulations of *Rhopalocystis* spp. are known in the Fezouata Shale since the pioneer works of Jean Chauvel in the second half of the 20th century. Here, we report occurrences of 'Cambrian-like' eocrinoids collected in late Tremadocian deposits corresponding to deeper settings. This new material shows the first definitive evidence of soft- part preservation in brachioles, and thus confirms that the food-gathering exothecal appendages of blastozoan echinoderms contained both a radial canal of the water-vascular system and its lateral extensions (tube feet).



Speaker

# Using climate modeling to reconstruct possible patterns of primary productivity and ocean circulation during the GOBE

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Recent studies suggest that the rapid rise in phytoplankton diversity observed at the Cambrian-Ordovician boundary may have profoundly restructured marine trophic chains, paving the way for the subsequent flourishing of plankton-feeding groups during the GOBE. Unfortunately, the fossil record of plankton is incomplete. Its smaller members represent the bulk of the modern marine biomass, but they are usually not documented in Palaeozoic sediments, preventing any definitive assumption with regard to an eventual correlation between biodiversity and biomass at that time. Here, we use an ocean general circulation model with biogeochemical capabilities to simulate the spatial patterns of marine primary productivity throughout the Ordovician, and we compare the model output with available palaeontological and sedimentological data. Fully understanding the GOBE also requires detailed knowledge about the spatial distribution of the organisms. The full potential of the palaeobiodiversity patterns remains underexplored due to the lack of knowledge about past ocean circulation. The latter conditions the dispersal of organisms, in creating preferential ocean migration pathways or, in contrast, by isolating specific regions and thus establishing major physical barriers. Here we present new maps of Ordovician ocean surface circulation based on numerical climate simulations. In providing clear, synthetic maps of ocean surface circulation in addition to raw model outputs, we aim to facilitate data-model comparison, to assist in interpretation of palaeontological datasets, and to promote renewed discussion about Ordovician biogeography.



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# Repartitioning Sepkoski's original dataset into life cycle modes: Testing the importance of dispersal potential as a driver for Phanerozoic marine biodiversity levels

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Which ecological trajectories underpinned the largest increases in Phanerozoic marine biodiversity, and are these coupled to the evolution of morphological innovations that favoured dispersal? To answer these questions, we present a repartitioning of Jack Sepkoski's original compendium. Instead of focusing on his renowned three evolutionary faunas, we concentrated on the underlying larval development stages, and notably their dispersal potential, through the Phanerozoic.

Our reasoning for this new mode of partitioning is based on two observations: Firstly, Sepkoski's dataset highlights the Middle Ordovician as a fundamentally important diversification interval. Secondly, recent data indicate that a brief interval during the Middle Ordovician marked a drastic change to icehouse conditions. As this may have initiated a Palaeozoic version of the Great Conveyor Belt, a link to the biodiversity rise could therefore be associated with new, more favourable conditions for primary producers. To test this on existing biodiversity datasets an obvious way forward would be to search for marked temporal changes within the plankton, such as those caused by the introduction of larval stages of marine organisms.

Sepkoski's approach, however, does not consider biases in the fossil record. Therefore, we apply an additional test to investigate whether the observed pattern in our life-mode subdivisions can be reproduced using corrections for such biases. Accordingly, our additional analysis is based on a new, highly resolved, biodiversity estimate for the Early Palaeozoic where a Capture-Recapture modelling approach has been applied to assess our larval subdivisions in high temporal resolution, while also accounting for biases in the rock record.

<sup>&</sup>lt;sup>•</sup> Speaker

### How does the skeleton influence soft tissues preservation? A case study from the Early Ordovician Fezouata Lagerstätte

Farid Saleh \*<sup>1</sup>, Bertrand Lefebvre <sup>1</sup>, Bernard Pittet <sup>1</sup>, Martina Nohejlová <sup>1</sup>

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Exceptional preservation consists of the preservation of soft to lightly sclerotised organic tissues (e.g. feathers, guts, skins) in the geological record. The transfer of such tissues from the biosphere to the lithosphere is the result of a succession of multiple, complex biological and geological mechanisms. These processes regroup mainly burial, decay and authigenic mineralization. Taphonomy is not only affected by extrinsic biological and chemo-physical parameters in the water column and the sediments, but also by intrinsic parameters related to the anatomy of the decaying organism (e.g. interactions between tissues). Stylophoran echinoderms, with their multi-plated, modular calcite skeleton, are good candidates to investigate the influence of original constructional heterogeneity on soft tissues preservation. About 300 specimens of stylophorans collected from a single lenticular horizon in the Lower Ordovician Fezouata Shale (Morocco) were analysed. In these echinoderms, the preferential preservation of the oesophagus can be explained by their modular anatomy, and more specifically, by the constructional properties of their proximal aulacophore. This decay-resistant module was made of tightly articulated, imbricate, tetramerous rings creating an isolated sub-microenvironment protecting the oesophagus and thus, delaying its degradation. This constructional feature probably explains why the oesophagus is more frequently preserved in stylophorans than other soft parts (e.g. gut, water-vascular system) in the Fezouata Lagerstätte. Consequently, skeletal heterogeneities should be taken in consideration when studying the tissue/organ selectivity of decay.



Speaker

#### Is the Great Ordovician Biodiversification Event (GOBE) an event?

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The Ordovician radiation has been recognized since the 1960s in Sepkoski's datasets and similar compilations. This radiation was also commonly named Ordovician biodiversification. In the 1990s, event geology and event stratigraphy were highly popular, which resulted in the proposal of a very successful International Geoscience Programme (IGCP n°410) that started in 1997, and that ran under the name 'The Great Ordovician Biodiversification Event.' Subsequently, this term was largely used and abbreviated by many as the 'GOBE.' This acronym is now used in many textbooks and the GOBE today is commonly used together with the 'Cambrian Explosion' to document the early Palaeozoic radiation of marine organisms. Like the Cambrian Explosion, the GOBE did not take place during a short time interval. Both these 'events' are thus not truly events. The GOBE actually includes different successive biodiversity phases in the pelagic and benthic realms, that are recorded for different fossil groups in different places; they are possibly decoupled. The analyses of biodiversity curves indicate that the GOBE can be presented as a sequence of diversifications of the planktonic (late Cambrian - Early Ordovician), level-bottom benthic (Early-Middle Ordovician) and reef communities (Middle-late Ordovician). The boundaries of these 'events' are diachronous (as for the entire GOBE). In addition, the GOBE may also include individual Biotic Immigration Events (BIMEs) that are the records of the large-scale dispersal of taxa from one biogeographic area to another (for example, the 'Richmondian Invasion' or the 'Boda Event'). The GOBE is thus the sum of the diversity trends of all individual fossil groups showing rapid increases, diachronously, during different intervals and across different regions. The GOBE spans the entire Ordovician, but it is not an event, but the sum of many sequential events.



Speaker

## Evidence for homoplasy in hybocrinid crinoid and blastozoan oral regions and its phylogenetic implications

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The earliest hybocrinid crinoids of late Early Ordovician age (two new genera and species based on nine specimens) from Nevada and Utah, western USA, have a typical hybocrinid cup shape and plating, five atomous arms, and a short pentameric stem, but no sutured orals around the mouth and between the ambulacral grooves on the cup peristome. Instead, these specimens have a tiny-plated flexible tegmen surrounding the mouth, anal pyramid, and radiating food grooves to the arms. Elongate plates are carried from the tegmen a short distance up the arms with the ambulacral cover plates and possibly floor plates. This is the same pattern seen in other Early Ordovician crinoids with numerous, poorly organized, cup plates (protocrinoids, early camerates, and early cladids). However, hybocrinids are among the first crinoids to organize the cup plating into two alternating circlets with only 12 tightly sutured plates. Later 5-armed hybocrinids, such as Hoplocrinus of early Middle Ordovician age, have many slightly larger tegmen plates forming a pavement around the mouth and food grooves. Only later in the late Middle Ordovician does the specialized hybocrinid Tripatocrinus with three recumbent ambulacra reduce the oral surface to only a few, small-medium, sutured plates. Normal hybocrinids with five erect arms only develop larger, flat, sutured orals in the early Late Ordovician, and these are the ones typically cited in support of the Universal Element Homology (UEH) model, proposing that larger sutured crinoid orals were derived from blastozoan groups with similar sutured orals. Because the earliest hybocrinids with typical cup plating had a tiny-plated tegmen, the sutured orals between later hybocrinids and co-occurring blastozoans are not homologous, but rather homoplastic. Proposed oral region homology as the key UEH synapomorphy linking crinoids to blastozoans can therefore be rejected.



Speaker

# Coordinated biotic and geochemical change during the Great Ordovician Biodiversification Event: the view from Laurentia

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The Ordovician Period records an extraordinary biodiversity increase known as the Great Ordovician Biodiversification Event (GOBE). A series of environmental changes to the Earth System is coincident with this diversity increase, notably a cooling global ocean, oxygenation, and increased nutrient supply from volcanism and continental weathering. The co-evolution of Earth and its biota during this interval have been studied in various contexts and on multiple paleocontinents. Depending on the lens of investigation, different patterns emerge. Here we summarize the current state of understanding focused on the Laurentian fossil and sedimentary records.

Ordovician deposits crop out extensively within Laurentia. These units have a long history of scientific study, which provides a foundation for modern paleontological and geochemical analyses. Recent paleontological studies, mainly focused on rhynchonelliformean brachiopods, have documented details of diversification, body size increase, development of ecosystem complexity, and intensification of intercontinental dispersal from the Dapingian through Katian stages. Diversification rates increase statistically during the *Histiodella holodentata* conodont Zone (middle Darriwilian Stage), which correlates with similar increases in Baltica and Gondwana.

Coincident with these biotic changes, Laurentian strata record significant change in the physical Earth system. Notably, oceanic temperatures decreased based on oxygen isotopic data measured from conodont apatite. Atmospheric oxygen levels increased to near modern levels coincident with the Middle Ordovician diversification of shelly fauna. Furthermore, a major drop in the strontium isotopic composition of the oceans occurred during the Middle–Late Ordovician, which is consistent with the weathering of juvenile volcanic rocks and delivery of nutrients to marine settings. This multi-proxy record is significant because it records near-simultaneous changes in fossil-rich shallow marine environments during exactly the interval of highest diversification rates.

By integrating biotic and geochemical data sets, a clear picture of the co-evolution of Earth and its biota during the GOBE emerges. Based on Laurentian records, the Darriwilian appears to be the critical interval of the GOBE. Future integration of the paleontological and geochemical records from other paleocontinents may elucidate whether this time interval is equally significant elsewhere as it is in Laurentia.



<sup>&</sup>lt;sup>\*</sup> Speaker

### A strange case of two fishes: enigmatic disappearance of bone tissue or an originally unossified osteostracan

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The Kalana Lagerstätte (Aeronian, Silurian, about 440 myr) in Estonia has revealed a diverse and exceptionally preserved non-calcified algal flora. Many of these algal fossils show spectacular preservation, exhibiting finest anatomical details. Although several fossils of soft-bodied animals have been discovered from Kalana, the majority of faunal fossils, like brachiopods, gastropods, leperditiid arthropods, corals etc., show 'classical' type of preservation with calcium carbonate skeleton only, mostly without preserved soft parts. The locality has also revealed two vertebrate fossils - one osteostracan head shield and a complete telodont. The preservation of these two fossils is contrasting. The osteostracan is preserved as a fine (~2  $\mu$ m thick) carbonaceous film, without any detectable internal structure. The telodont, on the other hand, shows well-preserved calcium phosphate dermal skeleton, with beautifully preserved sculpture and distinguishable multilayered architecture.

Bone is generally regarded as one of the best preservable organic tissues. Fossils, where original apatite has disappeared and/or replaced by carbonaceous matter have been reported in rare cases only. It has been argued that demineralization can occur due to acidic environment in the sediment. In our case, however, the geochemical environment is buffered by carbonate rock matrix and the rock adjacent to the fossil does not show any traces of dissolution. Even further, there are calcitic ostracod carapaces on the carbonaceous head shield. It has also been shown that bacterial mats can be involved in dissolving bony tissues of fish and replacing these with other minerals. Typically, in such case, hydrogen sulphide is locally generated through microbial sulphate reduction, which in the presence of dissolved iron will be precipitated as Fe-sulphide mineral, such as pyrite that replaces the original apatite in bone structures. However, there is no pyrite associated with the observed osteostracan fossil. Finally, there is also a theoretical possibility that the specimen lacked apatitic bony structures originally and the head shield was cartilaginous. In this case, however, it would be the first unossified osteostracan known by far.

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### A Katian microphytoplankton assemblage from Wanhe, Yongshan, east Yunnan Province, South China

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A moderately well preserved Late Ordovician acritarch assemblage was discovered from the Wanhe section, Yongshan, Yunnan Province.

The Wanhe section, located in Yongshan County in the northeast of Yunnan Province, is subdivided into the Pagoda Formation, 'Linhsiang' Formation, Daduhe Formation, Kuanyinchiao bed, Lungmachi Formation and Huanggexi Formation in ascending order, representing sediments from the Upper Ordovician to the lower Silurian. Thirty-eight samples are prepared for palynological analyses from the Wanhe section, and acritarchs were found in the upper part of the 'Linhsiang' Formation to the lowermost part of the upper member of the Daduhe Formation with the presence of chitinozoans representing an interval from the *Dicellograptus complanatus*, *D. complexus*, and *Paraorthograptus pacificus* graptolite biozones.

Eighteen species (assigned to 16 genera), and four acritarch assemblages have been identified from Wanhe section. The Assemblage 1 is represented by the sample AGM35 and AGM41 from the 'Linhsiang' Formation and is consist of *Baltisphaeridium adialstaltum*, *Buedingiisphaeridium balticum*, *Gyalorhethium granulispinuliferum*, *Navifusa ancepsipuncta*, *Oppilatala* sp. and others. The Assemblage 2 is represented by the sample AGM44 from the uppermost 'Linhsiang' Formation and AGM52 from the lowermost Daduhe Formation and is characterized by the occurrence of *Hoegkintia* sp., *Likropalla adiazeta*, and *Ordovicium* sp. The Assemblage 3 is represented by the sample AGM54, and is characterized by the occurrence of *Evittia remota*. The Assemblage 4 is lowest diversity and is represent the samples from the lower member of the Daduhe Formation.

The acritarch assemblages from the Wanhe section differ from other acritarch assemblages described from the Katian in other parts of China, such as western Tarim and northwestern Zhejiang. The absence of *Dactylofusa cabottii* from the Wanhe section may indicate a deeper water environment during Katian.

Although South China is considered to be located near the equator in the Late Ordovician, the diversity of acritarch assemblages is low, and even lower than some acritarch assemblages in high latitudes, such as Libya and the Czech Republic. The acritarch assemblage from Wanhe section is differ from the Gondwana and "peri-Gondwana" assemblages (Delabroye) in the lack of netromorph and other characteristic acritarch forms and differs from the Eastern Laurentian and Baltican assemblages (Delabroye) by low diversity. Acritarch paleogeography in the Late Ordovician is still poorly understood and our study clearly demonstrates that more research is needed to clarify these relationships.



Speaker

#### Late Ordovician Conodonts from the Dashetai area in Inner Mongolia, North China

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Continuous Upper Ordovician strata are well exposed in the Baiyanhuashan section, which is located in the North margin of the Ordos Basin. Twenty-four limestone samples were collected from the Erhagong and Baiyanhua formations for conodonts, among which 19 samples are productive. Conodonts, including 13 species belonging to 9 genera, with a stratigraphic range spanning the late Sandbian to the early Katian are present. The Baiyanhuashan fauna includes both typical endemic taxa restricted to North China and some species widespread in North American Midcontinent. This provides a good foundation for reassessing the correlations of conodont biostratigraphic succession of North China with the international standard zonations. Based on the Baiyanhuashan materials, we reconstructed the multi-element apparatus of the endemic age-diagnostic species Yaoxianognathus neimengguensis, and outlined two conodont biostratigraphic schemes for this critical section. Two endemic biozones, the Tasmanognathus careyi Biozone and the Yaoxianognathus neimengguensis Biozone, and three Midcontinent biozones, the Belodina compressa Biozone, the Phragmodus undatus Biozone and the Belodina confluens Biozone, were recognized. The Tasmanognathus careyi Biozone is broadly correlative with the upper part of the Belodina compressa Biozone, the Yaoxianognathus neimengguensis Biozone is at the levels equivalent to the Phragmodus undatus Biozone. Recognition of the present biostratigraphic schemes further revise the international comparations of the North China-type conodont biostratigraphy, meanwhile it provides a basis for world-wide correlations of the Upper Ordovician shallow-water conodont zonations established in Australia and Tarim.



Speaker

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#### *Saucrorthis* (Brachiopoda) fauna from the Northern Shan States of Myanmar and its significance

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Saucrorthis is an orthide brachiopod genus first recognized from the Shihtzupu Formation (Darriwilian, Middle Ordovician) in Guizhou, SW China, and the Saucrorthis fauna represents a group of brachiopods characterized by the eponymous genus and some other orthides and strophomenides (particularly plectambonitoids), all of which are pretty small in shell sizes, together with some other shelly fossils like trilobites, bryozoans, echinoderms, gastropods, bivalves and ostracods, representing a relatively deeper benthic environment. The trilobites, the second most abundant and diverse fossil group in the Saucrorthis fauna, are characterized by the presence of Neseuretus, a typical regional trilobite indicative of deeper water environment during the Darriwilian, although it could be found in relatively shallow settings in South China during the Early and early Middle Ordovician.

In South China, the second diversity acme of the Ordovician brachiopod radiation was manifested by the flourishing of the *Saucrorthis* fauna almost everywhere on the Upper Yangtze Platform where it could be differentiated into many different communities or associations at different localities with different paleogeographic settings. In northern Iran, *Saucrorthis*, together with the trilobite *Neseuretus* and some other shelly fossils, was documented from the upper Middle Ordovician representing the first diversity acme of brachiopod macroevolution there during the Ordovician.

Saucrorthis and several other brachiopods were first reported from Myanmar by Cocks and Zhan in 1998. The fossils studied by them were collected from the Naunkangyi Group by some pioneer British geologists in Southern and Northern Shan States, but all those fossils are distorted, to some extent. The material we have is all from the Middle Ordovician silty mudstone in Northern Shan States, not far away from Mandaley, mostly well-preserved without any distortion and deformation, and more diverse than formerly recognized. Detailed systematic study on this material sheds light on the brachiopod Ordovician radiation in Myanmar, and the relationship between Myanmar (Sibumasu) and some other paleogeographically related paleoplates like South China and northern Iran.



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### Fossilized appendages and guts in three phacopid trilobites from the Tremadocian lower Fezouata Konservat-lagerstätte (Lower Ordovician, Morocco)

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The Fezouata Shale has yielded remarkably diverse assemblages of non-biomineralizing and biomineralizing organisms of Early Ordovician age. Overall, some 160 genera have been documented, about a quarter of which are essentially soft-bodied. Exceptional preservation in the Fezouata Shale occurs in two main separated intervals, of late Tremadocian and mid-Floian age respectively. These intervals are best regarded as distinct Konservat-lagerstätten, since they contain different faunas and are separated in time by c. 9 Ma. Both assemblages are dominated by arthropods, including a diverse trilobite fauna (c. 25 genera).

Here we report the discovery of fossilized appendages and guts in 31 trilobite specimens from the lower Fezouata Konservat-lagerstätte belonging to the genera *Anacheirurus, Bavarilla*, and *Prionocheilus* (Order Phacopida). The preservation of appendages is generally poor, especially for their proximal parts covered by the dorsal exoskeleton. However, when appendages project from below the dorsal carapace, they exhibit delicate structures, such as annuli boundaries and lateral spines of antennae, or podomere boundaries, clustered endites and terminal claws of endopods. Lamellate exopods are rarely preserved, and when they are, their morphologies are largely obscured by the dorsal carapace. Appendages are typically preserved as thin, yellowish films of iron oxides, interpreted as oxidized pyrite.

Among preserved gut structures, *Anacheirurus* displays a parallel-sided, sediment-filled digestive tract, running under the entire trunk axis while the tract of *Bavarilla* (wide and sediment-filled) is associated with 10 pairs of digestive glands, which are atypically preserved as a sediment infill.

The new examples of fossilized 'soft'-parts of trilobites from the lower Fezouata Lagerstätte

complement previous observations in *Megistaspis* and *Symphysurus*, two taxa also belonging to the pilekiid-bavarillid biofacies typical of lower shoreface settings. Despite notable differences in size and affinities, the preservational styles are essentially the same in all specimens, suggesting that only a limited number of taphonomic pathways is responsible for the preservation of trilobite labile parts in these horizons. In addition to the work on the preserved soft parts, the morphological variability of preserved hard parts is currently also under study; in time, this will result in detailed systematic (re)descriptions of the taxa at hand.

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#### S39 - Timetrees

#### **Oral communications**

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#### Poster

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# The age and ancient biogeography of stoneflies (Insecta: Plecoptera)

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Stoneflies represent a textbook case of disjunctive distribution: as indicated by their names, the two main groups, Antarctoperlaria and Arctoperlaria, are distributed in the southern and northern hemispheres, respectively, with a few exceptions (e.g. the occurrence of Notonemouridae –Arctoperlariain the southern hemisphere, and of Perlidae –Arctoperlaria– in both hemispheres). It has been proposed that these two groups diverged during the Jurassic period, suggesting that late dispersal and/or selective extinction events are the main factors explaining this distribution. In order to test this hypothesis we contributed several descriptions and revisions of Mesozoic species. Among them is the first fossil representative of the Pteronarcyidae, discovered in the Jurassic of China. From the same locality we also identified the first genuine Notonemouridae. We also engaged in a vast revision of the wing venation of Antarctoperlaria, allowing us to critically evaluate the assignment of putative fossils. Based on molecular data we carried out a phylogenetic analysis which we calibrated using our updated palaeontological data. Our preliminary results indicate that the Antarctoperlaria–Arctoperlaria divergence took place much earlier than in the Jurassic, implying that an early vicariance is the most plausible explanation for the current distribution; yet, dispersal and partial extinction had to have taken place at a later stage.



Speaker

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### Exact distribution of divergence times from fossil ages and diversification rates

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Dating evolutionary events, in particular divergences, is a central question in biology. Since inferring the divergence times even for extant taxa relies at some point on fossil or geological calibrations, providing accurate priors for these times from fossil ages is essential to phylogenetic analyses.

Being given a phylogenetic tree of both extant and extinct taxa in which the fossil ages are the only temporal information (namely, in which divergences times are unknown) and the speciation (cladogenesis), extinction and fossilization rates, we present a method to perform the exact computation of the probability distribution of any divergence time of the tree under the Fossilized Birth and Death (FBD) model. This is, to our knowledge, the first method that computes directly and exactly this distribution which, up until now, could only be evaluated through sampling with MCMC approaches.

Our approach also allows to directly sample the divergence times from their distribution under the FBD model. Namely, sampling divergence times no longer requires MCMC methods. All the computations have polynomial complexities with regard to the size of the tree and the number of fossils. In practice, the software implementing our approaches can deal with trees containing several hundreds of taxa on standard computers.



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# The evolution of cockroaches and termites through fossils and phylogeny

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The timing of Blattodea (cockroach and termite) origins has been the cause of much debate, owing to controversies over fossil-calibration selection. By careful evaluation of purported crown- Blattodea fossils we determine that an overwhelming majority (80%) of fossils have been placed into crown groups with insufficient data. Yet we decide on four robust ingroup fossils and a variety of robustly placed outgroup fossils for date-calibration. We apply this dating analysis to a novel transcriptomic tree of 60 species and 500k amino acid sites. Our results tell a compelling story about the evolution of morphology, physiology, biogeography, and behavior in Blattodea.

Speaker

### Probabilistic models of correlated morphological character evolution for phylogenetic inference and divergence time estimation

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Despite the importance of morphology and the fossil record for understanding macroevolutionary patterns and processes and the history of life, statistical models of morphological evolution for use in Bayesian phylogenetic frameworks remain relatively simple and restricted. Here, we present a new discrete Markov model for modelling correlation between morphological characters. Under this Mc (Markov correlated) model, correlated clusters of characters evolve under latent processes from which observed character states are emitted probabilistically. Character clustering is determined using a Dirichlet process mixture model. We use the Mc model, as implemented in MrBayes v.3.3 (pre-release), to infer a phylogeny of mammals using a large binary dataset. We further perform divergence time estimation and compare the results under our model with previous tree topologies and dates in the literature.



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# The fossil and molecular records tell different stories of phylogeny and evolutionary history

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Evolutionary history studies depend on having reliable chronologies of macroevolutionary events such as the birth and rise of new traits and clades. Nevertheless, each macroevolutionary process is comprised of multiple datable components, including gene divergence, trait emergence, clade divergence, first fossil evidence, and variations in abundance, geographic distribution and diversity. These differ in mechanisms, drivers and the methods by which they can be detected and dated. Therefore, it is of paramount importance to clearly define what is dated and how, and what a date reflects. Moreover, palaeontologists and molecular phylogenetisists can see the same phylogenetic tree in considerably different ways, especially if there are cryptic or extinct lineages, which may result in considerably different evolutionary histories and interpretations. Distinguishing among the components of macroevolutionary processes and acknowledging the differences among dates can prevent misinterpretations and reveal the complexity of macroevolutionary processes. I demonstrate these issues through three examples. (1) Hundreds of millions of years that separate the emergence of oxygenic photosynthesis in cyanobacteria and the Great Oxidation Event that marks their success can be explained by the time needed for oxygenic cyanobacteria to segregate anaerobic nitrogen fixation and oxygenic photosynthesis. (2) That angiosperms and gymnosperms diverged genetically 50 million years before angiosperms evolved their key traits makes us take another look at how we understand angiosperm origins and early evolution. (3) Three studies that propose three distinctly different ages of the emergence of silicon accumulation in angiosperms reveal, when put together, a complex evolution of this trait and its possible environmental drivers.



Speaker

# Ranked tree shapes, non-random extinctions and the loss of phylogenetic diversity

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Phylogenetic diversity (PD) is a measure of the evolutionary legacy of a group of species, which can be used to define conservation priorities. It is defined as the sum of branch lengths of the phylogenetic tree of these species. It has been shown that an important loss of species diversity can sometimes lead to a much less important loss of PD, depending on the topology (balance) of the species tree and on the temporal distribution of its branch lengths. However, the loss of PD also strongly depends on the relative depths of the nodes in the tree, and on the order in which species are lost. Here, we propose a unifying framework to study these different effects. We introduce a new, sampling-consistent, three-parameter model generating random trees with covarying: topology, clade relative ages and clade relative extinction risks. This approach leads to a more accurate characterization of phylogenetic trees and allows us to better understand the conditions in which species extinctions lead to higher loss of PD. We propose a procedure to infer the three parameters from empirical ranked phylogenies and apply it to phylogenies of bird families. The parameters inferred predict higher future loss of PD than from random extinctions.



Speaker

### Using time to account for incompleteness when assessing rates of discrete character evolution

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Palaeontologists have used discrete morphological characters to capture whole-organism measures of evolutionary tempo since the 1940s. Such methods have improved markedly in the intervening decades and especially so with the increasingly widespread adoption of quantitative methods and fast computational implementations. However, a major difficulty in calculating rates is correcting for completeness: even if true rates are homogenous, disparities in completeness will appear as heterogeneous.

Accounting for completeness can be complex especially when examining a phylogenetic tree: how complete is a branch or a clade? However, ignoring completeness as many methods do, can potentially lead to misleading conclusions about evolutionary tempo. One proposed solution to this problem is to decompose a phylogenetic tree into character subtrees where only branches leading to observed values are retained. Such subtrees can then be aggregated so that the branch durations are able to perform two functions: accounting for available time and character completeness simultaneously.

Here I show an early implementation of this method and compare it to other recent approaches. I do so using the classic case study of lungfish which have long been recognized as undergoing high rates early in their history (the Devonian) with subsequent change being much slower. Furthermore, a coincident shift towards lower ossification results in relatively poorer (less complete) post-Devonian taxa, potentially explaining away the high early rate pattern. Here I use a 86-taxon, 91-character matrix to show clear shifts in apparent evolutionary tempo across the last 440 million years. Simple parsimony methods without completeness corrections conform to the classic high early rates pattern, but with additional high rate excursions at 330, 260, and 100 Ma. These latter peaks precede the appearance of better known fossil taxa or crown lungfish. Shifts to more sophisticated likelihood methods and an crude attempt to account for completeness diminish or diffuse these latter peaks whilst retaining the high early rates pattern. By contrast the subtree aggregation approach returns a time series with a proportionally larger confidence interval. This both suggests we should be less certain about such rate time series and allows that all of the latter peaks can be explained away as error. However, the high early rates pattern remains, confirming that phenotypic evolution was highest early in lungfish history.



Speaker

### Molecular clocks on Chelicerata suggest an early colonization of land by arachnids and support the monophyly of mites

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Animal life has marine origins, with only few phyla completing their entire life cycle outside water. The process through which organisms adapt to life on land is known as terrestrialisation, and it is one of the most extreme cases of adaptation to a new habitat that happened in animal history. The chelicerates (pycnogonids, horseshoe crabs, spiders, scorpions) are an ancient group of arthropods, with an astonishing fossil record dating back to Cambrian, and includes the second largest clade of fully terrestrial organisms, the arachnids. Morphological phylogenies support a single land colonization event by placing marine horseshoe crabs as sister group of arachnids, but phylogenomic studies nest this aquatic lineage within Arachnida (implying multiple terrestrialisation events). To identify how many times and when arachnids adapted to life on land we need to assess chelicerate phylogeny, and its evolutionary timescale.

Here, we present a timescale for Chelicerata designed to test how many times and when arachnids adapted to life on land. We used an expanded multigene dataset covering most chelicerate diversity and the largest set of fossil calibrations to date. Our results recover monophyly of Chelicerata, Euchelicerata and Arachnida, suggesting a single terrestrialization event. Furthermore, we found Acari as monophyletic (Parasitiformes+Acariformes) and recover Tetrapulmonata (Araneae+Pedipalpi) in alliance to Scorpiones (Arachnopulmonata) or allied to a clade composed by Scorpiones+Pseudoscorpiones. Our results reconcile previous results based on morphology and molecular evidence, suggesting a Cambrian colonization of land by arachnids, substantially predating trace or body fossil evidence.



<sup>&</sup>lt;sup>'</sup> Speaker

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# Current issues in divergence-time estimation with genomes and fossils

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Much progress has been made to improve the precision and accuracy of divergence-time estimates based on molecular data and fossil information. This progress is primarily driven by the development of new Bayesian phylogenetic methods for the integration of both types of data, and by the rapidly increasing amount of available molecular data thanks to genome sequencing. However, current approaches still rely on many assumptions that may rarely be met by empirical data sets and the impact of these model violations is often difficult to assess. For example, some approaches assume that the assignment of fossils to clades is known with certainty while other methods rely on the inclusion of all, or a random subset, of the fossils known for a clade in the analysis. With genomic data it is often assumed that all parts of the genome share the same evolutionary history; however, due to coalescent processes and horizontal gene flow, gene trees often differ from each other and are discordant with the species tree. While methods have been developed to account for gene-tree discordance due to coalescence, these methods still assume that all parts of a gene share the same history, which may be extremely unlikely in fast radiations. Thus, despite progress, recently published timetrees may still be affected by strong biases owing to these model violations.



Speaker

### The effect of sub-sampling fossil occurrence data on the accuracy of age estimates obtained from the Fossilised Birth-Death process (FBD)

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The FBD tree prior presents a model that allows for the calculation of the probability of observing a given tree containing fossil sampling events observed through time. This approach to the calculation of the probability of a tree allows for this process to be applied as a tree prior in Bayesian analyses, and to also be used for the estimation of divergence times using the ages of fossil occurrences and extant molecular data only. As this method requires only the ages of fossil taxa it is straightforward to obtain large quantities of applicable data through fossil occurrence repositories such as the Paleobiology Database (PBDB) or Geobiodiversity Database (GBDB). The FBD method has been applied in a number of published studies in which age estimates are obtained for relatively shallow divergences. In such cases it seems tractable to include all known fossil samples for the clades of interest. As the FBD process is applied to temporally deeper divergences this quickly becomes intractable as the number of known fossil samples will rapidly grow. In such cases it seems logical to simply sub-sample the available data to produce a reduced, tractable dataset. Unfortunately, the consequences of different approaches to subsampling the occurrence data are unknown, and as the distribution of fossil taxa through time is an important element of the FBD process this requires investigation.

Models of fossil occurrence through time have been derived from empirical data and can be used to generate a simulated fossil record on a given tree. Similarly, models of molecular substitution can be used to produce extant data. Through a simulation framework utilising these models, we determine the effect of different approaches to sub-sampling fossil occurrence data on the accuracy of divergence time estimates obtained with the FBD process.



Speaker

### Resolving phylogenetic and temporal conflict among anatomical regions reveals an end-Triassic origin of mammals

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The taxonomic constituency and temporal origin of crown mammals has been obscured by uncertainty over the affinities of monotremes. On an otherwise stable phylogeny of more plesiomorphic mammals we show extreme incongruence between cranial, mandibulodental, and post-cranial characters for the placement on monotremes. By considering prior hypotheses, homoplasy covariation, and evolutionary rates we identify potential sources of correlated phylogenetic error. Excluding these character complexes lends strong support and congruence between anatomical regions, for monotremes being sister to a clade that includes "eutriconodonts", multituberculates, spalacotheriids, and cladotheres (including Theria). Combining the morphological and molecular data to merge fossils into the modern mammal tree, and calibrating from both nodes and tips improves precision and places crown mammal origination during a rapid radiation close to the Triassic-Jurassic boundary. Thus, both the end Triassic and end Cretaceous mass extinction events are suggested as major diversification triggers for mammals. In addition, aspects of monotreme upper-appendicular anatomy that has been considered especially primitive may be better understood as highly derived, in association with their ecological habits, particularly their semi-aquatic ancestry.



Speaker

### Assessing the impact of stratigraphic age uncertainty on molecular estimates of divergence times

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Phylogenetic studies increasingly make use of the fossil record, in addition to extant samples, to improve estimates of divergence times. A critical issue with using fossil samples is that specimen age can rarely be determined exactly. Typically, a minimum and maximum age range are known for any given fossil. A common strategy for dealing with this uncertainty is to fix fossil ages to the median age of the interval, but the errors introduced using this method are difficult to quantify. Alternatively, hierarchical phylogenetic models, including the fossilized birth-death (FBD) process, allow the user to include the full range of possible sampling dates for each fossil using Bayesian inference. This enables fossil ages to be sampled along with all other parameters. This approach makes use of all the information available but is also more expensive computationally. In this study, we perform phylogenetic inference using the FBD model on simulated datasets with phylogenetic and stratigraphic features comparable to Cenozoic mammals. We compare the two approaches for handling fossil ages and assess their impact on estimates of the divergence times and the parameters of the FBD process, i.e. diversification rate, turnover and sampling proportion. Our results demonstrate that using median ages can lead to erroneous estimates of all model parameters, including divergence times. However, the true parameter values can still be recovered if fossil sampling times are treated as unknown and co-estimated along with other model parameters. This study highlights the critical importance of explicitly incorporating stratigraphic age uncertainty as prior information in Bayesian phylogenetic inference.



Speaker

#### The importance of fossils in dating the Tree of Life: from the arthropod radiation to gut bacteria

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The seemingly simultaneous appearance of animal crown group fossils in the early Cambrian, while reliable Neoproterozoic fossils remain limited, is known as Darwin's Dilemma. Recent work has combined geological age data with molecular sequences from living species to establish a timescale for the Tree of Life, with increasing evidence for bilaterian divergence in the Cryogenian and/or Ediacaran periods. Morphological datasets for over 200 arthropod fossils, employing tip and node dating (thus stronger phylogenetic evidence), suggest their divergence occurred in the late Ediacaran as well. Meanwhile, microbiota associated with animals play a pivotal role in their development (e.g. nutrient processing, immune system activation), but bacteria lack a fossil record entirely. Here I show that bacterial clades significant to the animal gut microbiota have estimated divergence times during the Cryogenian-Ediacaran, coincident with the inferred evolution of bilaterian gut morphology. New strategies are introduced to constrain bacterial divergences, including the horizontal transfer of genes into fossiliferous clades, and the cospeciation of bacterial symbionts with their fossiliferous animal hosts. 18 calibrations are derived from fossils which meet phylogenetic and straigraphic criteria comparable to the level of scrutiny in high-quality divergence time analyses of animals. Prior calibrations do not circularly invoke the Neoproterozoic, implying this result is genuine. I suggest that bacterial diversification was sparked by the opening of new niches in the form of bilaterian tissue differentiation. Directly or indirectly, the fossil record remains indispensable to date any branches of the tree.



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Speaker

### Divergences of early terrestrial arthropods based on combined fossil and molecular data

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Arthropods are most species-rich both geologically and in the extant animal world; they are also extremely morphologically disparate and ecologically wide-ranging, making them key players in the evolutionary history, at least during the Phanerozoic Eon. Early divergences of arthropod groups in the geological history, most likely in parallel with the colonization of vascular plants on land, are critical to the understanding of the origin of the terrestrial biosphere. Under the current phylogenetic framework, we analyzed fossil and genomic data of microcrustaceans (branchiopods), major myriapod groups (centipedes and millipedes) and some hexapods, resulting in a phylochronological sequence of early divergences in freshwater branchiopods, landdweling myriapods and some events in lepidopterans. Our studies result in the following early divergence dates in terrestrial arthropods:

1) The stem group of Branchiopoda is probably rooted in the latest Neoproterozoic Era, and the crown group branchiopods diverged during middle Cambrian to Early Ordovician, suggesting that a freshwater biota started at least that early;

2) Earliest divergence of crown group Diplopoda (Myriapoda) is estimated to range from late Cambrian to earliest Ordovician; i.e., the early land-dwelling arthropods evolved about same time or slightly later that the freshwater arthropods as mentioned above;

3) Crown groups of Chilopoda (Myriapods) first diverged during the Late Ordovician, indicating that carnivorous feeding habits evolved in land-welling myriapods in a later stage after their land colonization.



<sup>&</sup>lt;sup>\*</sup> Speaker

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#### Gene origins that predate the last universal common ancestor

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The last universal common ancestor (LUCA) is a much-discussed organism, both in terms of its physiology and metabolism, as well as where and when it existed. A candidate set of genes has been identified which are shared by all life and thus would have been present in LUCA, forming some of its fundamental building blocks. These genes have undergone several gene duplication events, which can be used in conjunction with molecular clocks, to date the timing of both the gene duplication events and the speciation events within the gene tree. Here we present the results of analyses on 8 key genes that would have been present in LUCA, including signal recognition proteins and ATPases, along with 11 robust fossil calibrations. These calibrations can be placed on speciation events which fall on either side of duplications. In each case this produces a timescale for the gene tree showing when, prior to their amalgamation in LUCA, the genes originally evolved. Preliminary results suggest that the gene families evolved in the Hadean eon, close to the origin of the Earth, with LUCA existing not long after. This was a time when the planet was newly formed and would have been a hostile environment for the organisms to have coped in. Though we cannot identify what other genes LUCA may have possessed, this timeline gives us an indication of the relative timing of acquisition of some of life's key genes.

39 // Poster



Speaker

### S40 - Vertebrate palaeophysiology

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Robert Brocklehurst // Breathing life into dinosaurs: XROMM ventilation kinematics of extant archosaurs and reconstructing rib motion in fossils
François Clarac <i>et al.</i> // The physiological roles of the dermal skeleton in the pseudosuchian transition to the amphibious ectothermic lifestyle: heat transfers when basking and acid-base balance during apnea
Alfred Crompton <i>et al.</i> <b>//</b> Speculations on the origin of the mammalian fauces: therians and monotremes compared
Jorge Cubo and Nour-Eddine Jalil // Bone histology of <i>Azendohsaurus laaroussii</i> . Implications for the evolution of metabolic rates in Archosauromorpha
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### Non-mammaliaform cynodont osteohistology and implications for the evolution of mammalian growth patterns

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Non-mammaliaform cynodonts appeared during the Late Permian about 256 million years ago and radiated into a diverse array of body sizes and ecological niches before evolving into the first mammals some 37 million years later during the Late Triassic. The acquisition of an increasingly mammalian skeletal morphology during the Triassic indicates that many features required to facilitate homeothermic endothermy were in place prior to the appearance of crown group mammals. The bone tissues of nonmammaliaform cynodonts reflect the diversity of this clade, but do they follow the acquisition of mammalian characteristics and show increasingly mammalian growth patterns during their evolution? During the Early Triassic, non-mammaliaform cynodonts were relatively small and growth attenuated within one to two years. Two major lineages diverged at this time, the Cynognathia and Probainognathia. The Middle Triassic Cynognathia evolved into large-bodied taxa that exhibit high growth rates and multiyear growth to somatic and presumably reproductive maturity, similar to large extant mammals. The Probainognathia includes the smaller bodied prozostrodontians, which themselves evolved into the tiny mammaliaforms during the Late Triassic. The Prozostrodontia also exhibit high growth rates, despite progressively smaller body sizes. They exhibit increasingly mammalian characteristics such as more efficient locomotory and masticatory structures allowing for increased activity levels and energy assimilation, maxillary vibrissae indicating improved sensory capabilities and improved thermoregulatory and reproductive controls (implied from the loss of a pineal foramen). However, despite being similar in size to small extant placental mammals that typically reach reproductive maturity within one year, early prozostrodontians still took more than one year to reach growth attenuation, even the Brasilodontidae, the sister group to Mammaliaformes. Thus, although the small Early Triassic non-mammaliaform cynodonts matured within one or two years, this strategy was abandoned when the lineage diverged into larger body sizes and appears to have taken a relatively long time to be regained. It is likely that future investigations will reveal a diverse array of life history patterns amongst the Mesozoic mammals and despite their rodentlike body plans, the extremely rapid growth attenuation typical of small placental mammals may not necessarily reflect the plesiomorphic state of this clade.



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### Breathing life into dinosaurs: XROMM ventilation kinematics of extant archosaurs and reconstructing rib motion in fossils

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Both modern birds and crocodilians have derived respiratory systems with divergent morphologies. This is coupled with divergent modifications to the ribcage, and differences in the mechanics of ventilation between these two groups. However, understanding the coordinated evolution of ribcage morphology and ventilation mechanics in living archosaurs has been hindered by a lack of integration between kinematic and anatomical data, which in turn creates difficulties in reconstructing motion in fossils. Here, we employ a joint-based approach to represent both bone morphology and motion. In vivo rib kinematics were recorded during ventilation in living crocodilians and birds using XROMM (X-ray reconstruction of moving morphology), with motion measured relative to the articular surfaces of the costovertebral joint; axes of rib translation and rotation were defined with respect to specific homologous landmarks on the ribs and vertebrae. This approach then served as the basis for "scientific motion transfer", applying motion patterns observed in modern archosaurs to their fossil relatives- specifically, non-avian dinosaurs- in a framework grounded in the anatomy of the costovertebral joint. This new approach provides a testable and repeatable way of predicting ventilation kinematics in extinct taxa. The XROMM results show that bony morphology is a better predictor of rib motion in birds than in crocodilians, although greater consideration should still be given to the soft-tissue anatomy of the costovertebral joint. Morphometric analysis of archosaur vertebral morphology, as well as soft-tissue correlates suggest that dinosaurs had costovertebral joints most similar to modern birds, and may have employed bird-like rib kinematics.



Speaker

### The physiological roles of the dermal skeleton in the pseudosuchian transition to the amphibious ectothermic lifestyle: heat transfers when basking and acid-base balance during apnea

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The pseudosuchians (the crown and stem-crocodylians) and the avemetarsalians (pterosaurs and dinosaurs) consist of two distinct sister lineages which evolved from one common ancestor 250 million years ago. This hypothetical ancestral archosaur is assessed to be both terrestrial and endothermic (" warm-blooded ") according to the study of the stem-archosauriforms' anatomy and to the estimation of their metabolic rate which is based on the analysis of their long bone histology. These latest assessments lead to argue that the crocodylians secondarily became both ectothermic and amphibious. Such a lifestyle transition in the Early Jurassic crocodylomorphs must have required the development of two main adaptative physiological functions: heat transfers when basking and apnea skills during diving (blood acidosis buffering in anaerobia). In this regard, it has been assessed that the development of the crocodylomorph dermal shield (osteoderms) in the Early Jurassic may be involved in both of these physiological processes. Indeed, these adaptative functions rely on one common anatomical support: an integumentary blood vessel proliferation within and straight above the osteoderm shield. As hypothesized by previous authors, this yet presumed vascular network may firstly convey the external heat to the general blood circulation when basking. Secondly, during prolonged apnea, the blood lactic acid is known be driven to the osteoderms in order to complex with the stored calcium thus resulting in buffering the blood acidosis which is due to the lactate accumulation in the plasma. Herein, we provide the quantification of this vascular network using histological sections on fresh crocodylian osteoderms. We analyzed the data with phylogenetic comparative methods evidencing that the crocodylian osteoderms house vascular clusters within a surrounding skin which is globally free from vascularization. Thus, we bring an anatomical evidence to the previous hypotheses and provide the essence of a new model to study the extinct vertebrate amphibious transitions.

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Speaker

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#### Speculations on the origin of the mammalian fauces: therians and monotremes compared

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In therian mammals, several muscles control the transport of food through the fauces: the tensor veli palatini tenses the soft palate between the pterygoid hamuli; intrinsic tongue muscles change the tongue's shape; and the palatoglossus acts together with extrinsic tongue muscles and the mylohyoid to draw the tongue against the soft palate and form a tight seal between the oral cavity and oropharynx. To determine the evolution of the fauces region of mammals, we studied serial sections of a pouch young marsupial, CT scans of non-mammalian cynodonts, ictidosaurs, mammaliaforms, and extant therians and monotremes. The heterodont dentition (incisors, canines and postcanines) of Permian therapsids suggests some processing of food occurred in the postcanine region, which would have required a way to prevent food from passing prematurely into their wide-open pharynx. Non-mammalian cynodonts may have achieved this by pushing the tongue against the pterygopalatine bosses of the pterygoids, but that would not have provided the tight seal achieved by therian mammals. Ictidosaurs and mammaliaforms of the Late Triassic were the first to attain such a tight seal in this region. The medial portion of the reptilian posterior pterygoideus muscle shifted its origin from the posterior surface of the transverse process of the pterygoid to a soft palate between the pterygopalatine bosses and formed the tensor veli palatini. We conclude that the pterygopalatine boss-not the ectopterygoid and not the lateral portion of the transverse process of the pterygoid-was the homologue of the mammalian pterygoid hamulus, and suggest that the palatoglossus arose at the same time as the tensor veli palatini. The lateral portion of the posterior pterygoideus in mammalian ancestors originated on the posterolateral border of the transverse process. When this process was lost in the transition to mammals, the origin of the muscle shifted to the pterygoid hamulus and palatine to form the mammalian medial pterygoid muscle. Monotremes extensively modified the fauces region: the palatine extends backward under the pterygoid portion of the pterygoid hamulus, and the hamulus portion retains its contact with the soft palate behind the palatines. The tensor veli palatini and palatoglossus are lost, but an enlarged mylohyoid helps the tongue break down invertebrates between the keratinized surfaces on the ventral surface of the palatine and dorsal surface of the tongue.



<sup>&</sup>lt;sup>\*</sup> Speaker

### Bone histology of *Azendohsaurus laaroussii*. Implications for the evolution of metabolic rates in Archosauromorpha

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Azendohsaurus laaroussii is an archosauromorph from the Upper Triassic (Carnian) of Morocco (Argana Basin). According to the recent phylogenetic analysis (Nesbitt et al. 2015), Azendohsaurus is the sister group of Trilophosaurus, forming the clade Allokotosauria which is the sister group of the clade Prolacerta – Archosauriformes. The histological analysis of Azendohsaurus laaroussii reveals many interesting features. The humerus is characterized by a well developed fibro-lamellar complex in the anterior, posterior, dorsal and ventral sides. The femur also shows a well developed fibro-lamellar complex in the anterior side whereas the dorsal, ventral and posterior sides show a "sandwich" structure with two layers (external and internal) made of poorly vascularized parallel-fibered bone containing mainly longitudinal vascular canals, and an intermediary layer formed by a fibrolamellar complex. The anterior, lateral and posterior sides of the tibia show a bone tissue formed by parallel fibered bone containing abundant longitudinal vascular canals included in small primary osteons, whereas the medial side is formed by an avascular parallel fibered bone tissue. Summarizing, the stylopodial bones (humerus and femur) contain abundant, well developed fibrolamelar complex formed at high to very high growth rates, whereas the only zeugopodial bone analyzed in this study (the tibia) shows a bone tissue formed at lower rates (as suggested by the presence of a matrix formed by parallel fibered bone including small longitudinal primary osteons). An optimization onto a phylogeny of the histological data of Azendohsaurus laaroussii (this study) and related taxa (data from recent literature) reveals that the primitive condition for Archosauromorpha involves the presence of a fibrolamellar complex. This condition may have been retained by the basal archosauromorphs Aenigmastropheus, Hyperodapedon, Teyumbaita, Azendohsaurus and Prolacerta, the non-archosaurian Archosauriformes Proterosuchus, Erythrosuchus, Chanaresuchus, Euparkeria and Rutiodon and by Ornithodira and basal Pseudosuchia. The basal archosauromorphs Stenaulorhynchus, Trilophosaurus and Vancleavea show reversions to the primitive condition of diapsids, involving a matrix composed of parallel fibered bone. These results suggest that high growth rates and elevated resting metabolic rates may have been acquired at the node Archosauromorpha instead of at the node Archosauriformes (as suggested previously).



Speaker

# The evolution of acellular bone in teleosts: a new structure-function relationship in fish bone histology?

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The skeleton of most teleost fishes shows a peculiar type of acellular bone, in which the main bone cells (osteocytes) are missing entirely. In the literature, acellular bone is thought to be a character of the diverse clade Neoteleostei. However, it is also found in other non-neoteleosts, such as pikes (Esocidae), while some neoteleosts such as tunas (Scombridae) have cellular bone. The evolutionary history of the character is therefore complex. We address two main questions:

1) What is the phylogenetic distribution of acellular bone in fossil and living teleosts?

2) Is there a functional explanation to this distribution?

We use a dataset of more than 500 fossil and extant taxa, mapped on a time-calibrated tree built from recent molecular topologies to reconstruct the history of acellular bone in teleosts. Cellular bone is primitively present in teleosts, and acellular bone evolved several times independently, with a main occurrence in Euteleostei (including Neoteleostei). As previously suggested, tunas acquired cellular bone secondarily. This has been hypothesised to be related to their endothermic metabolism, using modified muscles and special counter-current blood vessels to warm the brain cavity and most of the body. In order to test whether there is a link between this systemic endothermy and secondary cellularity in euteleosts, we studied bone histology in the opah (*Lampris guttatus*), another systemic endotherm. It also shows secondary cellularity, with features strikingly similar to those of tuna bone. In contrast, the close ectothermic relatives of *L. guttatus* possess acellular bone. These observations reinforce the hypothesis that systemic endothermy can be detected in neoteleosts by secondary reacquisition of osteocytes, suggesting a new structure-function relationship in teleost bone. Using bone histology as a correlate of metabolism and growth has the potential to help unravelling the physiology of extinct ray-finned fishes, a field that has been barely explored so far.

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<sup>\*</sup> Speaker

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### Introduction to the Symposium Paleophysiology : from a semantic paradox to a proper field of research

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Thirty eight years ago, I introduced our subject at the First International Symposium on Mesozoic continental ecosystems under the title "Paleophysiology: a mere intellectual game or a proper field of research?" The change in the titles over the decades emphasizes the progress of the field and its growing recognition as a legitimate domain of scientific endeavor, as illustrated by this Symposium.

It would be difficult to find two scientific disciplines more apart from one another than Paleontology and Physiology, not to speak of the doubtful "pecking order" that separate them on the axis of scientific respectability!

Paleontology is typically a descriptive-morphological science, rooted in the Deep Time of Geology and involved towards systematic and phylogenetic issues. A science of observation of empirical data directly taken from nature, its "demonstrations" use comparative methods based on cumulative evidences.

Physiology is typically the science of functions, not structures, it explores systems in action within the body on a short time scale. By essence an interventionistic science to get its data, its demonstrations use experimental evidences.

Starting from this situation, one may wonder what those two sciences may share and how some meaningful "hybridization" between the two could be reached. The answer is obvious : it is the same curiosity about how organisms "work" as "living machines" that is extended from the extant to the fossil realm.

This trend is not new. Cuvier (1769 -1832), the "father" of scientific vertebrate paleontology, already viewed the aim of this science as a reconstruction of fossils as living animals and had a much more functional view of comparative anatomy than a purely structural one. He states that "Living bodies are like experiments prepared at once by nature, as we would like to do in our labotatories, that show us the results of its additions or of its retrenchments". Although Cuvier's "experiments of nature" are merely comparative data with little more than a purely analogical value to the actual experimental approaches of physiology, he perhaps showed us the way to go towards a meaningful paleophysiology. Accordingly one will review 1/ the specific aims of paleophysiology and to what extent they are distinct both from physiology and from a more general paleobiology 2/ the methods that can be used for paleophysiological inference and 3/ the results and the general problems of testing they imply.



Speaker

### Applications of CPL microscopy to characterize diverse bone tissue textures in basal Amniota

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Correct characterization of bone tissue texture is important for interpreting skeletal growth in extinct tetrapods because tissue texture variations can reflect important life history milestones (somatic or reproductive maturity). These variations are widely accepted to be different in endothermic mammals and birds compared to ectotherms, as the latter tend to lack woven- fibered bone (WFB) in limb bone cortices and have abundant cyclically-deposited parallel-fibered (PFB) or lamellar bone with poor vascularity. I surveyed limb bone cortices of Permian synapsids, a group that includes the extinct forebears of mammals, and contemporaneous outgroups (basal eureptile Captorhinus, Diadectes, and a microsaur). Linear, elliptical, and circularly- polarized light (CPL) microscopic images were also compared among extant tetrapods of known thermophysiology. Both cross sections and longitudinal sections from extant ectotherms were studied with varied light settings. In basal amniotes, predictable patterns were observed that do not require special explanations of thermophysiology: (1) Nonlamellar tissues in juveniles and perinates, including WFB, are not limited to endotherms, with WFB showing a mixture of interference colors when viewed with CPL and occurring nearer to the perimedullary region where growth was most active; (2) Within groups, smaller-bodied species generally have a more abrupt transition to predominantly PFB and lamellar tissues, introducing a size/age bias that can confound phylogenetic optimizations of WFB distribution among early amniotes. Consequently, while important for reconstructing key life history events and aspects of bone physiology, tissue texture remains ambiguous with respect to thermometabolism in the absence of more desirable histometric and histochemical data.



Speaker

# Acid-base regulation in early tetrapods: a possible function of sculptured dermal bone

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PermoCarboniferous basal tetrapods are well known for their covering of sculptured dermal bone. The function of this dermal "armour", unlike anything seen in extant vertebrates, is obscure; simple protection from predation seems insufficient to account for its complexity. A recent hypothesis proposed that this bone was involved regulating acid-base balance. The issue of obtaining oxygen is commonly considered in the vertebrate water to land transition, but less appreciated is the need to eliminate carbon dioxide, and to avoid severe respiratory acidosis caused by hypercapnia (excess metabolic blood carbon dioxide).

Recent physiological studies of turtles and alligators show that calcium and magnesium carbonates in dermal bone can be mobilized to buffer of acidosis. Unlike extant reptiles, which encounter hypercapnia when submered in water, early tetrapods may have been subject to hypercapnia while on land less efficient mode of lung ventilation (likely buccal pumping in seen in extant amphibians) would impede carbon dioxide loss. Many of them retained gills, so carbon dioxide loss underwater would not have been problematic. Extant amphibians rely on cutaneous carbon dioxide elimination on land, but early tetrapods were considerably larger than amphibians today (so would have had proportionally less surface area for gas exchange), and would have been unlikey to have had the amphibians' thin, vascularized skin.

A prediction of the hypothesis that early tetrapods used their dermal bone to counteract acidosis on land would be in the distribution this feature: taxa that were more terrestrial (as judged by unrelated aspects of their skeletal anatomy) would have a greater extent of sculptured dermal bone. Observations confirm the prediction: sculptured dermal bone is seen mainly in terrestrial forms, with the exception of some specialized flattened aquatic forms that were presumed deep water dwellers, which may have been subjected to hypercapnia in these aquatic environments (as are fish today). Sculptured dermal bone is lost in the lineages leading to the tetrapod crown groups. In stem amphibians its loss is associated with small body size, where cutaneous loss of carbon dioxide would now be feasible. In stem amniotes it is associated with evidence of using the ribs for lung ventilation.



Speaker

#### The heart of osteostracans

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Osteostracans are a clade of armored Silurian-Devonian of jawless vertebrates that are currently considered as the sister group of jawed vertebrates, or gnathostomes. Their internal anatomy has been extensively studied in the last century using the highly destructive ground sectioning technique, notably providing evidence for a complex cavity, the 'intramural cavity' within the postbranchial wall that separates the oropharyngeal chamber from the abdominal cavity and was first interpreted as housing the pronephros, and then the heart. Here we provide the first synchrotron radiation X ray microtomographybased, 3D description of this cavity in a well-preserved specimen of the osteostracans Norselaspis glacialis from the Lower Devonian of Spitsbergen. It confirms the presence of two chambers separated by an asymmetrical septum that had led to the interpretation of the heart as being composed of a ventricle and an atrium placed side-by-side, as in lampreys. However, the new data show that the intramural cavity was closed dorsally, thereby preventing the passage of the venous blood from the sinus venosus to the atrium. It is suggested that the venous blood reached the atrium via paired vessels that passed anteroventrally through large groves lateral to the anterior opening of the intramural cavity towards the oro-pharyngeal chamber. These vessels may be either ventral jugular veins or homologues of the anterior cardinal veins. The dorsal closure of the intramural cavity was also a serious problem for the drainage of the paired capitis lateralis veins, which may have instead emptied posteriorly into the marginal vein sinus, whose role parallels that of the anterior cardinal vein of gnathostomes. Yet the position of the ductus Cuvieri remains unclear. The intramural cavity suggests that the atrium of the heart of osteostracans was not dorsal to the ventricle and ventral arterial trunk as in gnathostomes, but rather lateral to it, as in cyclostomes, thereby representing the probably plesiomorphic stem gnathostome condition.



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### Phylogenetic comparative methods and paleobiological inference of physiological traits

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Phylogenetic comparative methods (PCM), i.e. methods designed to take into account the influence of phylogenetic relationships between species in statistical analyses of quantitative datasets, have grown to become an essential part of evolutionary biology in the last decade. These methods, along with the improvement of associated software and outreach to new research communities, have allowed for a significant increase in the use of comparative statistics on paleontological datasets. The use of fossils has thus been rightfully advocated in many studies, to e.g. discuss the evolution of biomechanical constraints, improve ancestral state reconstructions (ASR), or describe the evolution of ecological communities in a paleoenvironmental context.

In recent years, the development of PCM has also given rise to new arguments in the classic debate of ancestral heat production strategies in vertebrates. The inferred endothermy of several groups of archosaurs or synapsids, originally discussed qualitatively during the last forty years, has been the subject of new discussions and estimations. Many specific procedures have been developed to estimate the thermometabolism of ancient vertebrates, and the various evolutionary constraints that may have given rise to the array of different physiological strategies in those groups. This profusion of dedicated methods and large-scale datasets has also generated many methodological discussions and contradictory results, and the ancestral condition for metabolic rate in amniotes remains highly controversial in the paleontological community.

In this presentation, several recent studies on the use of PCM in vertebrate paleophysiology are compared and discussed, both in the context of their respective methodologies and how their original hypotheses were discussed or challenged by the use of such procedures. The need for precise guidelines on the specific use of each procedure (e.g. phylogenetic generalized least squares, phylogenetic eigenvector maps, ASR) is also discussed in the context of a widespread use of PCM in paleontology. This approach highlights the difficulties of deciphering the respective influence of phylogenetic, structural, and environmental signals in physiological quantitative characters. Integrative approaches are likely to provide more information on this matter in the near future, by comparing the outcome of different procedures to the original definitions of such characters in a phylogenetic context.



Speaker

### Paleobiology of an extinct synapsid, the dicynodont *Moghreberia nmachouensis* (Therapsida: Anomodontia): new data on the origin and evolution of endothermy in Synapsids

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The maintenance of a high constant internal body temperature, linked to a high resting metabolic rate (i.e., endothermy), provided clear benefits in vertebrate evolution. This particular metabolism evolved at least twice in tetrapods (in synapsids and diapsids). The evolution of endothermy in diapsids was temporarily well-constrained with an acquisition in the archosauriform. But, in synapsids, indirect morphological evidence (e.g., insulative pelage, respiratory turbinates) only provide multiple discrete inferences of the occurrence of the endothermy, the debate thus still remains. We examined the qualitative histology of stylopod bones of the dicynodont Moghreberia, and two others (Oudenodon and Lystrosaurus) for comparative purposes, to infer their growth rate. The histology suggests increasing growth rates from Moghreberia [incipient fibrolamellar bone (FLB) in both stylopod bones], to Lystrosaurus (well-developed FLB in the femur but incipient FLB in the humerus), to Oudenodon (well-developed FLB in both stylopod bones). Nevertheless, qualitative histology does not provide precise inferences about the metabolic rate. We therefore performed the first quantitative inferences of resting metabolic rates on extinct synapsids (Moghreberia, Lystrosaurus and Oudenodon). Two statistic models (for the humerus and femur) were done on histological variables (size, shape and density of osteocyte lacunae in primary bone outside osteons) and a phylogenetic context (using phylogenetic eigenvector maps) to imply the massindependent resting metabolic rate. Histological data were measured in regions formed during the phase of sustained high growth rate. They were thus quantified in the outer cortex for 14 extant tetrapods species taken from previous studies, whereas they were made in the deep cortex in three new added adult extant mammals and the three subadult or adult cited dicynodonts. The best models were selected on the AIC value and validated (with 95% confidence intervals) using leave-one-out cross-validation. The predicted values are consistent with our qualitative histological observations: the metabolic rate inferred for Moghreberia (2.58 mLO2 h–1 g–0.67) is lower than for Lystrosaurus (3.80 mLO2 h–1 g–0.67), which is lower than for Oudenodon (4.58 mLO2 h-1 g-0.67). Optimization of these inferences onto the phylogeny better constrained the temporal (more than 260 Myr ago) and phylogenetic (Neotherapsida) frames of the acquisition of mammalian endothermy.

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### Selective forces behind the evolution of respiratory turbinates in mammals and birds

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Purported fossilised traces of respiratory turbinates have been used to argue for endothermy among various taxa of extinct amniotes. These studies claim that endothermy may have appeared in synapsid and archosaur lineages before the origin of Mammalia and Aves. Although evolved independently, respiratory turbinates of living mammals and birds serve the same function of temporal counter-current exchange. This mechanism helps to reduce heat and water loss in expired air, especially important to endotherms with high lung ventilation rates. But did respiratory turbinates evolve in response to high metabolic rates or other factors? Our comparative study of a diverse sample (> 150 species) of modern mammals and birds reveals that respiratory turbinate surface area (RTSA) scales isometrically with body mass (range = 2.6 g - 2,000 kg) in both endothermic taxa, but on average is three times greater in mammals than in birds. Within each clade, there is a strong phylogenetic signal in RTSA scaling, but there is no apparent effect of ecology (arid/mesic) or geographic distribution (tropic/polar). A residuals analysis reveals that RTSA correlates significantly with basal metabolic rate in birds (n=31), but not in mammals (n=38). In contrast, RTSA residuals correlate significantly with residuals of field metabolic rates in mammals (n=10), but not in birds (n=12). Because both data sets are limited, it is impossible to discern which of these metabolic signals may have been more important in extinct ancestors of mammals and birds. An alternative hypothesis had been proposed, which argued that respiratory turbinates may have evolved in response to a precipitous decrease in atmospheric oxygen levels across the Permo-Triassic boundary, or during the subsequent global hypoxia of the Mid-late Triassic/Early Jurassic. However, extant endotherms from high elevations and adapted to altitudinal hypoxia do not exhibit consistently greater RTSA compared to their lowland relatives. Neither do extant ectothermic archosaurs raised in chronic hypoxic conditions show phenotypic plasticity in the internal morphology of their nasal capsule. Our data, therefore, do not support the "hypoxia hypothesis" behind the origin of respiratory turbinates.



<sup>°</sup> Speaker

## Inferring the physiological capacities of extinct vertebrates: methods, limits, and framework

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What can we know of the physiological regimes of ancient vertebrates? Essential to the exploration of this question are (1) a phylogenetic framework for interpreting whole animals and individual tissues, (2) strong knowledge of variation in populations and among climates and geographies, (3) understanding variation during development and between sexes, and (4) a sense of the patterns of body size change, both phyletically and ontogenetically.

Extinct vertebrates leave us little but their hard tissues, from which physiological inferences must be wrested. Sufficient sampling of homologous bone tissues across taxa and ontogenies has revealed the growth rates and skeletochronological trajectories of more extinct species than those known from the living world. It has shown us that dinosaurs and other extinct taxa follow the same patterns and "rules" of growth as living taxa do. In general, larger species grow more rapidly than their smaller relatives, *ceteris paribus*. Only decades of painstaking histological work could have brought these insights.

Interpreting the physiological meaning of these data is more elusive. Physiological features have often been directly interpreted from the hard tissues, without considering developmental stage, adult size, or general patterns of the clade. Authors often neglect to define terms such as homeothermic, endothermic, and "warm-blooded," or use them interchangeably, or see certain terms as inextricably linked. Paleobiologists are chained to a relatively dichotomous set of terms developed long ago to describe the relatively depauperate living vertebrate fauna, which sees only two binary categories of five major groups: the "cold-blooded" fishes, amphibians, and reptiles, and the "warm-blooded" birds and mammals. Integration of all histoanatomical data with patterns of size, growth, and phylogeny provide our best opportunity to re-imagine not only vertebrate paleophysiology, but vertebrate physiology in general.



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### Altricial forelimbs – precocial hindlimbs: disparate growth and function in the ontogeny and evolution of avian locomotion

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The complexity of avian flight evolution is evident from comparing ratios and morphology of limbs and plumage in dinosaur-bird transitional theropods and the only living dinosaurs, modern birds. However, its ontogenetic aspects, i.e. how limbs develop to perform bipedal locomotion and flight, are almost unknown in extinct bird-like dinosaurs. Extant birds show diverse ontogenetic locomotor strategies along the precocial-altricial developmental spectrum, in which legs and wings develop at different rates in taxa following different strategies. Besides fully precocial (e.g. galliforms) and fully altricial (e.g. passerines) limb development, some birds, like anatines, hatch with precocial legs suited for running and swimming but develop their wings altricially with which only fully grown adults fly. While ossification degree and longitudinal limb growth have been related to these ontogenetic strategies, so far no in-depth attempt was made to identify their diaphyseal osteohistological correlates. Diaphyseal bone tissue reflects differences in growth rate and mechanical demands within the skeleton and is the most studied and usually well preserved region in fossils too, so studying it in growing modern birds is an invaluable information source for fossil inferences. As anatines are perfect subjects to explore how allometric growth and disparate function of the wings and legs are reflected in diaphyseal osteohistology, we investigated the humerus, ulna, femur, tibiotarsus and tarsometatarsus in an ontogenetic series of Rouen ducks (Anas platyrhynchos) bred and killed for a previous study at 4, 8, 30 and 50 days posthatching age (d). We studied intra- and interindividual development of cortical dimensions, vascularity, osteons and resorption-remodeling; features expected to be linked to disparate limb loading during growth. Our results show that leg bones consistently differ from wing bones in revealing remodeling and more advanced osteonal infilling, while wing bones only show extensive perimedullary resorption but no cortical remodeling. These histological disparities appear later than 8d, as they were first detected at 30d. Periosteal growth in leg bones reach asymptote by 30d, while wing bones keep on increasing in diameter. Other trends are less evident among different bones and/or throughout ontogeny. Our study is a first step to establish diaphyseal histological correlates of precocial-altricial development for analysing locomotor ontogeny in fossils.



<sup>&</sup>lt;sup>°</sup> Speaker

#### The independent evolution of endothermy in Plesiosauria: evidence from their unique long bone histology

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Sauropterygia were the longest-lived and most successful clade of Mesozoic marine reptiles, appearing in the late Early Triassic and going extinct together with non-avian dinosaurs at the end of the Cretaceous. The evolutionary and biogeographic history of Sauropterygia raises the question of their metabolic rate and thermophysiology. We studied plesiosaurian propodial histology from midshaft cross sections of seven small to medium-sized taxa representing much of plesiosaurian diversity and temporal range. Plesiosaurian primary cortical bone is a unique kind of radial fibrolamellar tissue (FLB) that later in ontogeny was replaced by dense Haversian tissue. Growth marks are distinctive, the first appearing at > 70% final cortical thickness, and annual growth mark counts indicate that asymptotic size was reached within 4-6 years.

After sampling of successive taxa on the Triassic plesiosaurian stem (*Neusticosaurus, Nothosaurus, Cymatosaurus, Pistosaurus*) qualitatively suggested a gradual increase in growth rate, quantitative estimates of metabolic rate and bone growth rate in plesiosaurs and these taxa were needed. We employed phylogenetic eigenvector maps (PEM), a method for estimating trait values (response variables) from a predictor variable while correcting for phylogenetic relationships. Our trait values are growth rate (expressed as local bone apposition rate) and resting metabolic rate. Our predictor variable is vascular density, measured in bone histological sections of the sauropterygians and extant comparative taxa. We quantified vascular density as proportion of vascular area (including lamellar infillings of primary osteons) to total bone area. Our models reveal bone growth rates and resting metabolic rates for plesiosaurs that are in the range of birds, suggesting that plesiosaurs were endothermic. Although our models are influenced by the availability of comparative data, which are lacking for large marine amniotes, potentially skewing our results, we note that endothermy had been suggested for plesiosaurs by other independent evidence in the past.

The oldest plesiosaur, a newly discovered taxon from the Rhaetian of Germany, already shows the same unique and uniform histology as all later plesiosaurs examined. This suggests that plesiosaur endothermy evolved in concert with the changes in their axial skeleton and limbs linked to the evolution of underwater flight. Endothermy thus may have been an adaptation to cruising in the open marine habitat, as predicted by the aerobic scope hypothesis of endothermy origins. Attaining > 70% of final size in the first year suggests energy transfer from parent to offspring, consistent with the parental care hypothesis of endothermy origins. Endothermy may explain plesiosaurian survival of the end-Triassic extinction event and their global radiation and dispersal.



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#### Bone histology of shell bones and dermal ossifications with implications for the palaeophysiology of turtles and archosauromorphs

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Increasing molecular evidence underpins an evolutionary, although still contested, scenario with a sister group relationship of turtles and archosaurs within Diapsida. Turtles and many archosauromorph reptiles carry dermal armour, usually in the form of a more or less rigid shell (and accessory ossicles in some turtle clades) in the former and a mosaic of individual or articulated osteoderms in the latter. Physiological studies on living representatives showed, among others, mechanical (e.g., locomotion, bracing system, defensive armour) and physiological (e.g., water retention, heat exchange, mineral storage) functions of integumentary hard tissues, including buffering of metabolic (e.g., lactic) and respiratory acidosis. Higher levels of vascularisation of turtle shell bones were proposed to allow for a larger buffering capacity, compared to larger endoskeletal and dermatocranial elements, and would benefit in heat exchange. Here, the histology of shell bones and osteoderms of extant and extinct turtles is compared to that found in diverse archosauromorphs, including doswelliids and proterochampsids, pseudosuchians, as well as armoured dinosaurs. Initial results indicate that external shell bone cortices are well vascularised in aquatic turtles, supported by a strong nutrient supply through the integument. This allows for higher shell growth rates especially early in development, compared to tortoises in which cortical vascularisation is less pronounced. Functional adaptations to the aquatic environment, however, often overprint the primary vascularisation signal, while overall shell bone reduction in marine turtles poses a disadvantage by reduced general storing and buffering capacity. Extant crocodylian osteoderms show well developed cortices comprised of slow-growing lamellar-zonal bone, but these can be partially destroyed through mineral mobilisation in ovipositing animals. Among fossil archosauromorphs, higher disparity in vascularisation and growth rates is apparent that could be linked to several functional or physiological aspects. The highest bone compactness is present in proterochampsid osteoderms (e.g., Pseudochampsa ischigualastensis), in paramedian osteoderms of Aetosauroides scagliai and large dermal ossicles of the sauropod Saltasaurus loricatus. The absence/very low rate of bone remodelling could indicate that these osteoderms were less physiologically relevant for heat exchange, mineral storage, or for providing buffering capacity.



<sup>&</sup>lt;sup>°</sup> Speaker

#### Bone as a buffer in Permo-Carboniferous tetrapods: insights from physiological studies of extant turtles

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We have previously argued that the involvement of mineralized tissues in acid-base homeostasis may have been important in shaping vertebrate design in Permo-Carboniferous tetrapods. Studies of extant vertebrate species have shown that dermal bone functions as a buffer, in part, by releasing Ca and Mg carbonates into the blood, partially demineralizing, and potentially altering the mechanical properties of the bone. In order to test the hypothesis that utilizing dermal bone as a buffer does not conflict with its protective role, we studied the mechanical properties of bone beams milled from the plastrons of anoxiatolerant painted turtles during anoxic submergence at 3°C. This turtle species is an extreme vertebrate example of dermal bone buffering of acidosis, in which it can utilize its large shell, comprised mostly of dermal bone, to buffer nearly 200 mmol/L lactic acid in its body fluids. The study revealed that the turtles could tolerate 130 days of anoxia without any measurable changes in the mechanical properties of its plastron, despite increases in blood plasma concentrations of lactate, Mg and Ca to  $152.0 \pm 3.5$ ,  $14.8 \pm 0.9$ and 42.2  $\pm$  2.0 mmol/L, respectively, and 15.4% and 15.2% decreases in the Mg and CO<sub>2</sub> contents, respectively, of dry shell. However, a mechanical trade-off was observed closer to the limits of anoxic survival (167 days), as maximum stress and elastic modulus decreased by 26.8% in 46.9%, respectively. This corresponded with blood plasma concentrations of lactate, Mg and Ca of 176.3  $\pm$  4.1, 14.1  $\pm$  0.9, and 46.3  $\pm$ 3.1 mmol/L, respectively. The Mg and total CO<sub>2</sub> contents of dry bone at this timepoint were decreased by 23.0% and 23.7%, respectively. There were no changes in the P or Ca contents of dry bone at any time. Therefore, we suggest that it would be possible for a Permo-Carboniferous tetrapod to mobilize significant mineral buffers from dermal bone without compromising bone strength, assuming the total amount and buffering properties of its dermal bone were not dramatically different from that in the painted turtle. This work was funded by NSF CAREER award 1253939.



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### Comparative tusk histology of *Lystrosaurus* from the Early Triassic of South Africa and Antarctica shows pronounced seasonality

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The Lower Triassic Fremouw Formation of Antarctica preserves a vertebrate assemblage that is strikingly similar to that of the *Lystrosaurus* Assemblage Zone of South Africa. Given the geographic proximity of the two within southern Pangea, this degree of faunal similarity is unsurprising. However, given their polar position during the Early Triassic, Fremouw vertebrates might be expected to have experienced more pronounced seasonality than their lower latitude conspecifics. By living in a polar light regime, Antarctic vertebrates during the Early Triassic may have had broad physiological tolerances that would accommodate this extreme seasonality. Differences in physiology between high and low paleolatitudes would likely be observable in the oral and osteohistology of the fossil remains.

Incremental periodic growth marks in dentine, often referred to as lines of von Ebner, record regular tissue growth as well as cessations in tissue growth that are often associated with stress. As such, these signals can be useful in revealing seasonal stress in extinct vertebrates. Here, we compared the paleohistology of the ever-growing tusks of *Lystrosaurus* from the Early Triassic of South Africa and Antarctica to test for physiological correlates of living in a polar light regime.

Using a standardized method to count periodic lines in the dentine, both South African and Antarctic *Lystrosaurus* tusks demonstrate periodicity in the deposition of stress lines. However, Antarctic specimens record these stress lines more frequently than South African ones and there are fewer incremental growth lines in between these indictors of stress. Additionally, Antarctic tusks display extended periods of growth in between the regular, incremental growth lines. These data indicate that Antarctic *Lystrosaurus* experienced more pronounced seasonality than did South African *Lystrosaurus*, perhaps as a response to extreme variation in food or water availability.

These results suggest that populations of *Lystrosaurus* that inhabited polar regions of southern Pangea had a flexible physiology to accommodate their polar habitat. However, their growth patterns remained relatively similar to South African contemporaries suggesting the ability to live in a wide range of environments, which is often associated with endothermy.



S40 // Oral

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#### Hindlimb osteohistology reveals details of tyrannosaurid ontogeny and independently tests the *Nanotyrannus* hypothesis

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Two mid-sized tyrannosaurid skeletons, collected from the Hell Creek Formation in Montana, are reposited at the Burpee Museum of Natural History (BMRP). Based on shared morphologic features, and because Tyrannosaurus rex is the only mega-carnivore known from the Latest Cretaceous of Montana, BMRP 2002.4.1 and BMRP 2006.4.4 are generally considered juvenile T. rex. However, some researchers suggest they represent mature individuals of the contested tyrannosaurid genus, Nanotyrannus lancensis, as the holotype skull (CMNH 7541) shares many morphological characters with the skull of BMRP 2002.4.1. Regardless of taxonomy, ontogenetic details of any tyrannosaurid genus remain poorly understood due to a lack of histological sampling, which would permit assessments of growth rate, physiology, and maturity status; the BMRP specimens were histologically examined with these aims in mind. Assessments of tibiae and femora diaphyseal transverse sections in circularly-polarized light reveal a matrix of fibrous, birefringent laminae containing randomly oriented osteocyte lacunae (i.e., rounded to elongate), whereas primary osteons are comprised largely of isotropic lamellae with rounded lacunae. Osteocyte lacuna density is uniformly high throughout the cortices and the rich network of vascular canals are arranged in longitudinal, laminar, reticular, and sub-plexiform orientations; although canal orientation and bone fiber arrangement varies locally about the transverse sections. Cortical structures observed in longitudinal sections are consistent with a woven-parallel fibered complex and longitudinal arrangement of lamellae comprising primary osteons. Zonal thickness between annual cyclical growth marks does not decrease progressively from inner to outer cortex as expected, and this erratic zonal spacing is consistent with observations from larger T. rex specimens. If all cyclical growth marks are accounted for, BMRP 2002.4.1 was 13 years of age, and BMRP 2006.4.4 was 14 years of age at death, but based on bone tissue and vascular canal patterns, there is no indication that either individual was skeletally mature when it died. This histological assessment aimed to permit a better understanding of tyrannosaurid ontogeny, and in doing so, independently tested the hypothesis that BMRP 2002.4.1 and BMRP 2006.4.4 are individuals of Nanotyrannus. Because of their histologically juvenile status, the parsimonious conclusion is that these specimens are immature Tyrannosaurus rex.

S40 // Oral

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## The origin of Mammalian endothermy: a phylogenetic approach

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The acquisition of mammalian endothermy is one of the most significant events in vertebrate evolution because it modified the energetic relationships between synapsids and their environment. The knowledge of this evolutionary event is crucial to understand related physiological, anatomical, behavioral and ecological traits in extant and extinct synapsids. In spite of the evolutionary relevance of this event, the phylogenetic and temporal frames of this acquisition is still debated. Previous studies used fossils from, at best, middle Permian. Here, we incorporated species from the late Carboniferous, using the oldest known fossil Synapsida (belonging to clades more inclusive than those analyzed to date). We used a paleohistological approach and quantified two newly defined variables both in the quoted fossils and in a sample of 17 species of extant tetrapods (for which we know the resting metabolic rate). These variables are the density of primary osteons and the density of woven bone and were used here as proxies for the fossils' metabolic condition. We used Phylogenetic Eigenvector Maps to infer the resting metabolic rate of the sample of extinct synapsids using the values known for the sample of extant tetrapods and the phylogeny. We have found that "basal" synapsids such as Clepsydrops and Ophiacodon had resting metabolic rates in the range of those of extant mammals, whereas Mycterosaurus was probably ectotherm. We analyze the implications of these findings for our knowledge of the origin and evolution of mammalian endothermy.



S40 // Poster

Speaker

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### A reference database of enamel texture microwear in extant rhinoceroses and its relevance for diet reconstruction of the fossil rhinocerotid *Stephanorhinus* (Mammalia, Perissodactyla)

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Climatic changes might affect the ecology, the geographical distribution, and the lifespan of land mammals. In Europe, during the late Pliocene-early Pleistocene interval, major climatic variations and associated shifts in vegetation have occurred, for instance resulting in the expansion of grasslands in Mediterranean regions. Here, we focused on samples of three Stephanorhinus species from French localities to study the impact of the Pliocene–Pleistocene climatic changes: S. megarhinus from Montpellier (early Pliocene, ~5.3-4.5 Mya); S. elatus (= "Dicerorhinus jeanvireti") from Vialette (late Pliocene, ~3.1 Mya); S. etruscus from Senèze (early Pleistocene, ~2.21-2.09 Mya). We aimed at reconstructing their diet using dental microwear texture analyses. Microwear is a short-term recorder of diet that can reveal subtle dietary differences, due to seasonality, individual, or populational variations. Thus, a repository of extant related species as living analogs, the diet of which is known, can be a valuable tool. We studied two distinct facets on upper and lower molars: a crushing facet with Hunter-Schreger bands (HSB) and a shearing one without HSB. We then built an unprecedented database on enamel texture microwear of 62 wild shot specimens belonging to the five extant rhinos species that cover a wide range of vegetarian diets. The fossil samples studied display significant differences (MANOVA) in dental microwear textures depending on the facet (p-value < 0.01) and the species (p-value< 0.05). The studied individuals of S. elatus and S. megarhinus exhibit similar texture microwear signal, meaning that they probably had similar feeding habits. The low values of anisotropy and the low to medium values of complexity of all fossils fall into the range of modern browsers Diceros bicornis and/or Rhinoceros sondaicus, suggesting browsing habits for the three samples. These results are consistent with the previous conclusions that S. megarhinus and S. elatus were largebodied Pliocene rhinos probably inhabiting non-fully open environments, even though no strong environmental constraint is available for Montpellier locality. Conversely, a rich palynoflora witnesses the dominance of a temperate deciduous forest at Vialette. Similarly, the inferred browsing diet for the smaller bodied S. etruscus would suggest no real shift in the diet, but the persistence of forest patches during the early Pleistocene interval around Senèze, whereas savannahs were covering most of Western Europe.



<sup>\*</sup> Speaker

#### Cases of pathological bone growth in *Isanosaurus* and *Spinophorosaurus* (Sauropoda)

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The histology of the long bone of sauropods appears uniform and conservative along the Sauropoda evolutionary tree. One of the main aspects of their bone histology is to exhibit a Fibrolamellar Complex (FLC) in the cortex of their long bones. However, we report Radial Fibrolamellar bone (RFB) in the outer cortex of the humeri of a young adult *Isanosaurus* (Histological Ontogenetic Stage - HOS - 8) and an adult Spinophorosaurus (HOS 12). RFB is regarded as a fast-growing bone tissue and has been documented in a few dinosaurian taxa, but never among Sauropoda. Its outermost position within the cortex raises questions, because such a rapidly apposited bone tissue would rather be expected in the inner cortex (corresponding to an early juvenile ontogenetic stage). Our thorough histological analysis of these specimens reveals some highly vascularized RFB yielding densely packed plump osteocyte lacunae that can even obscure the surrounding bone in both transverse and longitudinal sections. This osteocyte pattern is restricted to the RFB. Bone remodelling is more expressed in this cortical layer with more dense secondary osteons deposited in the RFB than more internally or externally. This contrasts with the other dinosaurian taxa affected by RFB which contains no secondary osteon in this bone tissue. The individual of Spinophorosaurus represents the first occurrence of RFB in Sauropoda buried in the outer cortex followed by a recovery of a 'normal' FLC after this event meaning this individual survived for some time after its phase of accelerated growth. This sequence of widely distinct modes of bone apposition suggests that these specimens are pathological.



<sup>&</sup>lt;sup>•</sup> Speaker

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#### Ecological and phylogenetic models to estimate resting and standard metabolic rates of extinct ectothermic Archosauria (Pseudosuchia: Aetosauria)

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Although much of what we know of the biology of extinct organisms can be inferred directly from the fossils themselves, other characteristics must be extrapolated from comparisons with living animals. This is especially true of metabolic rate (MR) in fossil vertebrates. Previously many workers have attempted to understand the metabolism of dinosaurs, but there has been little to no work on more basal archosaurs, in spite of the fact that it was the diversification of archosauromorphs over the first 30 million years of the Triassic that set the stage for dinosaur dominance during the latter Mesozoic.

Here we report our estimates of the MR of some well preserved aetosaur specimens. Our method relies on the fossil record for body mass estimates, but otherwise compares aetosaurs to an array of extant saurians with empirically measured MR pulled from the literature. We subdivide our approach in two different analyses, one emphasizing ecological characteristics and a second relying more on phylogenetic aspects, and running multiple linear regressions for both to obtain resting metabolic rate (RMR) and standard metabolic rate (SMR) from both analyses. For example, we find for a 120 kg specimen of *Typothorax coccinarum* an RMR of 1871 mL O2h–1, and an SMR of 973 mL O2h–1 utilizing the ecological analysis. On the other hand, focusing on phylogenetic aspect for the same specimen we find substantially higher values, with an RMR of 2253 mL O2h–1 and an SMR of 1599 mL O2h–1. In both analyses metabolic rate is most strongly influenced by body mass, but, from a relative weight analysis, we obtained estimates of the relative weights of other dependent variables involved in MR prediction, as well as a corroboration of the importance of phylogeny (6.6%), feeding mode (2.2%) and environmental adaptation (8.6%) of the total variance in the analysis based on phylogenetic aspect.

As we expected from the literature, the ecological equation shows the lower MR. We attribute this difference to the presence of armor, emphasized in the ecological analysis, in comparison to the phylogenetic analysis. However, our phylogenetic estimation could be a useful tool to estimate MR of all extinct ectothermic saurians and not only the heavily armored one.



<sup>&</sup>lt;sup>\*</sup> Speaker

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#### Another convergence: bone cortical compactness in extant sloths

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Bone remodeling, one of the main processes that regulate bone microstructure, consists in bone resorption followed by the deposition of secondary bone at the same location. Intense at an early ontogenetic stage, bone remodeling rate of most mammals decreases with ontogeny, which entails for the mature cortical bone to be characteristically compact. A previous analysis found that cortical bone in a few extant sloth specimens is heavily remodeled and characterized by numerous immature secondary osteons, suggesting that these animals were remodeling their bones at high rate until late in their ontogeny. This study aims at testing if this is generally present in extant sloths, using a quantitative analysis of the humeral cortical compactness (CC) among xenarthrans. The results of the investigation of humeral diaphyseal crosssections of 25 specimens belonging to nine xenarthran species including both extinct and extant specimens indicate that in extant sloths the CC is significantly lower than in the other sampled xenarthrans. No significant difference was found between the CC of the two genera of extant sloths (Bradypus and Choloepus). Our results are consistent with the hypothesis that the cortical bone of extant sloths in general undergoes intense and balanced remodeling that is maintained late (possibly throughout) their ontogeny. In the light of xenarthran phylogeny, low CC represents another convergence between the long-separated extant sloth lineages. Although the exact structural and/or functional demands that are associated with this trait are hitherto unknown, several hypotheses are suggested here, including a relationship to their low metabolism and to the mechanical demands imposed upon the bones by the suspensory posture and locomotion, which was independently acquired by the two extant sloths genera.

Speaker

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#### S41 - XXIst Century palaeohistology of mineralized tissue

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#### Histochemical staining of biomineralized and softtissues in fossil dinosaurs and birds: new avenues for XXIst century palaeohistology

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Since the 19th century, the field of palaeohistology has been essentially relying on the crafting of thick, petrographic sections of biomineralized tissues. In turn, the identification of specific fossilized tissue types has been based mostly on qualitative variables, such as osteocyte lacunae shape, collagen fiber arrays detected using polarized light, or vascular orientation and density. Alternatively, histochemical staining is routinely used on extant vertebrate bone to identify skeletal tissues by revealing components of their extracellular matrix.

Very few attempts to stain fossilized tissues have been made, because it is assumed that biomolecules recognized by these stains will not survive more than ~1 million-years, or that the thickness of ground sections (~100 $\mu$ m) or alteration of skeletal components would prevent any significant staining reaction. However, successful histochemical staining has recently been made in two types of bone in the theropod dinosaur *Tyrannosaurus rex*, by using demineralization and paraffin histology methods (5 $\mu$ m slices) modified for fossilized tissues.

Here, we present new data that demonstrates successful staining in bone, cartilage and dentine from a hatchling dinosaur skull of *Hypacrosaurus stebingeri* from Montana (MOR 548). Three different histochemical stains were used: alcian blue, a relatively non-specific stain that reacts to the presence of glycosaminoglycans; picrosirius red, which identifies collagen based upon fiber orientation; and a modified Masson's trichrome that highlights differences between connective tissues. Morphological integrity of cellular components is preserved in these paraffin slides, such as odontocyte processes in dentine.

For the first time, we also apply this method to originally unbiomineralized soft-tissues, including ovarian follicles and wing patagia preserved in fossil birds from the Jehol biota of Northeastern China. This 21st century palaeohistology method has the potential to revolutionize the way that tissues are identified and interpreted in vertebrate palaeontology, to increase our understanding of molecule preservation in the fossil record, elucidate the chemistry driving diagenetic changes and underlying taphonomic processes responsible for soft tissue preservation, as well as reveal the evolution and development of important soft tissue structures.



Speaker

### Patterns and processes of the convergent microanatomical and histological traits in the landwater transition

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Secondary adaptation to an aquatic lifestyle led to numerous convergences in amniote evolutionary history. Among these, several concern bones. These changes occur in bone outer shape but also in its microanatomical and histological features. The distribution of the osseous tissue in the bone is indeed strongly modified in the process of adaptation to an aquatic lifestyle and several specializations occur (bone mass increase, spongious organization) with various degrees of intensity and different patterns of distribution in the skeleton, pending on the functional constraints underwent by the organisms. The plastic nature of bone microstructure indeed leads to a wide spectrum of epigenetic changes. An increase in growth speed, associated with metabolic changes, also occurs through this change of milieu, which is observable in the nature of the osseous tissue. Some marine reptiles show strong trends towards endothermy, probably linked with associated increased swimming efficiency. This study documents the trends in microanatomical and histological changes associated with a terrestrial to aquatic transition in modern and fossil amniotes using distinct methodological approaches and discusses the possible processes involved in the light of the wide diversity of patterns observed.



Speaker

#### Trabecular 3D architecture and diaphyseal structure - the forelimb of extant and extinct xenarthrans (Mammalia)

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Trabecular architecture (i.e., the main orientation of the bone trabeculae, their relative number, mean thickness, spacing, etc.) has been shown experimentally to adapt with extreme accuracy and sensitivity to the loadings applied to the bone during life. However, the potential of 3D trabecular parameters used as a proxy for the biomechanics of an organism to help reconstruct the lifestyle of extinct taxa has only been seldom exploited, as present studies are limited to primates. Here we investigate xenarthrans, for which functional and ecological reconstructions of extinct forms is particularly important in order to broaden our macroevolutionary understanding of their main constitutive clades, i.e., the Tardigrada (sloths), Vermilingua (anteaters), and Cingulata (armadillos and extinct close relatives). The lifestyles of modern xenarthrans can be classified into three categories, the fully terrestrial and highly fossorial armadillos, the (partly) arboreal and hook-and-pull digging anteaters, and the fully arboreal (suspensory) and non-fossorial sloths. The degree of arboreality and fossoriality of some extinct forms, "ground sloths" in particular, is highly debated (interpretations are so far based on gross morphology and ichnofossils). We used high-resolution computed tomography to compare the epiphyseal 3D architecture and midshaft structure of the forelimb of extant and extinct xenarthrans. The comparative approach we used aims at inferring the most likely lifestyle of extinct taxa, taking into account the potential effects of body size and phylogeny. Our first observations suggest that lifestyle inferences will be challenging: The Early Miocene sloth Hapalops presents some structural parameters that fall outside the range described by extant taxa, and the gigantic size of the Quaternary sloths Lestodon and Glossotherium most likely biases allometric regressions (used to correct for the influence of size). This is confirmed by a phylogenetically informed discriminant analysis.



S41 // Oral

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## Bone histology and growth of deer: preliminary results from bone histology

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Over the last decades, data from bone tissue and skeletochronology begin to improve our knowledge of life histories of both extinct and extant vertebrates. To date, the majority of studies are biased towards dinosaurs and extant reptiles, while relatively few research focuses on mammals. This is mostly due to the common view that the growth of endotherms is continuous until maturation. However, it has been demonstrated that changes in bone types and growth arrest marks are also present in mammals because of life history events and seasonal changes in their physiology. Hitherto, only few bone histology studies addressed the family Cervidae, mostly focusing on extinct genera, and we know relatively little about extant deer. Accordingly, the aim of this work is to fill this gap by providing new data on the growth and life history of deer using bone histology of the genus Cervus. Here, we collected information about epiphyseal closure, eruption pattern and growth marks in long limb bones of different aged captive (with known life history data) and wild Cervus elaphus to create a basis for correct interpretation of life histories in fossil cervids. Our results indicate that skeletal maturity in females is reached earlier than in males (3.5 and 4.5-5.5 years, respectively) and, that at this age, epiphyseal fusion and dental eruption are completed, and tissue patterns in long bones change importantly. Our results also show that the attainment of sexual maturity in C. elaphus is attained slightly earlier than skeletal maturity, in accordance with the growth vs. reproduction trade-off. These data yield for the first time key information about life history and growth in extant deer, and provide the basis for a better understanding of the life histories of extinct deer and its variations over evolutionary time.



Speaker

#### New data on the skeletal distribution, microstructure, and chemistry of medullary bone in Neornithes – Paleobiological implications

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Medullary bone (MB) is a specialized tissue produced by female birds during the egg-laying cycle that acts as a labile reservoir of calcium for the eggshell formation. In the literature, it is commonly described as a highly vascularized and strictly woven bone tissue, endosteally deposited in the medullary cavity of long limb bones. MB has also been defined by a unique molecular signature. Some of its molecular markers, such as the glycosaminoglycan keratan sulfate (KS), have not been reported in the calcified matrix of other bone types.

Using these microstructural and chemical criteria, MB-like tissues have been identified in several specimens of non-avian dinosaurs. However, MB's definition mostly results from its study in domestic bird species that are not representative of bird diversity. Moreover, some avian pathological bone (PB) tissues meet the microstructural criteria, thus casting doubt on previous observations of MB in the fossil record.

With a sample of over 55 bird species, the present work constitutes the first taxonomically comprehensive study of MB. Using micro-computed tomography and histochemical techniques (chemical staining and immunochemistry), we assess the skeletal distribution of MB and evaluate the extent of microstructural and chemical variation of this bone tissue in Neornithes. Using similar techniques, we also studied the bone pathologies of 22 bird specimens, in order to test the hypothesis that MB is chemically different from avian PB tissues.

Our results reveal that the skeletal distribution of MB varies interspecifically. This bone tissue can be found in most skeletal elements and is uniformly present in the proximal part of the tibiotarsus of all studied specimens during the laying cycle. At the histological level, MB presents a lamellar component (associated to the woven bone matrix) in some large ratite specimens. Finally, our preliminary chemical analyses reveal that some avian PB tissues may contain KS, complicating the reliability of chemical approaches to MB identification. Our tests will be replicated and other techniques will be implemented to verify these results.

The data of this groundwork will be used to reassess previous identifications of MB-like tissues in fossil archosaurs.



<sup>\*</sup> Speaker

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# New material of *Huanghetitan ruyangensis* Lü *et al.,* 2009 and the preliminary study of bone histology

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*Huanghetitan ruyangensis* is the second large-sized sauropod dinosaurs of the Ruyang Gigantic Sauropod Dinosaurian Fauna, which comes from the late Early Cretaceous Shang Donggou Formation. The holotype consists of nearly complete sacral vertebrae, anterior caudal vertebrae and a complete dorsal rib of 2.93 meters long which was regarded as the sauropod with deepest body concavity. The vertebral column of the new material of *Huanghetitan ruyangensis* is naturally articulated with 7 cervical vertebrae and six dorsal vertebrae, the fused scapula and coracoid, and one ulna are scattered near the vertebral column. They clearly belong to one individual. The new material provides much more information of *Huanghetitan ruyangensis*, especially the characters of the scapula and coracoids, ulna, and the cervical vertebrae. The rib bone histology of *Huanghetitan ruyangensis* shows it should has a very fast growth rate.



Speaker

### The first hard evidence for a developmental link between teeth and dermal odontodes: 3D synchrotron dental histology of the Silurian stem osteichthyan Lophosteus

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If teeth and dermal odontodes share a single evolutionary origin, it should be possible to find intermediate structures in early vertebrates, but none has been found to date. Here we show how ontogenetic data obtained by 3D modeling of synchrotron microtomography scans of Lophosteus superbus from the Late Silurian of Estonia, the phylogenetically most basal stem osteichthyan, reveal links between teeth and dermal odontodes that are not obvious from the adult morphology. A marginal jawbone of an adult Lophosteus carries small conical teeth that undergo repeated shedding and replacement, and large stellate ornament odontodes that are not shed. 3D virtual dissection reveals that the earliest odontodes to form are two longitudinal rows of non-shedding linear ridges, located over the growth center of the bone. The lingual ridges appear to consist of fused unicupspid odontodes, the labial ridges of similarly fused multicuspid odontodes. Tooth formation begins immediately lingual to the lingual ridges; the first teeth, which are resorbed semi-basally, are arranged in transverse files and set up the multiple rows of tooth positions that then undergo repeated site-specific resorption and replacement in a typical osteichthyan manner. Immediately labial to the labial ridges, isolated multi-cusped odontodes are added, the side cusps gradually becoming smaller and arranged in radial rows to achieve a stellate appearance. The ridges thus differentiate into two morphologies in opposite directions, becoming teeth and ornament respectively. We suggest that the position of the ridges reflects the initial ectoderm-endoderm boundary. The morphological gradation implies the existence of a morphogen concentration gradient between endoderm and ectoderm. The replacement teeth, the first-generation isolated odontodes, and the main cusps of the ridges are aligned in the same alternate files. Later, successive generations of ornament overgrow the labial tooth rows, indicating the invasion of ectoderm. At the invasive front line, both overgrowing odontodes and replacement teeth have side cusps on the labial face of the lingually recurved main cusp. The half-tooth half-ornament morphology suggests the overlap of the signal spheres of the two epithelia. Therefore, teeth and ornament are initially not separate systems in Lophosteus, but diverge in response to molecular signals in the developmental environment. We suggest that this may illuminate the evolutionary origin of teeth.

S41 // Oral

<sup>&</sup>lt;sup>\*</sup> Speaker

### Dental hypermineralized tissue in actinopterygians (bony fish) and neoselachians (cartilaginous fish): homology or convergence?

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Selachian enameloid is divided into two main units, Single Crystallite Enameloid (SCE) and bundled Crystallite Enameloid (BCE). The latter may show three components: Tangled- Bundled Enameloid (TBE), Radial-Bundled Enameloid (RBE), and Parallel-bundled Enameloid (PBE), the RBE appearing to be the most plesiomorphic condition. Actinopterygian acrodine, on the other hand, is devoid of SCE and correspond to a BCE only unit, where only TBE and PBE have been recognized so far. As the acrodine lacks an equivalent of SCE, it cannot be homologous to the entirety of selachian enameloid, unless it has lost its SCE unit secondarily. The same is true of its RBE component. So the question remains whether the similarities in microstructure between the two kinds of tissue reflect simply a functional adaptation or a common ancestry. One argument favouring the former hypothesis is the composition of their mineral phase that is reported as being different: hydroxyapatite with a variable fluorine content for acrodine, and fluorapatite for selachian enameloid. To further verify this, we studied the composition of the enameloid of teeth of the modern Isurus Oxyrinchus (Selachimorpha), Rhina ancylostoma (Batomorphii) and Sparus aurata (Teleostei) using Raman spectroscopy. Fluorapatite was identified only in the teeth of *Isurus oxyrinchus*, whereas the teeth of the other cartilaginous fish, the shark ray Rhina ancylostoma shows a biopatatite quite similar to that of the teleost Sparus aurata, although incorporating more CO3 than the latter. Although preliminary, these results suggest therefore that an enameloid made of fluorapatite is not characteristic of all cartilaginous fishes. More studies are needed to test this hypothesis on modern taxa, but unfortunately they cannot be extended to fossil teeth because diagenesis leads to the replacement of hydroxyapatite by fluorapatite, blurring the original signal. Anyway, it seems that the mineral composition of enameloid cannot be used to confirm a convergent apparition of selachian enameloid and actinopterygian acrodine, even if this is still the most likely hypothesis based on our present understanding of the fossil record, as the dentition of several basal chondrichthyans and osteichthyans appear to be devoid of enameloid.



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#### Osteocyte lacunae and genome size in teleosts: towards a tool to detect genomic events in the fossil record?

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Cell volume is thought to covary with various factors, including metabolic activity, growth rate, developmental complexity and body size. Empirical quantitative studies on red blood cells and bone cells (osteocytes) of tetrapod vertebrates have also established a significant statistical relationship between their volume and genome size.

Osteocytes can be easily investigated in the case of fossil vertebrates, because the cavities that they leave in bone (osteocyte lacunae) are preserved after fossilisation. Estimated volumes of osteocyte lacunae have been used to reconstruct genome size in a variety of fossil vertebrates, including non-avian dinosaurs, stem-group tetrapods and lungfishes. Here, for the first time, we focus on teleosts, a vertebrate clade for which the relationship between cell and genome size is yet largely unknown. Teleosts are a particularly interesting model, because they experienced drastic changes in genome size in the course of their evolutionary history. Most notably, a whole-genome duplication event occurred before the origin of crown teleosts, a potential turning point resulting in the evolutionary success of this enormously diverse clade. Moreover, the fossil record includes a well-known series of stem-teleosts representing the phylogenetic and temporal interval in which the duplication event must have occurred. We assembled a dataset for teleosts and their close relatives, encompassing taxa with duplicated and non-duplicated genomes, Devonian to Recent. Sets of homologous bones have been CT-scanned with synchrotron light to reconstruct osteocyte lacunae in three dimensions. This accounts for variations in cell shape and orientation, critical parameters not fully addressed by "classical" histological 2D thin sections. All measurements have been taken on two series of bones (dentaries and ribs, chosen because they are easy to obtain and homologise) because research on various taxa including teleosts show that osteocytes sizes vary significantly from one bone to another. Within a given bone, when various sources of intra-specific variability are taken into account (growth rate, primary or secondary bone) a difference in osteocyte lacuna volume is observed between lineages, whether fossil or extant. Whether this variation can be explained with genome size is established by preliminary results based on extant taxa. Applying this relationship to fossils will allow us to detect such an extreme genomic event as the teleost-specific whole-genome duplication and to locate it in time and phylogeny.

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## Evolution of the epiphyseal development of the mammalian humerus

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One of the characteristic traits of the mammalian skeleton is the development of complex Secondary Ossification Centers (SOCs) in their long-bone epiphyses. The presence of vascularization within pre-ossified cartilaginous epiphyses is presumably linked to SOC development. Based on the literature, the epiphyseal vascular pattern seems to differ between the main extant mammal groups: monotremes, marsupials and placentals. However, long-bone epiphyses have only been studied in a few species, most often on the basis of histological thin sections in different bones and at different ontogenetic stages, making difficult to assess their evolution and diversity. We analyze here the three-dimensional (3D) epiphyseal vascular mesh of the humerus in a stem amniote (Seymouria), a stem mammal (Galesaurus) and eight extant species of mammals, most of which had not been studied so far. The species selected differ in posture, growth-rate strategies and lifestyles. Ontogenetic series were included in the study when possible. We used propagation phase-contrast synchrotron radiation microtomography to generate 3D models of complete bones at relatively high resolution (voxel size: 3-13µm). Three types of canals were identified based on their 3D topology within the metaphyseal and epiphyseal areas: 1) "communicating canals", piercing the growth plate and connecting the medullary cavity to the SOC; 2) "epiphyseal canals", invading the epiphysis; and 3) "metaphyseal canals", crossing the shaft cortex of the metaphysis. Preliminary results indicate that the number, size and mapping of the types of canals strongly differ between the mammal taxa. The timing of appearance of the canals, however, seems to correlate with the lifestyle regardless of their phylogenetic position. The data also suggest that some communicating canals were not necessarily associated with the formation of a SOC and could play other roles than triggering or supporting the appearance of SOCs, such as hematopoiesis. We propose that the characteristic large tubular marrow processes found in stem tetrapods evolved, in stem amniotes, into a system of cylindrical tubes interconnected to larger chambers. In extant mammals, the system further differentiates into a marrow cavity from which a network of smaller vascular canals irrigate the growth plate. This evolution would correlate with bone elongation and morphology changes of the humerus resulting from posture shifts in mammal evolution.

S41 // Oral

<sup>.</sup> Speaker

### Cranial medullary bone in the turkey informs identification in fossils

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Female birds deposit a reserve of calcium for eggshell formation called medullary bone. It is enriched with anionic groups, sensitive to estrogen, and forms along the endosteal margin (marrow cavity) of limb bones. Medullary bone was once thought to be an avian adaptation. It now appears to be ancestral in birds dating back 245 Ma based on recent reports of similar looking (and presumably functioning) tissue in the limb bones of the extinct relatives of birds- non-avian dinosaurs and pterosaurs. However, one species of pterosaur, *Bakonydraco galaczi*, shows it in the mandibular symphysis. This is an unusual location and suggests that it may not be medullary bone.

To test the hypothesis that medullary bone is restricted to limb elements, we collected the skeletons of egg-laying turkeys (*Meleagris gallopavo*). From each individual, 19 cranial and postcranial elements were sampled including the mandibular symphysis, articular, occipital, coracoid, ulna, pubis, femur, cervical vertebra, and rib. Undecalcified sections were prepared and stained with toluidine blue to label medullary bone. Additionally, we prepared decalcified sections tagged with antibodies against diagnostic markers of medullary bone (keratan sulfate and estrogen receptor alpha).

Our results show that the proximal limb elements contain abundant medullary bone. However, it also occurs in cranial bones. Among them, the articular shows typical medullary bone as well as a novel form that we call "intramural medullary bone". This tissue fills cortical resorption cavities despite bearing characteristics of medullary bone-non-lamellar texture, keratan sulfate, and estrogen receptor alpha.

Based on these results, we reject the hypothesis that medullary bone is restricted to limb bones. Instead, medullary bone is more widely distributed across the cranial and postcranial skeleton than previously thought. Given the distribution in the turkey, the mandibular tissue found in *Bakonydraco galaczi* may be medullary bone. The expanded scope of where to find medullary bone in the skeleton will accelerate future discoveries of it in the fossil record.



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#### Renewal and growth of the dental plates of the holocephalan *Harriotta* and microstructure of tissues forming special hypermineralised dentine

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Among the cartilaginous fishes (Chondrichthyes), the Holocephali are the sister group to the Elasmobranchii (sharks and rays), with *Harriotta* an extant Rhinochimaerid possessing a dental plate that exhibits a different distribution of hard tissues compared to *Callorhynchus* (Callorhinchidae). We used a variety of optical methods with transmitted, reflected and polarized light on serial ground sections, BSE imaging and elemental analysis, and density rendered CT-scans, from dental plates of juveniles and adults. We investigated renewal of the tissues from the soft tissue interface and their degree of mineralization from forming to oral surfaces. Adult dental plate tissues are continually formed from pulpal tissues deep to the wear surface (aboral). Hypermineralized dentine (pleromin) is arranged as stacks of separate ovoids, also continuous lingual pads (tritors) punctured by subparallel vascular pulp tissue. Ovoids and pads form within, and are supported by, a trabecular dentine framework that itself becomes progressively more mineralised, as vascular spaces infill with dentine (osteodentine). None of the tissue types conforms to that of bone, contrary to previous suggestions. At the anterior, lingual margin is a thick sheet of hypermineralized tissue that was previously thought to be enameloid, but is similar to the tritors.

Ovoids and pads possess arrays of very fine tubules, penetrating into the mineralizing tissue from large cell spaces and wider tubules at their forming surfaces. Both lack a collagen fibre matrix and form a granular, disorganised, cluster of crystals that have a different shape and composition (ß-tri calcium phosphate) from hydroxyapatite crystals that typify all other mineralized vertebrate tissues. Elemental analysis plotted onto the hypermineralized dentine shows magnesium ions are in the predominantly calcium and phosphate rich zones as mineral density increases towards the oral surface. High resolution shows that the process of mineralization is mediated by multitudinous small vesicles and membranous tubes, these form amongst the mass of odontoblast tubules in the tissue.

The specialised dentine in the ovoids and pads is identical, but different from all chondrichthyan dental plates and teeth. How the distribution pattern is regulated is unknown but ovoids and tritors seem to form a succession series, although all accounts agree there is no indication that successional teeth contribute to the renewal of the dental plate morphology.

<sup>\*</sup> Speaker



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### Explore the trabecular architecture: new data from reptiles

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The lifestyle of extinct tetrapods is often difficult to assess without clear adaptations such as swimming paddles. For example, the external anatomy of salamanders gives no data about their lifestyle. According to the Wolff 's law, the trabecular bone architecture follows the principal stress trajectories generated from external loads. Theoretically, a terrestrial tetrapod will show a marked main trabecular orientation, while an aquatic tetrapod will show a trabecular orientation more isotropic. The Wolff 's law has been extensively studied in mammals and birds, but rarely in reptiles and amphibians. These animals with transverse posture like that of first tetrapods have various lifestyles (aquatic, amphibious, generalist terrestrial, fossorial and climber).

We sampled 10 squamates, 8 turtles and 2 crocodilians. Their humeri have been scanned on the technical platform of tomographic imaging RX of the Muséum national d'Histoire naturelle. We selected spherical volumes of interest (VOI) centered in the proximal metaphyses. We analyzed many trabecular parameters: spacing (Tb.Sp), thickness (Tb.Th), number (Tb.N), degree of anisotropy (DA), average branch length (Av.Br.Len), bone volume density (BV/TV), bone surface density (BS/TV) and connectivity density (Conn.D).

Length, spacing and thickness show a positive allometric scaling in squamates ( $R^2$ =0.95; 0.76; 0.78 respectively) and turtles ( $R^2$ =0.73; 0.64; 0.86 respectively). A negative allometric scaling is shown for the connectivity in squamates ( $R^2$ =0.74) and turtles ( $R^2$ =0.81). The anisotropy show a gradient in Turtles: the highest in aquatics, intermediate in amphibious and the lowest in *Geochelone*. It is unclear in the squamates anisotropy (because there are few trabeculae in the small specimens), but the amphibious *Amblyrhynchus* show a value higher (0.84) than the terrestrial *Varanus* (0.70 and 0.63). The bone volume density show a significant phylogenetic signal within reptiles (Blomberg's K: 1.058), with the lowest average value in squamates (0.22) and higher in other reptiles (0.39).

These allometric scalings, previous emphasized in mammals and birds, can be expanded for the other amniotes. The degree of anisotropy seems to be an interesting clue to find ecologies. Several explanations about the phylogenetic signal of the bone volume density are proposed. To conclude, this study will help to determine uncertain ecologies of many fossils.

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#### Exercise, growth and histology in the developing hind limb bones of ducks – a case study

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Within physiological regimes, exercise is known to induce bone deposition and remodeling, in line with the general interpretation of 'Wolff's law' on the adaptive functional responses of bone to mechanical loading. However, 'Wolff 's law' has lately become an intricate concept that tries to grasp and unfold a more complex relationship, including the changing responsiveness of bone tissue to exercise through ontogeny. Exercise-induced changes in growing bone tissues are also influenced by trade-offs between growth and function. Most studies on this subject used mammalian models, while birds, the only living representatives of dinosaurs with a variety of ontogenetic locomotor strategies on the altricial - precocial developmental spectrum, have scarcely been investigated in this respect. With the aim to explore how exercise affects the growing avian bone tissue and what this could tell us about locomotor development in fossils, we studied the histology of the femur (Fe), tibiotarsus (Ti) and tarsometatarsus (Tmt) at 4, 8, 30 and 50 days posthatching age (d) in three ontogenetic series of Rouen ducks (Anas platyrhynchos) bred for a previous locomotor experimental study. In the latter experiment, ducks were raised in three groups with different exercise setup: 1) control (C) (free walking, no swimming); 2) swimmer (S) (free walking & swimming + forced swimming 10x10 min/day) and 3) walker (W) (free walking + forced walking 10x10 min/day, no swimming). We found tendentious osteohistological differences among the groups in cortical dimensions, resorption and remodeling, while trends in vascular architecture and osteonal development were less obvious. Relative cortex thickness was consistently the lowest in W and highest in S, although at 50d thickness ratios converge on very similar values irrespective of bone or group identity. The amount of posthatching periosteal growth measurable only at 4d and 8d was always the lowest in W. Corticomedullary border was the most distinct with the least perimedullar resorption bays in W. No remodeling was observed up to 8d; however, compacted coarse cancellous bone and secondary osteons are already abundant in Ti and Tmt at 30d, and are more prevalent in both exercised groups than in C. Finally, at 30d-50d primary vasculature in Fe is locally more laminar in C, longitudinal in S, and reticular in W. Pioneering in extant bird bone histology, these findings also aid locomotion-related paleohistological interpretations.



<sup>&</sup>lt;sup>°</sup> Speaker

## Sclerochronology of dental and dermal skeletal organ systems in deep-time

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Dental developmental patterns and processes are mainly studied in mice as modern model organisms. Deep-time analyses of dental development in early vertebrates are rare and mainly inferred from gross morphology of multiple specimens interpreted as successive stages or through traces of growth stages seen in skeletal histology of individuals.

The application of synchrotron radiation X-ray tomographic microscopy (SRXTM) allows the visualization of histological patterns in great detail. Lines of arrested growth, remodeling and resorption are visible in virtual sections and can be traced manually or semi-automatically to reconstruct surfaces. Application of SRXTM to extant taxa including mineralized and soft-tissues allows an interpretation of the developmental process. The reconstruction of traces in one fossil results in growth models reflecting the morphology of developmental stages, however the development of their mineralization cannot be reconstructed in detail.

We show models of dental and dermal systems and discuss possibilities to study growth patterns and changes of morphology during growth. Growth vectors can be traced and compared in dental systems of early gnathostomes like placoderms, basal chondrichthyans, basal osteichthyans and extant forms. Growth patterns in the dermal skeleton of early gnathostomes can be traced and compared. Degrees of tooth resorption and bone remodeling can be determined and tested in congruence with the phylogeny.

Future research will include semi-automated segmenting and growth pattern reconstruction. Quantitative studies will be enabled including recent and fossil taxa comparing growth patterns and inferring developmental processes.



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Speaker

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## Could Archaeopteryx fly actively? New insights based on long-bone cross-section geometry

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Where did avian flight originate? What was the first form of dinosaurian flight? How did it evolve? These questions remain debated, with new fossil discoveries frequently reviving the discussion. We accessed the inner structure of wing bones of the iconic feathered dinosaur *Archaeopteryx*, using state-of-the-art imaging methods, to resolve its flight mode. *Archaeopteryx* is a Jurassic (150 million-year-old) fossil that combines dinosaurian and avian anatomical features. It inhabited a tropical archipelago in the lagoon of Solnhofen, preserved in the present-day Southern Germany. Numerous hypotheses on its flying abilities have been proposed, with many depicting *Archaeopteryx* as a passive glider, gliding down from trees. However, no direct evidence was provided so far.

As limb bones develop and evolve in response to biomechanical stresses, we decided to investigate the midshaft cross-section geometry of the wing bones in 3 *Archaeopteryx* specimens and 32 additional archosaurian species exhibiting a large range of locomotory patterns, among which crown birds, *Compsognathus*, dromaeosaurs, pterosaurs and crocodiles. We used a non-invasive method to image the inner bone structure of these samples and obtained detailed scans of the long bones using phase-contrast synchrotron microtomography at the European Synchrotron Radiation Facility (France). Multivariate analyses, including data sourced from literature, were applied on the following parameters to resolve *Archaeopteryx'* flying abilities.

The dense **vascularity** – measured as the number of canals per mm2 of cortical bone – in the long bones of *Archaeopteryx* strongly resembles that of crown birds. This suggests substantial metabolic performance in *Archaeopteryx*. The *relative cortical thickness* – i.e. the cortical bone area divided by the total area of the bone cross-section – discriminates volant from non- volant archosaurs, thereby identifying *Archaeopteryx* as a flying dinosaur. The *mass normalized torsional resistance* – expressed as the polar moment of area relatively to the mass of the animal –, when combined with the relative cortical thickness, clusters taxa based on their locomotory modes. All studied specimens of *Archaeopteryx* plot closest to the short-flying birds such as pheasants. *Archaeopteryx* could thus be considered as an active flyer.

Our study demonstrates that active dinosaurian flight originated at least 150 million years ago, earlier than previously thought.

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\* Speaker



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#### Spatial variability and scaling of osteocyte lacunae: a new protocol based on 3D microtomography in teleost fishes

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Osteocytes are involved in multiple aspects of bone physiology, notably growth, resorption, remodeling and homeostasis. It has been proposed that these functions are reflected in their morphology, size, distribution and abundance. Osteocytes could then potentially be used as a useful proxy to infer various metabolic parameters and life history traits, for example in fossil vertebrates in which only the cavities they leave in bone (osteocyte lacunae) are preserved.

To explore variability of osteocyte lacunae and whether they scale with life history traits, metabolism and genome size, we constituted a 3D histological dataset of more than 80 fossil and recent actinopterygians with microtomographical data obtained at the European Synchrotron Radiation Facility (ESRF).

This approach provides several advantages: (1) 3D data show osteocyte lacunae volume, shape, orientation and abundance with a much higher confidence than "classical" histological 2D thin sections; (2) the synchrotron beam achieves the sub-micron resolution ( $^{\circ}0.7\mu$ m) and- enhanced phase-contrast necessary to accurately reconstruct osteocyte lacunae in 3D; (3) microtomography allows minimally to non-destructive sampling of the specimens, unlike histological thin sections.

We established a standardised protocol to accurately segment and reconstruct osteocyte lacunae and other histological features in 3D in the software *VGStudioMAX*. The module "Porosity/Inclusion Analysis" is used to automatically measure the volumes of all segmented osteocyte lacunae. This allows efficient calculation of the median volume of the osteocyte lacunae and visualisation of its variation within a given bone.

As an example, we present results obtained on the carp, *Cyprinus carpio*. Nine bones have been chosen from a single adult individual, including dermal and endochondral bones. Similar to what has been observed in other taxa, median osteocyte lacunae volume is significantly different from one bone to another. Within a given bone, osteocytes vary in size and shape as well. For example osteocytes are generally smaller and more regular in shape in cortical bone than in secondary bone close to vascular canals and muscle insertions. Within a zone of cyclical growth, osteocytes are larger and more irregular close to lines of arrested growth. This reinforces the hypothesis that osteocytes are bigger in areas of increased metabolic activity and/or quicker growth.

Thanks to this dataset focusing on osteocyte variability in 3D and on an unprecedented phylogenetic scale, we expect to increase our understanding of their role in bone growth and maintenance, especially in the understudied teleost model.

\* Speaker

S41 // Oral

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# Osteohistology sheds light on the origin of high growth rates in Iguanodontia

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Iguanodontia are a group of herbivorous dinosaurs, of which Iguanodon bernissartensis from the Early Cretaceous of Belgium, Germany and the United Kingdom is probably one of the most iconic members. Iguanodontia have their origin in the Middle Jurassic, and flourish from the Early Cretaceous onwards. Many iguanodontians evolved high growth rates and very large body sizes, most notably hadrosaurs, but due to lacking samples in the phylogeny, it remained unclear when this precisely happened. We collected samples from a wide range of Early and Late Cretaceous iguanodontians, including hadrosaurs, to better understand this process. Our hadrosaur samples were taken from typical bonebed assemblies from Far Eastern Russia and Mongolia. Bone histology of Olorotitan, Amurosaurus and Saurolophus shows highly vascularized cortical bone, consisting mainly of a woven-parallel fibered complex with plexiform to laminar vascularization, indicative of high growth rates. Olorotitan and Amurosaurus show very few lines of arrested growth (LAG) even in the biggest specimens (femur length ~1 m). It remains unclear if this indicates an uninterrupted juvenile growth phase, or if mass increase was extremely high in the first years, but the high average growth rate is in accordance with high growth rates reported for North American hadrosaurs (e.g. Maiasaura, Hypacrosaurus). Long bones of the iguanodontids Iguanodon bernissartensis and Mantellisaurus generally show a fast growing woven-parallel fibered complex with numerous longitudinal to circumferential primary osteons arranged in a laminar to plexiform pattern. We also found a variable number of growth marks in specimens of similar size and histologic maturity. These marks occur as vascularization shifts, annuli, and/or lines of arrested growth (e.g. 3 to 4 in the ribs of large specimen RBINS I52, and up to 7 in femur WMN P61446 (80/436) from Nehden). The abundance of erosion rooms is less pronounced than in hadrosaurs, but Iguanodon bernissartensis definitely grew faster than Tenontosaurus, at rates more like those of hadrosaurs. This suggests that iguanodontians evolved high growth rates at least during the Early Cretaceous, an event that may be correlated with the diversification of the angiosperms.



Speaker

# Three-dimensional virtual histology of the osteostracan *Dartmuthia* revealed by synchrotron radiation microtomography

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Osteostracans are generally considered the sister group of jawed vertebrates and are therefore important for understanding the evolution of gnathostomes from a jawless ancestor. Thyestiida is a morphologically diverse group of osteostracans, and display the widest geographical and temporal range. Previous studies have demonstrated the importance of three-dimensional (3D) virtual modeling to understand the detailed histology of the thyestiids Tremataspis and Oeselaspis. However, their disparate histological structure make it difficult to infer primary homology between their canal systems, and how such different organizations of dermal skeleton can be found in closely related taxa. In this study, dermal elements of the seemingly histologically intermediate Dartmuthia have been modeled in 3D. These elements have a sculpture composed of tubercles and ridges with a similar composition as the entire surface cover in Tremataspis, while the areas in between are more similar to the majority of the outer layer in Oeselaspis. However, the intermediate areas also have canals divided by a septum similar to those seen in Tremataspis, albeit of a more limited extent. This study forms part of a larger investigation where synchrotron data from a range of thyestiid osteostracans will be investigated with the goal of understanding differences in 3D histology within the group and the functions of the canal system. This may also help elucidate thyestiid intrarelationships, as well as forming the basis for similar investigations of other osteostracans and subsequently how they compare to other early vertebrate groups.



Speaker

#### Cells in another dimension – characterizing putative early jawed vertebrate dentine cell spaces in 3D

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Skeletal histology and the definition of mineralized tissue types is traditionally based on studies of thin and polished sections. This allows the characterization of composition, crystal structure and cell spaces in highest resolution. However, the projection of three-dimensional structures in two dimensions is sensitive to the direction of the cutting plane. The application of high-resolution synchrotron radiation X-ray tomographic microscopy (SRXTM) overcomes this problem permits the visualization of the topographic interrelationships of the tissues and their structures.

Here we present preliminary data characterizing dentine cell types in 3D, with a test of the described cell types in the putative gnathostome *Skiichthys halsteadi* from the Ordovician Harding Sandstone of Colorado. Qualitative analysis characterizing the hard tissue histology of this taxon illustrates a network of unipolar cells arranged in layers of dentine connected by cell processes and canaliculi. A gradient in X-ray density characterizes each dentine layer.

Preliminary comparison with acanthodian mesodentine and acanthothoracid placoderm semidentine, also visualized in 3D, results in the categorization of *Skiichthys* dentine as semidentine and may suggest a phylogenetic assignment to the placoderms. A hypermineralized layer of enameloid caps *Skiichthys* tubercles with a characteristic enameloid-dentine junction and a notable change of X-ray density.

The application of synchrotron tomography and visualization of dentine cell types in 3D enhances our knowledge and understanding of tissue types. Future quantitative research will allow an interpretation of the growth and function of cell networks.



41 // Poster

<sup>&</sup>lt;sup>•</sup> Speaker

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### Dental growth of Middle and Late Pleistocene equids from Germany: first insights from enamel histology

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Dental growth and development is recorded, among others, in enamel tissue. It is rhythmically deposited by enamel-forming cells (i.e. ameloblasts) following a circadian periodicity, which leads to the formation of daily incremental markings. These histological features have been widely used to infer rates and timings of tooth formation in fossil taxa. In mammals, dental development and key life history events, such as weaning or age at maturity, are tightly linked. Therefore, enamel formation time is considered a good proxy of overall life history. Other enamel growth variables, like the rate of enamel extension, are intimately related to the pace of life too. Despite enamel being crucial for reconstructing the life history of past organisms, most histological research has focused on brachydont teeth, while hypsodont species still remain poorly studied. Among high-crowned mammals, equids are of special interest due to their characteristic evolution. During the Pleistocene of Europe, for instance, Equus species progressively decreased in size. This size shift has traditionally been related to climatic and resources variations because of the close relationship between body size and environment. Body size, however, is also an important life history trait that co-varies with other biological traits. Nevertheless, body size changes of European Pleistocene equids have been little analyzed under a life history framework. Here, we study enamel histology on first lower molars of different Equus species from the Middle and Late Pleistocene of Germany (E. altidens, E. suessenbornensis, E. steinheimensis and E. germanicus), with the aim to shed light on the life history changes that might have accompanied body size modifications of these European extinct equids. Fossil material was recovered from classical German paleontological sites (e.g. Steinheim an der Murr, Süssenborn) and is currently housed at the Staatliches Museum für Naturkunde (Stuttgart, Germany). Histological sections were prepared from each tooth for microscopical examination under polarized light. Daily and supra-daily (Retzius lines) incremental markings were identified in all samples, allowing calculation of different enamel growth parameters (e.g. daily secretion rate, enamel extension rate), and reconstruction of rate and time of tooth formation. The results obtained have provided valuable information about the pace of life and the dental development of these fossil European equids.



Speaker

#### Can we infer the posture of fossil taxa based on the 3D pattern of their long-bone epiphyseal vascularisation?

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The development and histology of long-bones and their epiphyses are key factors for understanding the evolution of tetrapod locomotion. In mammals, the epiphyses ossify through ontogeny to form a Secondary Ossification Centre (SOC). Although SOCs play a major role in the development and mobility of the skeleton, the underlying developmental processes for this ossification remain poorly understood. To fill in this lack of knowledge, we investigated a variety of humeri from extant mammals, including an ontogenetic sequence of the armadillo (*Dasypus*), in addition to fossil outgroups, using propagation phase-contrast synchrotron microtomography at the European Synchrotron Radiation Facility (Grenoble, France).

Through the ontogenetic sequence of *Dasypus*, we show that epiphyseal canals invade the cartilage cap and form clusters at the location of the future SOCs prior to ossification. Moreover, both proximally and distally, the main articulations, respectively the humeral head and trochlea, develop before the tubercles and epicondyles. When present, major canals piercing the growth plate are in association with the humeral head, such as in the subadult *Dasypus*, hedgehog (*Erinaceus*) and echidna (*Tachyglossus*), as well as with the distal articulation in the latter taxon. Based on aforementioned data, a correlation between vascular organisation and the long-bone articulation is thus apparent.

The humeri of the stem amniote *Seymouria* and the stem mammal *Galesaurus* share a similar tetrahedral or "hourglass-like" morphology, and both lack SOCs. This similarity in overall morphology could be interpreted as a similarity in locomotion. However, in contrast to *Seymouria, Galesaurus* does possess numerous canals extending up to both the proximal and distal metaphysis. These canals pierce the respective metaphyseal surface centrally in a slight depression bordered by two prominent tuberosities. If the vascularisation to articulation relationship in extant mammals can be used as a proxy, one could infer the position of the articulations in the forelimb of the stem mammal *Galesaurus*, highlighting that its posture was already more alike crown mammals than the sprawling posture characteristic of stem amniotes.



<sup>&</sup>lt;sup>\*</sup> Speaker

# S42 - "Early" vertebrates: from fossils to genome

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Allison Bronson <i>et al.</i> // Well-preserved symmoriiform cartilage from the Late Mississippian Fayetteville Shale of Arkansas, USA
Alessio Capobianco <i>et al.</i> // Phylogenetic affinities of marine osteoglossomorphs and the role of marine dispersal in osteoglossomorph biogeography
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### Homology and morphofunctional significance of accessory hyoid-arch elements of actinopterygians: new data from µCT on fossil and recent forms

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The homology of the skeletal elements intercalated between the hyomandibula and the ceratohyal(s) of osteichthyans, and actinopterygians in particular, has been a matter of scientific debate for over half a century. Previous studies on extant ray-fins have resulted in a morphological framework for the distribution and arrangement of such accessory hyoid-arch elements (symplecitc, interhyal) across different lineages. However, the condition in early actinopterygians remained largely speculative, due to the delicate nature of these ossifications, and/or limitations of traditionally employed analogue techniques for extracting relevant information from fossils. Past studies have established the presence of a symplectic, and its involvement in the formation of a double lower jaw joint, as key synapomorphies of neopterygians and halecomorphs respectively. Earlier, albeit weak, evidence for a more stemward origin of the actinopterygian symplectic, and its potential homology with that of other bony fishes (e.g., coelacanths) has been dismissed on the basis of poor preservation, or misidentifications of such structures in fossils. In order to reappraise the distribution and morphofunctional significance of these accessory hyoid elements across ray-fins, we performed micro computed tomographic ( $\mu$ CT) investigations on fossil and recent examples. Our data from Permian-Triassic taxa indicate that an independent symplectic and a double jaw joint evolved lower in the actinopterygian tree of life than previously thought. Moreover, the discovery of a neopterygian-like arrangement between the symplectic and interhyal in early crown actinopterygians suggests that the highly kinetic endochondral portion of the feeding apparatus of neopterygians is more generalized than previously hypothesized. We establish new morphological and topological criteria for distinguishing between symplectic and interhyal in fossil actinopterygians. Finally, our novel anatomical observations, combined with developmental data from the literature, allow for a critical view on the arrangement and homology of accessory hyoid elements of extant non-neopterygian actinopterygians.

<sup>°</sup> Speaker

42 // Oral

#### Well-preserved symmoriiform cartilage from the Late Mississippian Fayetteville Shale of Arkansas, USA

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Paleobotanists, invertebrate paleontologists, and oil geologists have studied the Fayetteville Shale for many decades, but the vertebrate fauna of the formation has only recently been addressed. This black shale yields a diversity of fishes, including acanthodians, sarcopterygians, and chondrichthyans, represented by teeth, denticles, and skeletal elements including fins, crania, and branchial arches. Many of the cartilaginous fishes are in excellent condition, and often three- dimensionally preserved, due to the formation's depositional environment. In particular, several chondrichthyan fossils with unique character combinations have added to our understanding of shark evolution. One of these chondrichthyans, a symmoriiform represented by two specimens, has an operculate structure somewhat similar to that of holocephalans. This fossil also preserves a complete lower dentition, with small teeth and denticles present between tooth families. This particular operculate symmoriiform has a mosaic of chondrichthyan features, potentially useful for understanding the relationship between elasmobranchs and holocephalans.

Speaker

### Phylogenetic affinities of marine osteoglossomorphs and the role of marine dispersal in osteoglossomorph biogeography

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Osteoglossomorphs are among the earliest diverging branches of modern teleost fishes. Living members are restricted to freshwater environments and distributed across most continents, making them especially interesting for historical biogeography. Whether the modern distribution of osteoglossomorphs has been primarily shaped by the breakup of Gondwana or by more recent dispersal between continents is still an open question. The relatively rich osteoglossomorph fossil record expands the geographic distribution of the group to Europe and Northeastern Asia, and more surprisingly reveals numerous marine forms restricted to the early Paleogene. Despite the likely relevance of the osteoglossomorph fossil record for inferring the evolutionary and biogeographic history of the group, many key taxa (including most marine species) are poorly studied and excluded from phylogenetic analyses. Thus, the evolutionary history of osteoglossomorphs remains still largely unknown.

Here, we discuss new osteological data revealed by micro-computed tomography ( $\mu$ CT) of 3Dpreserved osteoglossomorph fossils, which allow for detailed reconstruction of cranial regions– such as branchial skeleton and basicranium–that are highly diagnostic but usually difficult to observe in fossils. Through comparative analysis with extant osteoglossomorphs, we highlight phylogenetically informative characters that could help to resolve uncertain areas of the osteoglossomorph tree.

Specifically,  $\mu$ CT scanning of the skull of a new marine osteoglossid (Osteoglossomorpha; Osteoglossidae) from the early Eocene (Ypresian) of Mali suggests a possible affinity with Arapaiminae, a sub-clade inhabiting freshwaters of Africa and South America. Features that link the new marine species to arapaimines include the absence of an ossified basihyal toothplate, the presence of ossified Baudelot's ligaments and the extreme anterior expansion of the first parapophysis.  $\mu$ CT analysis of *Brychaetus muelleri*, a well-known marine osteoglossid from the Ypresian London Clay Formation of England, revealed the presence of some of these features, but failed to identify others. The potential close relationship of at least some marine osteoglossids to arapaimines bears significant implications for biogeographical reconstructions, as it would suggest a key role of marine dispersal–followed by freshwater invasion–in shaping the current geographic distribution of the group.



<sup>&</sup>lt;sup>°</sup> Speaker

#### The first functional analysis of the lateral line system in fossil fish

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The lateral line is a mechanosensory system used by fish for predator evasion, prey detection, shoaling and navigating their environment. Fish display an extremely diverse range of lateral line morphologies ranging from simple grooves on the surface of the body to elaborate and complex ramifying tubes enclosed in dermal tissue and bone. Recent work has demonstrated that the degree of complexity of ramifying lateral line tubes may behave as a signal filter, the effects of which are dependent on the dimensions of the canal system. Here we employ a simple fluid mechanics model using Hagen-Poiseuille flow to calculate the mean flow and pressure inside a fossilised lateral line canal that, in turn, stimulates the canal neuromasts - the functional hair-like cells in the lateral line. We calculate solutions for the Devonian lungfish Dipterus valenciennesi and compare it with that of the extant Australian lungfish Neoceratodus forsteri. The former has a complex lateral line canal network while the latter has a simple canal system. The solutions describe an increase in bilateral flow in the lateral line canal of the extant lungfish compared to the Devonian lungfish Dipterus indicating a greater stimulus to the canal neuromasts in Neoceratodus. We interpret this to represent a change in behaviour from the Devonian lungfish, a highly active animal with a low sensitvity system to avoid overstimulation, to a more sedentary lifestyle in the extant Australian lungfish, the latter requiring a more sensitive lateral line system to compensate for a less active hunting strategy. The flow regime of a simple lateral line canal system from an entirely separate fish group, represented by the placoderm Shearsbyaspis is also analysed to test if a simple lateral line canal morphology evokes the same functional response as seen in Neoceratodus. The technique offers great potential for investigating the diversity of sensory function of fish lineages in different environments and how sensory systems diversify and change during key evolutionary events.

Speaker

#### Acanthodian diversity in Strud (Devonian, Famennian, Belgium)

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More than 50 specimens of acanthodians have been collected in Strud locality (Belgium), famous for tetrapodomorph found in Upper Devonian levels. Acanthodian remains consists mainly of tiny *Devononchus* spines (Diplacanthidae). Their size added to paleo-histological arguments suggest they may owing to juvenile specimens. A part of a squamation and a posterior part of a body were also found. A high proportion of acanthodians in regard with other vertebrates is considered as a proximal environment index. A peak of diversity in vertebrates is recurrent in levels dated from *postera- expansa* zones in Ardenne before the D/C boundary.

Speaker

#### Drawing back the veil: diverse internal cranial structure in Carboniferous-Permian fossils and its bearing on the earliest actinopterygian radiation

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During the more than 100 million years of the Carboniferous and Permian, actinopterygians became major contributors to aquatic vertebrate faunas and made conspicuous anatomical innovations in gross body and skull shape. Most paleontological assessments and all molecular studies also point to the origin of one or more major actinopterygian crown radiations during this interval. However, the late Paleozoic fossil record of ray-finned fishes remains one of the most poorly known episodes of vertebrate history. Heavily compressed specimens dominate the study of Permo-Carboniferous actinopterygians, but such fossils severely limit the kinds of information that can be passed on to downstream functional and systematic analyses. Despite the ubiquity of compression fossils, several Carboniferous and Permian localities do yield understudied, three-dimensional remains. As part of an effort to better constrain patterns of early actinopterygian evolution, we have examined a wide variety of Permo-Carboniferous fishes using micro-computed tomography scanning (mCT), with an emphasis poorly known but functionally and phylogenetically significant components of cranial anatomy: neurocranium, suspensorium, and hyoid and gill arches. This work reveals surprising levels of internal anatomical diversity that might not be predicted from examination of relatively conservative external structure. mCT reveals clues about the evolution new feeding ecologies in the early Carboniferous, including dental plates and palatal bites reminiscent of lungfishes and tongue-bite mechanisms of the kind generally associated with some teleost groups. Exceptional preservation of soft tissues in late Carboniferous fossils provide clues about the evolution of neural anatomy in early ray-finned fishes, and question the widely held assumption of a close correspondence between brain and endocast anatomy in the group. Finally, early Permian fossils show derived features of the hyoid arch and jaw articulation typically associated with neopterygian subgroups, but otherwise seem to be distantly related to those Mesozoic clades. Collectively, these results point to the considerable untapped potential of internal cranial structure to deliver new information bearing on the initial radiation of actinopterygians, foreshadowing the group's remarkable success during its subsequent evolutionary history.



#### Endoskeletal anatomy of platysomids supports a Carboniferous origin for Chondrostei

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Chondrostei is one of the four major actinopterygian groups, with around 25 extant species. Molecular divergence estimates indicate that chondrosteans diverged from other ray-finned fishes in the Carboniferous, a time period in which actinopterygian fossils are known in abundance. Despite this extensive record, a conspicuous gap remains on the chondrostean stem. Although saurichthyids have traditionally been afiiliated with the group, recent analyses posit a stem neopterygian affinity. As such, the oldest recognised fossil chondrosteans are Early Jurassic (~195 Ma) in age, some 135 million years after the predicted origin of the group, and already display profound anatomical specialisations. Playtsomids have recently been suggested as branching from the chondrostean stem, albeit with limited support. Despite the abundance of platysomids in the fossil record (~15 species known from worldwide deposits), most are known only from two dimensional and largely postcranial remains, with the head skeleton either disarticulated or badly crushed. Here, we use CT scanning to investigate the internal anatomy of a threedimensionally platysomid cranium preserving the braincase, hyoid arch, gill skeleton, palate and shoulder girdle. The elongate parasphenoid is held almost vertically, articulating with a narrow median vomer anteriorly and bearing a bifurcate posterior stalk. The triangular maxilla is underlain by a fenestrate Ishaped palate, which is mobile with respect to the braincase and cheek. The gill skeleton supports a large basihyal toothplate, contributing to a tongue bite. CT scanning of Chondrosteus, an unequivocal chondrostean, reveals a previously misidentified beak-like maxilla, reminiscent of that seen in platysomids. Phylogenetic analyses uphold a chondrostean affinity for platysomids, as well as providing support for a close relationship between bobosatraniids and the broader chondrostean group. Our results extend the chondrostean fossil record back ~130 million years, highlighting unexpected morphological diversity at the roots of Chondrostei, with downstream effects helping to refine palaeontological timescales relating to the origin and divergence of the living actinopterygian radiations.



Speaker

#### The rise of crown features in stem gnathostomes

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Recent advances in the early evolution of jawed vertebrates have reached a general consensus that three of the four major gnathostome groups form the crown gnathostome clade including ourselves. Still, a large gap is present between the crown and stem gnathostome, now including the placoderms that were dominant jawed vertebrates in the Devonian 'age of fishes', and the jawless "ostracoderms" that are more closely related to jawed vertebrates than living jawless fishes. This gap, often in the form of dubious homology between structures and especially those belongs to the dermal skeleton, significantly hampers the effort of tracing the origin of crown gnathostomes. The discovery of the so called "maxillate placoderms" from the Silurian of China partly fills the gap by demonstrate that characters such as the marginal jaw bones, previous found only in bony fishes, have deeper origin in the gnathostome stem. But the phylogenetic position of the maxillate placoderms, and its relationship to other placoderm groups is not firmly established, largely due to a lack of endoskeletal information. Here, we exploit the state-of-the- art technologies in computed tomography, three dimensional reconstruction and 3D printouts to investigate several Silurian-Devonian placoderms, based on the rich and unique Silurian and Early Devonian fossil collection from South China and Australia, with an emphasis on the largely untapped but character-rich endoskeleton and the endocast data. The new data, based on the comparison of character status in undisputedly homologous structures across jawless stem, jawed stem and crown jawed vertebrates, shows unexpected character status in olfactory tracts, inner ears, endolymphatic system in the investigated taxa that are previously considered as crown features. The deeper origin of these conditions further fills in the gap between the stem and crown gnathostomes. The result reveals a larger diversity of endoskeletal morphology in the "placoderm" assemblage that were covered by similar pattern of dermal skull roofs. The alternative interpretation of the origin of crown gnathostomes and corresponding character acquisition sequences may help to recover the long-lost chapters in this section of vertebrate evolution.



Speaker

## Squamation and dilemma of the Devonian asterolepid antiarchs: better swimming abilities or finer protection

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The squamation was known in a few representatives of Asterolepiformes, including *Pterichthy-odes milleri*, *Asterolepis ornata*, and *Remigolepis walkeri*. Study of a new material allows description of the squamation of *Byssacanthus dilatatus*, *Asterolepis* cf. *dellei* and *A. radiata*. Morphotypes of scales and five zones of squamation were established for *A. ornata* based on the studies of both juvenile and adult specimens from the Lode clay pit.

Byssacanthus and Pterichthyodes have thin rhomboid scales with rounded anterior margin and strongly vascularized middle layer composed of cancellous bone. Ornamentation consists of a network of tiny sinuous ridges and elongated tubercles in Byssacanthus scales; of long median crest and rounded tubercles in Pterichthyodes scales. The overlapping areas in the Byssacanthus scales are wide but in Pterichthyodes scales these are narrow. The scales in Byssacanthus squamation vary from the isometric in the anterior part to the longitudinally elongated with pointed anterior margin in the caudal fin. Relatively short and high trunk armour of Byssacanthus and Pterichthyodes consisting of thin dermal plates was accompanied with a quite short tail. Morphology of scales most probably shows adaptation to reduce turbulence during swimming.

All species of *Asterolepis* with known squamation demonstrate two morphological types of relatively thick scales from five zones of the tail. Flank scales of *A*. cf. *dellei* and of *A*. *radiata* show overall similarity to, but are smaller than those of *A*. *ornata;* scales of *A*. *radiata* differ in the more pronounced ornamentation of ridges and tubercles on the scales from proximal part of squamation, and more smooth scales from the area below the dorsal fin. Fulcral scales of *A*. cf. *dellei* are much higher and elongated in comparison with scales of *A*. *ornata*. Overall morphology of a relatively long, but more flat trunk shield, consisting of thick plates with highly vascularized cancellous bone layer, and of a long tail with thick scales, containing massive basal and superficial layers, but very thin cancellous bone layer may correspond to the adaptation of *Asterolepis* for better protection against predators rather than for better swimming abilities.



Speaker

### The endoskeletal development of pectoral and pelvic fins of the coelacanth *Latimeria*: an extant model for paleontological interpretations

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Among vertebrates, the sarcopterygians represent a clade characterized by a mono-basal articulation of the fins or limbs to the girdles. This group is subdivided into three extant clades: tetrapods, lungfishes and coelacanths. The latter appeared during the Early Devonian and was thought to have disappeared by the end of the Cretaceous. However, two extant coelacanth species are known so far: *Latimeria chalumnae*, discovered in 1938 in the Mozambique Channel and *L.menadoensis*, discovered in 1995 off Indonesia.

The coelacanth clade is well known in the fossil record with more than 40 genus with worldwide occurrences. However, the inner structure of the paired fins is poorly known with only two recored fossil species with preservation of fin endoskeletal elements (*Laugia* from the Triassic of Greenland, *Shoshonia* from the Devonian of US). Coelacanths are the nearest living marine relatives of tetrapods. Indeed, the proximal endoskeletal elements of their paired fins and of tetrapod limbs are considered as homologous.

The first step of this research project aims to describe the ontogenetic development of pectoral and pelvic fins of *Latimeria chalumnae*. This study is based on tomographic data (CTscan, Synchrotron, MRI) of a unique ontogenetic series with five different stages. The anatomical description of the endoskeletal elements of fins during the development will be completed by dissection of paired fins of adult specimens. Preliminary results show different allometric growth ratios and ossification rates in the formation of the pectoral and pelvic fins. Comparisons between the developments of proximal endoskeletal elements of paired fins of non-tetrapod sarcopterygians and of limbs of first tetrapods will contribute to a better understanding of the evolutionary steps of the terrestrialisation in vertebrates.



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# Yes, we can homologize skull (and other) bones of actinopterygians and tetrapods

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It is difficult to tease apart the homologies of bones across Osteichthyes, often even within Actinopterygii. For a long time, it seems, anatomists stopped trying; numerous separate (sometimes contradictory) nomenclatures were used in different decades for different taxa or by different authors. However, numerous recent discoveries provide grounds for optimism.

The tetrapod stem is much more densely sampled than 25 years ago, confirming unambiguously that the large bones of the actinopterygian skull table – which lie in roughly the same places as the frontal and parietal of crown-group tetrapods – are homologous to the parietal and postparietal. This affects the next more lateral series as well: as recently proposed, the "dermosphenotic"/"infraorbital 5" is the intertemporal (which participates in the orbit margin in a few early tetrapods), the "dermopterotic"/"intertemporal" is the supratemporal and the "supratemporal" is the tabular.

Further, the base of the tetrapod stem clarifies the original spatial relationships of other bones: the bone dorsal of the (anterior) naris is plesiomorphically not the nasal, but the so-called anterior tectal, and the one ventral to it is the so-called lateral rostral (apparently the septomaxilla of crown-group tetrapods), making it likely that these are the homologs of the actinopterygian "nasal" and "antorbital" respectively. Unlike in tetrapods, the squamosal of many other sarcopterygians has a long contact with the maxilla and could be homologous to the (second) "supramaxilla".

Outside the tetrapod stem, the placoderm-grade animal *Entelognathus* has shown that some homologies can be traced beyond Osteichthyes; I further propose that the unpaired "vomer" of various actinopterygians is the "prerostral plate" seen in "placoderms" and the Silurian osteichthyan *Guiyu*, the actual paired vomers being represented by the "vomerine toothplates".

The braincase remains underresearched even within crown-group tetrapods, and neomorphic bones seem more common there than in the dermal skeleton; still, it seems clear that the best candidates for homologs of the opisthotic are the "autopterotic" and/or perhaps the "epiotic"/"epioccipital" of actinopterygians, not the "intercalary" sesamoid.

I propose further homologies throughout the skeleton based on ontogenetic data and the fossil record, and hope to start a discussion on this promising field. Confidently identified homologs would provide a boost for phylogenetics and evolutionary biology.



Speaker

#### A new onychodontid (Osteichthyes; Sarcopterygii) from the Middle Devonian of Morocco

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In 1976, Lehman described new fossil vertebrate remains from the Middle Devonian (Eifelian) outcrops of southern Morocco. Amongst the material, which included 'placoderms', chondrichthyans and 'acanthodians', he identified the presence of onychodontids, a specialized and phylogenetically important group of marine sarcopterygians (lobe-finned fishes), probably closely related to coelacanths. The remains were then redescribed by Aquesbi in 1988 and attributed to a single individual; however, she did not erect a species name for the material. Onychodontids represent one of the earliest diversification stages of the sarcopterygian radiation at the beginning of the Devonian; nevertheless, they are among the least well-understood groups of early osteichthyans (bony fishes). This is due to their cartilaginous, and thus perishable, cranial endoskeleton which causes the skull bones to disarticulate after death. Well-preserved onychodontid fossils from Euramerica (*Strunius* from Germany and *Grossius* from Spain) and Gondwana (*Qingmenodus* from China and specially *Onychodus* from Australia) have started to alleviate the gaps in our knowledge of these elusive fishes. It is thus now possible to adequately compare the Moroccan material with other onychodontids and early osteichthyans.

New preparation of the specimen has revealed features and bones that were not previously known and justifies its attribution to a new genus and species. Dermal skull bones are well preserved and enable a partially complete reconstruction of the snout, cheek and skull roof. They are ornamented with numerous rounded tubercles. New histological data illustrates the presence of enamel covering the crescent-moonshaped odontodes in the scales. Several branchial bones are also exceptionally preserved, adding to our knowledge of early osteichthyan endoskeleton.

Phylogenetic placement supports the onychodontid attribution of the specimen and enables to test evolutionary scenarios among early osteichthyans. This Moroccan new species, representing the first occurrence of onychodontids from Africa, constitute important material from a new Gondwanan locality that furnishes key information not only on onychodontid morphology and interrelationships but also on their paleobiogeographical distribution and Devonian faunal affinities between Euramerica and Gondwana.



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# The power of otoliths in situ for the reconstruction of fossil teleost evolution

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The fossil record of bony fishes (teleosts) consists of two lines of evidence: articulated skeletons and sagittal otoliths. Articulated fish skeletons can yield osteological data comparable to that of extant species and are widely used to illuminate the evolution of certain characters or to resolve phylogenetic relationships. However, preservation of articulated fishes requires particular taphonomic conditions resulting in a highly heterogeneous and gap-filled fossil record. Otoliths are known to be specific for species and genera in the majority of instances and sometimes even for higher systematic units. They have the advantage of being abundant in the fossil record where aragonite, of which they are composed, is preserved and sediments are unconsolidated. This results in a much more continuous record through space and time with often a much richer archive of taxa.

However, both otoliths and fish bones have largely been studied independently from each other. Here, we present three recently described cases of articulated skeletons with otoliths *in situ* and demonstrate how this contributes to a better understanding of the evolution of teleost fishes.

1. Ponto-Caspian gobies from the Sarmatian of the Paratethys elucidate the early developments in this group of highly successful adaptive fishes. The *in situ* finds are also essential for the calibration of abundant isolated otolith finds.

2. Micro-CT scanning results from three dimensional fossil fish skulls from the Late Cretaceous elucidate how modern techniques can contribute to the linking of skeletons and otoliths. Two examples are selected; one shows good congruence with the earlier interpretation of isolated finds while the other demonstrates the importance of calibrations, both for the assessment of isolated otoliths, as well as for the phylogenetic analysis of the entire fossil fish.

3. Otolith finds, partly *in situ* otoliths from the Late Jurassic Talbragar *Lagerstätte* in Australia demonstrate key changes in otolith characteristics in the early teleost history. They also show how otoliths were overlooked, although being very abundant in a Lagerstätte that has been the focus of research for over100 years.

These examples suggest that otoliths *in situ* may be much more common than previously thought.

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# Exceptional basal body preservation in Early Triassic conodont elements from Oman: functional and developmental implications

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Conodonts are a group of extinct, jawless, marine vertebrates that are considered as stemcyclostomes. They are known in the fossil record from Cambrian to Triassic mainly by their apatitic teeth-like feeding structures, called conodont elements. They feeding apparatus include an anterior group of so-called S and M elements, which were used to grasp the food and two posterior pairs of so-called P elements, which were used to process the food.

Conodont elements are mainly composed of two tissues: the crown and the basal body. The basal body is a laminated structure less likely to be preserved than the crown because of its lower mineralization. Thereby, elements with preserved basal body are found only in exceptional cases in the fossil record. To date, no S or M element has ever been documented for post- Devonian conodonts, leading some authors to raise the question of an evolutionary trend towards unmineralized basal bodies in conodonts, which would imply a major developmental shift.

Here we report neospathodid conodont elements from Dienerian (Early Triassic) rocks of Oman with exceptional basal bodies preservation. We demonstrate the presence of basal body within the entire apparatus (including S and M elements) in the genus *Novispathodus*, and most likely in all the gondolelloidea family. This discovery suggests that the apparent absence of basal body in post-Devonian conodonts was presumably due to a preservation bias only. Furthermore, we show that the morphology and extent of the basal body in *Novispathodus* are in agreement with previous predictions of the conodont apparatus feeding motion and do not contradict a cyclostome-like functional model. Based on a review of the occurrences of basal body in the literature, we suggest a general pattern for the morphology of the basal body in conodont elements that may reflect the mechanical constraints associated with these feeding motions.



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# Saws and scissors: Late Paleozoic experimentation with symphyseal dentition in edestoid fish

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Chondrichthyans of Late Paleozoic oceans evolved unique dentitions for catching and eating soft bodied prey. A diverse but poorly preserved clade, edestoids are noted for developing biting teeth at the midline of their jaws. *Helicoprion* has a continuously growing root to accommodate more than 100 crowns that spiraled on top of one another to form a symphyseal whorl supported and laterally braced within the lower jaw. Reconstruction of jaw mechanics shows that individual serrated crowns grasped, sliced, and pulled prey items into the esophagus. A new description and interpretation of *Edestus* provides insight into the anatomy and functional morphology of another specialized edestoid. *Edestus* has opposing curved blades of teeth that are segmented and shed with growth of the animal. Set on a long jaw the lower blade closes with a posterior motion, effectively slicing prey across multiple opposing serrated crowns. *Edestus* and *Helicoprion* provide context for other edestoids that currently lack cranial fossils to contextualize their dental structures. The symphyseal dentition in edestoids is associated with a rigid jaw suspension and may have arisen in response to an increase in pelagic cephalopod prey during the Late Paleozoic.



Speaker

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## The skull of the 'acanthothoracid' placoderm Weejasperaspis gavini, from the Early Devonian (Emsian) limestones of Burrinjuck, NSW

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'Acanthothoraci' is a poorly defined subgroup of 'placoderm' fishes (the monophyly of both is questioned in recent phylogenetic analyses). Acanthothoracids are a basal placoderm subgroup, because of their short dermal shoulder girdle, and their dorsal nasal openings if these are assumed primitive for gnathostomes. Acanthothoracids from Burrinjuck comprise two groups based on ornament: the 'brindabellaspid' type (smooth rounded tubercles), and the 'weejasperaspid' type (elongate crenulated tubercles and ridges). The latter includes two genera (Weejasperaspis White 1978; Murrindalaspis Long 1984), placed in a separate family Weejasperaspidae White 1978. Weejasperaspid ornament sometimes breaks down into stellate tubercles, characteristic for the ornament of Romundina, the best known Northern Hemisphere acanthothoracid. Weejasperaspis and Murrindalaspis were based on isolated dermal shoulder girdle bones, and skull morphology was largely unknown. Here we report a new incomplete skull and endocranium of Weejasperaspis. The parallel-sided skull-roof is deeply embayed posteriorly, with projecting posterior paranuchals, an assumed acanthothoracid character. A similar embayed posterior skull margin in some early osteichthyans (e.g. Meemannia) has posterior projections formed by supratemporals, but these are homologised with the anterior paranuchals based on skull pattern analysis using the Silurian osteichthyan-like 'placoderm' Entelognathus from China. The new Weejasperaspis has paired preorbitals in front of a median post-pineal. The anterior rostral capsule is missing, but the nasal notch in the sclerotic capsule shows the nostrils were more lateral than in Romundina, and could not have been surrounded posteromesially by the rostral plate. The parasphenoid is preserved, with various grooves and foramina on the ventral braincase surface.

The new cranial information of Weejasperaspis will clarify understanding of basal placoderm relationships, and shed light on the phylogeny of early gnathostomes.

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Speaker

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## The youngest marine record of double-armoured herrings: an Eocene paraclupeid fish (Teleostei, Clupeomorpha, Ellimmichthyiformes) from Monte Bolca

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Double-armored herrings of the order Ellimmichthyiformes constitute an extinct clade of clupeomorph fishes with a broad paleogeographic and paleoenvironmental distribution in marine, estuarine and freshwater deposits worldwide. This clade comprises more than 40 species spanning from the Early Cretaceous to the middle Eocene. After the end-Cretaceous mass extinction and until their final extinction, double-armored herrings experienced a drastic drop in their diversity and disparity, with the Paleogene taxa being restricted in the freshwaters of North and South America and China. A new doublearmored herring is documented based on a single partially complete specimen from the early Eocene Pesciara site of the Monte Bolca Konservat-lagerstätte, northeastern Italy. The fossil is characterized by a unique combination of features (ornamentation of the skull bones; medial fusion of the contralateral halves of the neural arches of the abdominal vertebrae; endopterygoid teeth; parhypural fused to the first preural centrum; presence of a short series of six predorsal scutes increasing in size posteriorly; postpelvic scutes bearing very prominent spines) that supports its recognition as a new genus and species of the family Paraclupeidae. The phylogenetic analysis (62 morphological characters coded for 32 taxa) suggests that new paraclupeid taxon from Monte Bolca documented herein is closely related to the Early Cretaceous genus Ellimmichthys. Moreover, it represents the youngest marine occurrence of the family Paraclupeidae and, more generally, of the order Ellimmichthyiformes, suggesting that the shallow marine biotopes of the Tethys might have favoured the persistence of certain fish lineages that were severely affected by the end-Cretaceous mass extinction.



Speaker

## Preliminary analysis of the morphology and ultrastructure of a putative arthrodiran (Placodermi) egg case

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Six arthrodiran egg cases were reported from the Cleveland Shale (Famennian) of Ohio, U.S.A. Using scanning electron microscopy (SEM), the recognition of obliquely arranged layers of collagen fibers formed the basis for assignment to the vertebrates. The search for a producer of these cases was based on the distinct morphology of the cases compared to the known morphotypes among the chondrichthyans and a single specimen possessing a tiny fragment of apparent tuberculated bone within the egg case. Suggesting an arthrodiran producer, the nature of the tubercles is distinct from the surface ornament in other vertebrates, but a common feature among the arthrodires within the fauna. Samples of the bone were not extracted for further analysis.

The purpose of this study is to test the hypothesis for the origin of these egg cases. To this end, the morphology of the specimens is being described to provide a comparison to known chondrichthyan egg cases. The ultrastructure and composition are being analyzed using microXRD using TEM to determine the nature of phosphatization, thin sectioning for both light microscopy and SEM analysis, and energy dispersive spectroscopy (EDS) to evaluate the elemental variations within individual laminae.

On a macroscopic scale, the egg cases appear to possess a single marginal rib and are preserved opened-like-a-book with the rib serving as a hinge. There appears to be a symmetrical arrangement of surface ornament centered on the hinge. The outer edges have a feathered-edge appearance, thus lacking the bilateral symmetry seen in chondrichthyan egg cases. The cases appear to be made up of several layers potentially representing lines of weakness in the once continuous covering. The separation of layers appears to be a preservational artifact. Samples of each layer are being analyzed to reconstruct an intact section. The individual layers consist of alternating bands of color with individual bands further subdivided into fine laminae. This pattern parallels that seen in the extant spotted dogfish (*Scyliorhinus caniculus*) where the approximately 2 mm egg case wall consists almost entirely of alternating layers of collagen fibers. The analysis to date documents the asymmetry of these egg cases, unlike the condition in extant and fossil chondrichthyans. On the other hand, the ultrastructure of the egg cases presents either a vertebrate plesiomorphic condition or convergence on a common structural design for collagenous egg cases.

IPC 5

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#### The apparatus composition and architecture of *Erismodus quadridactylus* and its implications for the prioniodinin apparatus bauplan

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The apparatus composition and architecture of prioniodinin conodonts is poorly understood, largely because few prioniodinin taxa are represented by articulated 'natural assemblages', but also due to the highly variable gradational morphology of their constituent elements that makes apparatus reconstruction problematic. We describe a natural assemblage of *Erismodus quadridactylus* (Stauffer, 1935), a basal prioniodinin conodont, from the Sandbian (Late Ordovician) of North Dakota, USA. The assemblage demonstrates that the apparatus architecture of *Erismodus* is similar to those of Late Palaeozoic prioniodinins, namely, *Kladognathus* Rexroad and *Hibbardella* Bassler, but also has similarities with ozarkodinin apparatuses. There is evidence to suggest that *E.quadridactylus* also shared topological similarities to 'prioniodontid' architecture, with respect to the position of its inferred P elements. This apparatus reconstruction suggests, at least with respect to the M-S array, an 'ozarkodinin-type' bauplan is likely more widely representative across ozarkodinids. Furthermore, element morphotypes traditionally considered to lie within the S array are M elements, whereas others traditionally interpreted as P elements are found in the S array. These observations are used as a basis for revising the prioniodinin apparatus bauplan and for refining concepts of element homology among other prioniodinin condonts and their closest relatives.



Speaker

#### "Early" vertebrates from the Late Cretaceous of Saxony – the fish inventory revisited

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Shallow marine sediments that prevail in the so-called Elbtal Group accumulated during the early Late Cretaceous (Cenomanian–Coniacian, 95–89 Ma) in present-day Saxony (East Germany), in the area around Dresden (Meißen – Dresden – Czech border). The sandstones, marly siltstones, marls and marly limestones were deposited in a narrow sea strait connecting warm Tethyan waters of the Bohemian Cretaceous Basin with temperate Boreal waters of the Northwest European shelf.

Vertebrate fossils are known from the Late Cenomanian–Late Turonian interval, but their occurrence is restricted to some distinct levels within the Elbtal Group. Disarticulated osteichthyan and chondrichthyan remains occur in high-energetic deposits of the D<sup>Ö</sup>lzschen Formation (Upper Cenomanian, transgressive and "Pläner" facies) and in the micritic limestones of the Strehlen Formation (Upper Turonian, "Plänerkalk"). More complete actinopterygians are occasionally found in marly siltstones and marls in stratigraphically intermediate position.

The diverse fish assemblage is documented by at least two types of holocephalian tooth plates and fin spine fragments; teeth, spine fragments and vertebrae referable to at least 17 shark species; and no less than ten species of actinopterygians. Coelacanth remains, mentioned in literature, appear to have been lost.

Highest diversity is observed in the Upper Turonian Strehlen limestone ("Kalk von Streheln"), equally known for its rich invertebrate fauna, supporting complex trophic networks. Indeed, the limestone yields abundant remains of small, mid-sized and large predators from only few cm-long enchodontids to several m-long ichthyodectids and lamniform sharks. The large durophagous shark *Ptychodus* is widespread over the whole fossiliferous Elbtal Group succession. In contrast, the trophic guild of mid-sized durophagues, represented by pycnodontiform actinopterygians as well as hybodont and heterodontid sharks, is more diverse in the Late Cenomanian Dölzschen Formation. The intermediate marls and siltstones exhibit the least diverse faunas, consisting of rare pycnodonts, teleosts, *Ptychodus*, and lamniform sharks. However, these strata are the least known because collecting traditionally focused on the D<sup>ö</sup>lzschen and Strehlen formations. Since most outcrops were temporary or have been exhausted, and most available collections come from the 19th and early 20th century, these results may further be influenced considerably by collecting biases.



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## New discoveries from an Early Devonian placoderm illuminate the evolutionary origin of teeth

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The origin and development of teeth is one of the most important event for gnathostome evolution. However, how and when the teeth evolved remain debatable. As one of the most primitive groups of gnathostomes, arthrodire placoderms provide crucial evidence for the understanding of evolutionary origin and the development of teeth. However, the lack of fossil evidences from early arthrodires hamper our understanding in the initial stage of teeth evolution. Here, we investigate the articulated dental plates of an unnamed Early Devonian arthrodire V244, from Burrinjuck, New South Wales, Australia, by using high resolution X-ray computed tomography and digital segmentation. The most impressive features of the dental plates of V244 are the smooth-sided pulp cavity underneath the nonshedding teeth, and the interconnecting longitudinal blood vessels in the basal bone. These features recall the similar arrangement in stem osteichthyan Andreolepis. Besides, the dental plates of V244 are quite different from those of advanced arthrodires in following aspects: the ossification centres are towards the centre of the bones, and numerous radiating tooth rows have been identified. In the dental plates of V244, the continuous growth lines from the denticles to the base of the anterior supragnathal are present. Oral denticles have a dense core as that of the external tubercles. Vascular spaces occur at the base of the denticles on both dental plates. A radiating structure within the denticles may indicate semidentine, but this could not be confirmed because cell spaces were not identified. Our preliminary study reveals that the dental plates of early arthodire V244 share many similarities with those of stem osteichthyans, which sheds light on the teeth evolution, and gives a better understanding on the evolution of placoderm dentition and the evolutionary development of 'true' teeth.

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## Old questions answered for the enigmatic *Palaeospondylus*: new data demonstrates crowngroup vertebrate character

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Palaeospondylus gunni Traquair, 1890 is a problematic Devonian vertebrate whose affinities had been unresolved and a source of constant debate. Importantly, a recent publication proposed this fossil species to be a stem-group hagfish (Myxinoidea). However, our new data contest this by the presence of three semicircular canals in the otic region of the cartilaginous skull of *Palaeospondylus*, as one essential characteristic of jawed vertebrates. We further question this assignment as new tomographic data reveal characters of crown-group gnathostomes (Chondrichthyes+Osteichthyes) in Palaeospondylus, including a first arch jaw articulation, a longer telencephalic region of the braincase, an otico-occipital fissure that separates otic and occipital regions, and vertebral centra. More specific chondrichthyan characters include a precerebral fontanelle and postorbital articulation of the palatoquadrate, while similarities in the structure of the postorbital process to taxa such as Pucapampella, and possible presence of the ventral cranial fissure, suggest Palaeospondylus can now be resolved as a stem chondrichthyan. The internal skeleton in Palaeospondylus is specified by enlarged cell spaces surrounded by mineralized cartilage, although previously this was thought to indicate an early stage in osteichthyan endochondral bone formation, these new chondrichthyan characters of the braincase may instead suggest the unusual skeleton represents a stage in the loss of bone characteristic of the Chondrichthyes.



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## A phylogeny for Heterostraci: evolutionary relationships of extinct jawless vertebrates on the gnathostome stem

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Heterostracans are the most diverse group of fossil jawless fish (ostracoderms). They are also one of the earliest branching clades on the gnathostome stem, making them key to our understanding of early vertebrate evolutionary patterns. Their phylogenetic relationships are poorly understood, meaning that the pleisomorphic state for heterostracans, gnathostomes, and potentially even vertebrates as a whole, is unknown. Here, we propose a phylogeny using a combination of discrete and continuous characters for all described heterostracan genera (137 taxa) including Pteraspidiformes, Cyathaspididae, Psammosteidae, Amphiaspididae, Traquariaspididae, the heterostracan problematica and representatives of other stemgnathostome lineages. Our results indicate the Cyathaspididae are paraphyletic and the Psammsoteidae fall within the Pteraspidiformes. Clustering methods identify two equally parsimonious solutions with respect to rooting of the Heterostraci: tesselate forms, or Ctenaspididae as sister group to all other heterostracans. Stratigraphic congruence metrics supports the the later. The novel large scale phylogeny is the first to include representatives from all heterostracan clades and provides a framework to investigate major evolutionary transitions such as dispersal histories.

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#### Historical perspectives to modern day conditions in the southern Southwestern Atlantic: glimpses from Late Quaternary molluscan assemblages of Argentina

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Different approaches (diversity, palaeobiogeography, bioerosion, geochemical variations) to Late Quaternary molluscan assemblages of Argentina, especially from interglacial episodes during MIS5e (Last Interglacial, ca. 125 ka B.P.) and MIS1 (Mid-Holocene, ca. 7-4.5 ka B.P.) along underpopulated Patagonia, provide palaeobiological-palaeoenvironmental data for the southern Southwestern Atlantic (SWA). In summary, all the data together with new patterns of  $\delta^{18}$ O and  $\delta^{13}$ C variations in modern, Holocene, and Late Pleistocene shells of Protothaca antiqua (Bivalvia) and the coeval Pleistocene Tegula atra (Gastropoda) suggest responses to palaeoclimate-palaeocirculation, providing a historical perspective for changes in SWA since the Last Interglacial. The modern  $\delta^{18}$ O trend responds to salinity and secondarily to SST; the highest modern  $\delta^{13}$ C values link to salinity and to coastal fronts (yielding higher nutrients concentration/chlorophyll-a/primary productivity). For the mid-Holocene, the influence of the Hypsithermal is confirmed (palaeobiogeography, bioerosion, isotopes); in northern Golfo San Matías, the highest  $\delta^{18}$ O and  $\delta^{13}$ C values support a Golfo San Matías Front stronger than today; lower  $\delta^{18}$ O values in northern Golfo San Jorge (GSJ) compared to Late Pleistocene values suggest mid-Holocene warmer waters; overall higher  $\delta^{13}$ C, an enhanced productivity. Fort the Late Pleistocene (particularly MIS5e), a southwards increasing  $\delta^{13}$ C trend is apparent, the highest values matching with coastal fronts (Northern GSJ, Southern GSJ) and areas of maximum chlorophyll-a concentrations today; consequently, the fronts were already active, significantly enhanced, due to colder waters and higher upwelling levels from southern GSJ southwards. Last Glacial millenial-scale (sub-Milankovitch) episodes, responsible for abrupt changes of SST, ice melting and surface-ocean stratification in western Antarctica and the Weddell Sea-Antarctic Circumpolar Current, could account for the different Holocene isotope, bioerosion and palaeobiogeographical patterns, and for the extinction of Tegula atra (cold Pleistocene biostratigraphical marker, dispersed from the SEP to the SWA by rafting on kelps; controlled by SST, light, winds, nutrient concentration/productivity). Macroscale changes inferred from the overall sources of evidence illustrate responses to recent drastic climate and sea ice changes around southernmost SWA and western Antarctica leading to modern conditions.



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#### Peer Community in Paleontology (PCI Paleo): a community-driven, transparent, free and open platform for peer-review in paleontology

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The academic publishing system is becoming increasingly costly for institutions, users, and ultimately the taxpayer. This system is undergoing major changes, including a push for Open Access. However, the progressive transition from a reader-pays (subscription journals) towards an author-pays model (Gold Open Access or Hybrid) is unlikely to significantly reduce the overall cost of academic publishing. The current system also fundamentally lacks transparency and is relatively slow.

A faster, more transparent, completely open access, and free publishing system is now possible thanks to modern technologies for only a fraction of the cost. These tools just need to be implemented for biological sciences. Preprints have successfully been used for more than 25 years by physicists, mathematicians, astronomers, and computer scientists as a way to rapidly diffuse research results and to promote early feedback from a wider audience. They have more recently penetrated the field of biological sciences, but some justifiably criticize their non-peer-reviewed nature. Fortunately, peer-review is already a self-organized service provided by the community and can easily be implemented to evaluate preprints.

The Peer Community In (PCI) project calls for the creation of non-profit communities of researchers to peer-review articles available in preprint servers. PCI Evolutionary Biology, the first of these communities, now counts more than 360 scientists reviewing preprints in their discipline. Launched in early 2018, Peer Community in Paleontology (PCI Paleo) is backed up by an international Managing Board and a growing group of recommenders (= editors). This is the third community of the PCI project.

The PCI Paleo workflow is very similar to that of conventional journals, except that it is completely free and transparent. Manuscripts are first posted as preprints on an open online server and submitted to PCI Paleo for peer-review. They are then evaluated by an editor and at least two external referees. Revised versions are posted on the open server after each round of peer-review. If the paper is accepted, a final version is uploaded on the server and permanently linked to a recommendation text (written by the editor) and the peer-review reports, which are published by PCI Paleo. Papers recommended by PCI Paleo are therefore peer-reviewed, fully citable (DOI) and Open Access, obviating the need to publish them in conventional journals (although this remains a possibility).



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# Early tetrapod relationships: new results based on well-preserved specimens

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The origin(s) of lissamphibians (frogs, salamanders and caecilians) among their fossil relatives (i.e extinct non-amniotic tetrapods, called early tetrapods) is a century old question which is still actively debated. Currently, three hypotheses are discussed: an origin among temnospondyls; one among lepospondyls; one where frogs and salamanders are among temnospondyls and caecilians among lepospondyls. This latter hypothesis, involving a polyphyletic origin of lissamphibians, therefore questions their currently accepted monophyly. Even if the phylogenetic position of some groups seems to be well defined (e.g. Temnospondyli), several still have a highly variable position (e.g. Chroniosuchia, Anthracosauria), even with a questioned monophyly (e.g. Lepospondyli).

The preservation could explain this lack of robust relationships: fossil amphibians are mostly known by their skull roof, involving that their taxonomy and phylogeny are mainly based on skull roof characters. Unfortunately, these characters are frequently found convergent, hence rarely form exclusive synapomorphies or are not applicable in the analyses because absent in some taxa. This leads to frequent irrelevant optimizations and alters the phylogenetic signal of non-skull roof characters. Moreover, the coding of rarely well preserved anatomical regions (such as endocranium) leads to a high amount of missing data. To overcome these issues, we conducted a phylogenetic analysis based on the best-preserved representatives of each group of early tetrapods, with the inclusion of lissamphibians and amniotes based on literature. Thanks to the good preservation, we observed and defined new palatal, occipital and endocranial characters (such as the shape of the sphenethmoid anterior extremity), and we redefined previously used characters. In total, we built a matrix of 48 taxa and 209 characters.

Our preliminary results show that the palate and occiput are much more conservative than the skull roof, and thus more informative for high-ranked relationships. Hence, certain phylogenetic positions have been specified: for example the taxa Chroniosuchia is found closer to Amniota than previously thought, and the monophyletic Lissamphibia has a robust position among Temnospondyli.

This study allows to better understand the evolution of poorly known anatomical regions (e.g. basicranial joint) among early tetrapods. Thus, it will help to investigate the phylogenetic signal bore by poorly preserved characters.



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#### Crossing borders: Early Pliocene - Middle Pleistocene expansion of the genus *Nyctereutes* (Mammalia, Canidae) across the Old World

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Nowadays the genus Nyctereutes limited in diversity (monospecific) and geographically (only present in Eurasia). Nevertheless, the fossil record of Nyctereutes testifies to a considerably wider areal, a (paleo)diversity similar to that other extant Canidae genera and to the progressive appearance of adaptations to an omnivorous diet, particularly in dentognathic features (e.g., the development of the subangular lobe). The earliest occurrences of the genus come from the Early Pliocene localities of the Yushe basin (China, ~MN14-15). The two different species that co-occur in this basin, N. tingi and N. sinensis : the former is primitive compared to the latter, which already possesses the dentognathic adaptations to omnivory comparable to those of extant N. procyonoides. The Western European records of the genus start in MN15, with the primitive N. donnezani recorded in few French and Spanish sites. Numerous features seem to justify the specific distinction between the two taxa, although many shared characters suggest a close affinity and similar dietary preferences between N. donnezani and N. tingi. In contrast to the Asian record, in Europe, during the late Pliocene, primitive and derived forms of raccoon- dogs never coexisted: N. donnezani was replaced by the widespread N. megamastoides. The latter has generally been regarded as the European counterpart of N. sinensis (for comparable development of craniomandibular features). The African diversity of Nyctereutes is relatively abundant. Possibly, the two earliest African records of the genus are those of Upper Laetoli Bed of ?N. barryi and of the primitive N. lookwoodi (Ethiopia), both from the Early Pliocene. Other findings are the Early Pleistocene derived N. abdeslami and N. terblanchei from Morocco and South Africa, respectively. During the Early Pleistocene, the findings become more and more scarce and the diversity declined as the previous species disappear. The extant N. procyonoides appears in Middle Pleistocene deposits in China. Although many scholars have investigated the evolutionary history of this genus, many issues are still matters of debate and fertile grounds for research (e.g., the phylogenetic relationships between the species, etc.). Unlike previous works, our study deals with the problem on a larger scale [i.e., (inter)continental] and, thanks to new or recently described material, aims to tackle the difficulties encountered in literature, suggesting new hypotheses on the phylogeny, dispersion, and radiation of Nyctereutes across the Old World.



Speaker

### Mycelial fossils in the Palaeoproterozoic deep biosphere

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Fungi have recently been shown to be a significant component of endolithic biotas in the Phanerozoic deep biosphere. Pores and fractures in rocks of the igneous oceanic subseafloor crust are commonly occupied by mycelia-forming filaments having morphological and chemical characteristics of fungi. Consortia of fungi and prokaryotic chemoautotrophs suggest close symbiotic interactions between autotrophs and heterotrophs in the deep biosphere. The fungi display cryptoendolithic (cavity-dwelling) and chasmoendolithic (fracture-dwelling) as well as euendolithic (rock-boring) modes of life. We search for ancient equivalents to these biotas in Palaeoproterozoic crustal igneous rocks, particularly in vesicular basalts, these being likely to have provided suitable habitats for endoliths. Basalts from the 2.5-2.2 Ga Kuruman, Ongeluk, and Hekpoort formations of the Kaapvaal Craton, South Africa, have yielded filamentous networks comparable to those of Phanerozoic endolithic fungi, but their considerably greater age makes an assignment to fungi problematic. The Kuruman and Ongeluk structures are particularly well preserved morphologically, showing fungus-like features: branching and anastomosing filaments forming entangled networks. The Hekpoort filaments are more varied in morphology and dimension than those of Kuruman and Ongeluk, and their formation may have been influenced by both biogenic and abiogenic processes. The Kaapvaal basalts have undergone low-grade metamorphosis (up to lower greenschist), and the content of the vesicles reflect the replacement of original structures and the formation of seconday mineral phases. When criteria of biogenicity are fulfilled, endolithic fossils in crustal rocks give insights into an environment that has probably existed as long as life itself on Earth. Though its biota has likely been repopulated many times from the surrounding marine environment, the cryptic deep environment may also have served temporarily as a refugium during periods of global environmental crises.

<sup>°</sup> Speaker

### Morphological phylogenetics, character construction and serial homology: a case-study on the evolution of cingulum on placental upper molars

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Morphological data are essential to place phylogenetically extinct taxa that are currently inaccessible to molecular analyses. However, phylogenetic analyses based on morphology face many challenges and require methodological improvements. Morphological integration, and most particularly serial homology, certainly count among classical difficulties encountered for this type of analysis. Serial homology generally consists in repetitive features sharing a large proportion of their genetic architecture and developmental pathways, and which initially exhibit high levels of covariation. Cladistic analyses of morphological traits, which are critical to include fossil taxa in phylogenies, require independence between characters being scored in the analyzed matrices. For these reasons, selecting and scoring characters on serially homologous structures represent a tricky task. Teeth constitute one of the main examples of serially homologous structures in vertebrates. Because of their high morphological diversity and good preservation in the fossil record, teeth constitute a much used phylogenetic proxy in mammals. Though their covariation patterns remain poorly known, repeated structures at successive dental loci are routinely scored as separate characters within cladistic analyses. Here we report the results of a large-scale investigation of the distribution of cingular crests on the upper molars of ca. 280 placental extant and fossil species. The analyses of phylogenetic co-distributions of the cingular crests on successive molars (M1, M2 and M3) showed highly correlated evolution in the entire sample, demonstrating the non-independence of these features at a macroevolutionary scale. Likelihood analyses applied on a baseline phylogeny further showed that the serial variation of the cingular crests on M1-3 should be better scored within a single composite character but with constrained paths for transitions. Current molecular and developmental knowledge related to dental morphological variation is also in good agreement with this result. Finally, we argue that similar cases of non-independence among characters may be found in many other examples of serially homologous structures. This work thus highlights how essential studies on patterns of variation and integration can be to character construction and modelling, and thus to morphological phylogenetics.



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Speaker

## Handbook of Paleoichthyology, vol. IA, "Agnatha" I, H.-P. Schultze ed., Verlag Dr. Friedrich Pfeil, München (FRG) - State-of-the-art with new perspectives in Eco-Etho-Phylo-Evo-Devo

Alain Blieck \*+<sup>1</sup>, David Elliott <sup>2</sup>, Philippe Janvier <sup>3</sup>, Susan Turner <sup>4</sup>, Vadim Glinskiy <sup>5</sup>, Gai Shi-Kun <sup>6</sup>, Marion Chevrinais <sup>7</sup>, Damien Germain <sup>3</sup>, Jean Goedert <sup>8</sup>

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The Handbook of Paleoichthyology vol. I " Agnatha " was ordered by its editor Prof. Dr. H.-P. Schultze in the early 1990s after L. B. Halstead-Tarlo deceased. H.-P. Schultze asked one of us (A. Blieck) to coordinate the volume, what he accepted. He was, however, unable to fulfill this challenge until he was pensioned on 2014. Later, in 2017, he asked P. Janvier, who had finished in 1997 his early version of the chapters that he was in charge of, whether or not he was ready to come back to the project and finally make the work. The delay was due to A. Blieck's inaction. P. Janvier said 'yes', thus, the decision to reorganize the authorship with both other senior authors D. Elliott and S. Turner. The latter copublished vol. IB on Thelodonti in 2007 with both T. Märss and V. N. Karatajūtė -Talimaa. We added two younger scientists to vol. IA, viz. V. Glinskiy as a Russian-speaker for psammosteid heterostracans, and G. Shi-Kun as a Chinese-speaker for galeaspids. On April this year, during the annual congress in Brussels, Belgium, of the French Association of Palaeontology, A. Blieck " recruited " three other younger experts in phylo-evo-devo (M. Chevrinais), palaeohistology (D. Germain) and S32,34 isotopic biogeochemistry for palaeoenvironmental problems (J. Goedert). This ideal team will be able (1) to review all known fossil basal, Palaeozoic vertebrates, a.k.a., 'fishes', as systematic, biostratigraphic, palaeobiogeographic, palaeoecologic, palaeoethologic, that is, geobiological objects, and (2) to propose completely new perspectives on various taxa such as tunicates, cephalochordates, Myllokunmingia, monophyletic cyclostomes, basal naked vertebrates, and paraphyletic ostracoderms, i.e., anaspids, pteraspidomorphs, osteostracans, galeaspids, ?pituriaspids and thelodonts. This volume of the Handbook of Paleoichthyology is ambitious enough as to propose an actual model for other systematic handbooks, and furthermore for all other palaeontological handbooks.

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### On the origin and evolution of the lateral sensory line system of vertebrates

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The crown-group Gnathostomata has representatives which bear an electronically active lateral sensory line system (LSLS) that irradiates all through their head and body as, e.g. in the stemward-group sharks and in the crownward-group teleosts. In both cases, the external pores function as electroreceptors that help the fish to locate up-down and right-left in water in order to survive in its environment. The great white shark (GWS) Carcharocles carcharias, aka the megatooth shark, growing to 6.1 m (20 ft) in length & 1,905 kg (4,200 lb) in weight, feeds upon fish, sea turtles, dugongs & large whales. GWS has an extra sense given by the ampullae of Lorenzini which enables to detect electromagnetic fields emitted by the movement of living animals. GWS are so sensitive they can detect variations of half a billionth of a volt. At close range, this allows the GWS to locate even immobile animals by detecting their heartbeat. C. megalodon, aka the big tooth, lived from -23 to -2.6 My, i.e., from the Early Miocene to the Pliocene. It is sometimes thought that it still exists in very deep oceanic environments, in, e.g., the French comics QR Carthago edited by Les Humanoïides Associés. Homologous systems are known among all extant vertebrates, i.e., from crownwwardmost Homo sapiens to stemward most Lampetra fluviatilis. The system, originally selected in marine aquatic environments, evolved through darwinian process and is adapted to terrestrial environments as well. The question that we focus on here is whether or not morphologically and functionally homologous systems did occur and evolved in fossil craniates (= vertebrates because cyclostomes are now considered as monophyletic). The answer is 'yes'. We accredit the lateral sensory canal system (LSCS) of Ordovician to Devonian pteraspidomorphs, that is made of pores, pit lines and/or canals, as an homolog to LSLS. This is based upon a thorough personal experience of pteraspidomorphs & an 'Indiana Johns-like' exploration of literature. This may be 'drilled' down to the root of the system. It is intellectually modellized by help of a cladistic analysis whose light shines. We thus reconstruct the sequence of morphological states of characters down to the original state called 'unossified lateral line system' (LSO). It probably 'appeared' as early as the Ediacaran at ca. -635 My. We even date the successive nodes of the cladogram.



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## Evolution of the terrestrial vertebrate diversity of Marie-Galante Island (French West-Indies) during the last 40 000 years

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Marie-Galante Island (Guadeloupe, French West-Indies) has recently been the object of several paleontological investigations in order to characterize the evolution of its terrestrial vertebrate paleobiodiversity during the last 40 000 years. This paper consists in a synthesis these recently obtained results obtained by crossed studies of several large vertebrate fossil assemblages (mammal, bird, squamate, and amphibian) collected in Late Pleistocene and Holocene deposits. Our work reveals a previously inconspicuous now-extinct Pleistocene and Holocene vertebrate biodiversity. We observed that this past diversity was recently modified to become very different from what it is nowadays. Indeed, while a small number of extinction or extirpation events can be related to the Pleistocene-Holocene climatic transition, the faunal community of the island is nearly completely modified during the last millenaries. These modifications include the arrival of several exogenous taxa, and an extinction/extirpation rate of native species between 54% and 100% depending of taxa.

Our results suggest that human impact was the main factor driving the evolution of the island terrestrial faunal diversity. We also demonstrate a possible impact of Pre-Columbian human populations on the faunal diversity of Marie-Galante Island which however remains minor in respect to the overwhelming modifications possibly related to the European colonization and subsequent anthropization of the island.

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## New insights in the evolutionary history and the paleobiology of the ground sloth *Simomylodon uccasamamensis* (Xenarthra, Mylodontidae) from the Pliocene of the Bolivian Altiplano

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Fossil remains of ground sloths have been discovered in numerous localities throughout the Americas, but knowledge of these animals remains poor in the tropical latitudes, in comparison with other extinct folivoran taxa from more northern and southern regions. During the Pliocene, mylodontine ground sloths were spread from North to South America but, in the central regions of South America, wellpreserved craniodental remains had not been discovered yet, impeding reliable assessment of their taxonomic attributions and phylogenetic affinities. Recent paleontological expeditions to Pliocene deposits of the Bolivian Altiplano (i.e., localities of Choquecota, Pomata-Ayte, Casira, Inchasi and Ayo Ayo-Viscachani) provided several new well-preserved craniodental remains ascribable to the mylodontid species Simomylodon uccasamamensis. The analysis of this material, and its comparison with other moderate-sized Mio-Pliocene Mylodontinae from North and South America, allowed us to reliably differentiate Simomylodon uccasamamensis among these taxa on both morphological and morphometric grounds, and to revise the taxonomic attributions of several specimens from Bolivia and Argentina. Morphometric analyses show that the species Simomylodon uccasamamensis, together with the poorly-known Glossotheriopsis pascuali, is the smallest Mio-Pliocene mylodontine, whereas new phylogenetic analyses stress the close relationship between Simomylodon uccasamamensis and the late Miocene mylodontine Pleurolestodon acutidens from Argentina. Preliminary studies on the enlarged sample of this Andean mylodontid species suggest the presence of moderate sexual dimorphism, recognizable in both shape and size. These observations are in accordance with those made for some Pleistocene ground sloths (e.g., Paramylodon and Eremotherium), suggesting that sexually dimorphic taxa were already present in the Pliocene Epoch. Simomylodon uccasamamensis also appears to be an endemic taxon of the Andean highlands during the Pliocene, consistently recovered from this area throughout the Montehermosan, Chapdamalalan, and early Marplatan South American Land Mammal Ages. This ground sloth may have found its ideal ecological conditions in the Bolivian Altiplano, during a span of time falling between the South American Mio-Pliocene faunal turnover and the Great American Biotic Interchange.



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#### The skeletal maturation of Paranthropus robustus

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In 1938, the taxon *Paranthropus robustus* was established by R. Broom following the discovery of the partial cranium and associated mandible TM 1517 at the cave site of Kromdraai B, in Gauteng, South Africa. A few weeks after his announcement, Broom reported the discovery, nearby and in the same matrix, of a distal humerus (TM 1517g), a proximal ulna (TM 1517e), and of a distal hallucial phalanx (TM 1517k). Such postcranial material was attributed to the same individual representing the holotype. Since the early descriptions, while the partial skull has been dentally attributed to a late juvenile individual of uncertain sex, no specific analysis investigated the postcranial remains for the presence of still growing bone. However, such evidence would corroborate the suggested association of craniodental and postcranial remains and would provide, for the first time, information on skeletal growth patterning in *P. robustus*.

In the hominin fossil record there are few craniodental specimens sampling immature individuals unequivocally associated to postcranial materials, an essential condition for appropriately assessing the taxon-specific patterns of odontoskeletal maturation. We thus aim at finely characterize the inner structure of the specimens TM 1517g, TM 1517e, and TM 1517k in order to tentatively detect any remnant of a recent, or an even still incomplete, epiphyseal closure. In this perspective, in 2017 we scanned the three specimens at the South African Nuclear Energy Corporation (Necsa), Pelindaba, at resolutions ranging from 8.7  $\mu$ m to 35  $\mu$ m voxel size.

In TM 1517, the M2 mesial radicular apices are fully formed, while the M3 roots only reached c. 60-70% of their total length, which in extant humans corresponds to a developmental stage of  $18\pm3$  years (sexes pooled). 3D-based imaging results show that the distal humerus was likely completely fused, while the ulna and, to a lesser extent, the hallucial phalanx still display a subtle remnant of growing bone.

These new data thus support their attribution to the same individual representing the type specimen. However, given the specific tooth growth pattern displayed by TM 1517, our results also indicate a certain degree of asynchrony with respect to the human and chimpanzee postcranial maturational patterns. Nonetheless, given the likely bimaturational condition characterizing *Paranthropus*, the still uncertain sex attribution of TM 1517 represents an additional complicating factor.



Speaker

### Systematic study of fossil elephants from Dhok Pathan Formation, Middle Siwalik deposits of Pakistan

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Fossil site Dhok Pathan is an important locality in the Middle Siwalik deposits of Pakistan. This important type locality is situated in District Chakwal and is 27 Km from Talagang. The thickness of this locality is 950-1200 metres. The Dhok Pathan Formation is mainly composed of claystone, sandstone and siltstone. The age of this locality is approximately 7.9-5.1 Ma. This Formation was deposited in sub-tropical and semi-arid climatic conditions. This locality was selected to explore in detail and compare with European mammalian assemblage. The main focus was the collection of new fossil remains of order Proboscidea. We have discovered two different species such as *Stegolophodon cautleyi* and *Stegolophodon stegodontoides* after extensive fieldwork. Collected fossil specimens have been identified morphologically. Different aspects such as geographic distribution, taxonomy and palaeoenvironment have been interpreted. Results and data have also been compared with published work.

Speaker

### The third specimen of *Ikrandraco avatar* (Pteranodontoidea) from the Early Cretaceous Jehol Biota, China

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In the Early Cretaceous Jehol Biota, an interesting species of the toothed pteranodontoid pterosaur, Ikrandraco avatar, was known for its unusual structure, which is so far unique to this taxon. Unlike other pterosaurs, this species has a low and elongated crestless skull with a lower jaw that has a developed dentary crest with a hook-shaped posterior process. The special dentary crest is larger than those in any other known pterosaur species. This mandibular structure is analogous to those of some modern birds with a throat pouch, indicating the presence of a similar soft tissue and feeding mode on this pterosaur. It shows a distinct foraging habit for pterosaurs, what increase the potential feeding modes of pterosaurs. Here we describe a new laterally compressed pterosaur specimen from the Lower Cretaceous Jiufotang Formation, northeast China, which preserved skull, mandible and two cervical vertebras. It could be assigned to Ikrandraco avatar, based on the large mandibular symphysis on the lower jaw, strongly inclined quadrate, a well-developed crest on the ventral margin of the dentary, dentary crest with an extraordinarily thin ventral edge, and a notch on posterior margin of the dentary crest proving the existence of the hookshaped process. The new specimen shows some differences from other Ikrandraco avatar specimens that we have known. For example, the dentary crest of the new specimen is deeper than those of the holotype and the referred specimen, but shorter than that of the holotype. Except for the influence of taphonomic compression, this distinction could also be attributed to intraspecific variation. The phylogenetic analysis found Ikrandraco avatar among the Pteranodontoidea, outside but closely related to the Anhangueria, and belonging to the Pterodactyloidea. Besides this new specimen, there are only two specimens of Ikrandraco avatar. The study on the new specimen gives more information on understanding the morphology and feeding habits of Ikrandraco avatar.



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### Ecological interactions between Pleistocene carnivore and herbivore communities in western Eurasia: Implications for the human ecological niche

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The ecological and evolutionary interaction during the last 3 million years between communities of large-sized herbivores (67 species, proboscideans and rhinocerotids excluded) and carnivores (30 species with body mass above 10 kg) from western Eurasia is analyzed. This frame can bring information about the ecologic context of early human dispersal. The ecologic and systematic structures of herbivore and carnivore communities during the Late Pliocene and Early Pleistocene show little evidence on mutual evolutionary influence triggered by climate change. Herbivores were highly sensitive to climate fluctuations that caused a high species turnover due to extinctions of local stenobiont forms and dispersals of new large-sized oriental species. The body size structure of the whole herbivore guild sifted significantly toward the large-sized body class. The dispersal of first hominines into the European subcontinent (1.1 - 1.4 Ma) coincided with this restructuration of the herbivore guild. Unlike herbivores, carnivores were long-living ubiquitous species with a large distribution range and show a lesser dependence on climate shifts caused by the 41 kyr climatic cycles. This archaic predator assemblage lasted in Europe until ca. 1.2 - 1.0 Ma. The high-amplitude 100 ka cycles caused a significant increase of carnivore species turnover marked by the extinction of specialized felid predators, however, the main ecological parameters of the carnivoran guild (mean body mass and species richness) changed insignificantly. Early Pleistocene predators faced to the "large body size – cursorial ability" evolutionary dilemma that impeded the adaptation of solitary carnivores to megaherbivores in the open landscape conditions. Such dilemma was solved independently in the lineages of Felidae (Panthera leo), Hyaenidae (Crocuta crocuta), and Canidae (Canis lupus, Lycaon lycaonoides) by acquiring ethological characteristics such as social behavior and cooperative hunting that in combination with large body mass (lions) or high cursorial abilities (spotted hyena and dogs) to take a larger prey. Such a scenario will be put in parallel with the arrival and permanent settlement of human groups in Western Eurasia. Factors as ecological flexibility (especially in diet) and sophisticated social behaviour of early hominines were particularly advantageous in the specific faunal ecosystems of Western Eurasia.

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### X-ray tomography contribution to the palaeobiology of Upper Cretaceous planktonic foraminifera

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External test characters of Upper Cretaceous planktonic foraminifera are commonly compared to those of extant species. Similarities are used to interpret their life position: globular pustulose forms (*Whiteinella* and *Muricohedbergella*) are supposed to have inhabited the upper part of the water column, whereas heavier keeled species (*Rotalipora* and *Thalmaninnella*) would have evolved below the thermocline. However, this model cannot be applied to all time intervals. Indeed, during, Paleogene forms with a well-developed keel (*Morozovellids*) were common in the upper part of the water column.

With the development of non-destructive X-Ray tomography, it is now possible to qualitatively and quantitatively characterize all the ontogenetic stages of the planktonic foraminifera. Indeed, morphological test changes and internal volumes can be precisely constrained for each chamber. CT techniques were therefore used to study, for the first time, the growth patterns of three well-preserved Cenomanian species (*Whiteinella aprica, Rotalipora cushmani* and *Thalmaninnella greenhornensis*) from the Greenhorn Formation of the Great Plains (South Dakota, US). The ontogenetic succession of their chambers has been compared to those of recent fossil species (Miocene up to Holocene) still inhabiting oceans. Surprisingly, the results would show that the globular *W. aprica* and the keeled *R. cushmani* have the same growth pattern which is similar to the thermocline dweller *Globorotalia menardii. Th. greenhornensis* growth pattern is clearly different and belongs to the deep dwellers group.

Those results are important as they will allow a better understanding of the extinction steeps of rotaliporids (*Rotalipora and Thalmaninnella*) during the onset of the Oceanic Anoxic Event 2.

Speaker

### Anomia-associated bryozoans from the upper Pliocene (Piacenzian) lower Tamiami Formation of Florida, USA

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Extensive commercial mining conducted northeast of Sarasota, SW Florida, USA, since the late 1960s have exposed the Plio-Pleistocene rich marine shellbeds of the Tamiami Formation, a complex geological body containing mixed carbonate and siliciclastic beds. Specifically, material used for this study was collected from the lower Tamiami Formation (Units 10/11), whose malacofauna is characterized by a mixture of subtropical and temperate species and is leached of much of its aragonitic component. The age of the lower Tamiami Formation is estimated as being  $3.0\pm0.5$  Ma, corresponding to the late Pliocene (Piacenzian).

We picked 866 shells of the bivalve Anomia simplex d'Orbigny, commonly known as the jingle shell, visibly and densely encrusted by bryozoans, from Phase 10 excavations of the SMR Aggregates quarries (27.373907, -82.376859; WGS84) in July 2017. The bryozoan fauna associated with the Anomia shells consists of 25 cheilostome species, comprising eight anascan- and 17 ascophoran-grade cheilostomes, all with sheet-like colonies. Five of the bryozoans are new species. Most species are rare, represented by a single or a few colonies, while only a few species are very common and abundant. Outer surfaces of the Anomia shells are encrusted in 96% of the shells analysed, while inner surfaces are encrusted in 58% of the shells analysed, although 25% of the shells have cemented sediments that prevent observation of the entire inner surface. A large number of overgrowth interactions can be observed between the bryozoans, both intraand interspecific. In addition, a smaller number of interactions are also present between bryozoans and other groups of organisms such as barnacles, corals, serpulids and encrusting foraminifera. These interactions record competition for substrate space and can be categorized into winlose overgrowths, reciprocal overgrowths and mutual growth cessations (stand-offs). Win-lose overgrowths were found to be more common than stand-offs in interspecific encounters, while stand-offs are more common than win-lose overgrowths in intraspecific encounters. Intraspecific encounters often result in the fusion of the two colonies, with the development of rows of kenozooids along the contact edge. A main aim of this study will be to establish a ranking of species in a competitive hierarchy.

IPC 5

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### The Great American Biotic Interchange (GABI) revisited: a perspective from the stable isotope record of Argentine fossil mammals

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The South American late Cenozoic fossil record constitutes an exceptional natural laboratory to study mammalian paleoecology in the context of changing biotic and abiotic forces. South America remained largely isolated from other landmasses for more than 50 Ma. The initial emergence of land resulted in the early exchange of South American and North American terrestrial taxa at the Late Miocene, and then the permanent establishment of the Isthmus of Panama (~3.1-2.7 Ma) triggered a massive faunal interchange beginning at the end of the Pliocene. This event is known as the Great American Biotic Interchange (GABI). In this study, we investigate the paleoecological response to the GABI of South American endemic and North American immigrant fossil mammals through the application of stable isotope techniques. We focus on a long-term fossil record from the Pampean Region (La Pampa and Buenos Aires provinces, Argentina) spanning from  $^{-9}$  Ma to  $^{-12}$  Ka. Selecting a single region allows us to evaluate variability in taxa resource and habitat use through time within a same geographical and geomorphological context. The tooth enamel carbon isotope record and niche assessment point to a major shift in resource use by most of endemic herbivorous taxa (caviomorph rodents, notoungulates, xenarthrans), which switch from a pure C3 diet to an intermediate C3-C4 diet at the Late Miocene-Early Pliocene and track the expansion of C4 plants in South America. In contrast, litopterns kept a C3-dominated diet throughout the studied interval. A flexible dietary behavior shown by North American herbivorous taxa including C4 vegetation (gomphotheres and equids), or a wide range of C3 resources (cervids) may have favored the successful settlement of some immigrant groups in the Pampean area. Bayesian mixing models applied to evaluate predator-prey interactions reveal that endemic Sparassodonta (i.e., Borhyaenoidea) preferred prey from pure C3 environments, whereas North American Carnivora (i.e., Felidae) consumed prey from mixed C3-C4 areas. This study provides the first integrated stable isotope record of more than 350 specimens of 11 orders/superorders of Pampean endemic and immigrant mammals. It demonstrates the value of isotopes as a proxy for paleoecological traits, including shifts in resource and habitat use throughout the GABI, which have been difficult to assess by other means.

<sup>&</sup>lt;sup>\*</sup> Speaker

### The bones of Doñana National Park (Spain): postmortem modifications in bones and carcasses from a modern Mediterranean ecosystem

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The fossil record is our primary window to study life in the past and to infer episodes of faunal and floral change associated with past environmental shifts. Nevertheless, before obtaining evolutionary or environmental information from the fossil record, it is necessary to evaluate the taphonomic processes that have transformed information from living ecosystems to death assemblages to buried fossil assemblages.

Death-assemblage surveys in modern ecosystems are of particular interest because they document comprehensive information on the multiple processes affecting organic remains and controlling their eventual recycling or preservation. In the case of land vertebrates, long-term bone surveys did not start until the 1970s with the work carried out by A.K. Behrensmeyer and others in Amboseli National Park, Kenya.

We seek to add another long-term monitoring program to the handful of ongoing studies of vertebrate taphonomy in modern ecosystems. The study site is Doñana National Park (DNP), a UNESCO World Heritage Site and Biosphere Reserve, in a Mediterranean ecosystem in Andalusia, Spain. The Park area of approximately 54,000 ha contains one of the largest wetlands in Western Europe. The primary habitats differ according to their geomorphological location: shifting dunes, bushland and pine woods developed on stabilized dunes, marshland, and an ecotone in the boundary between the aeolian sands and the marshes. In these landscapes, several depositional settings with fossiliferous counterparts in the geological record are recognized (e.g., river margin, floodplain, dunes, and beach).

We will present the results of the first field season that included 20 transects in different habitats at DNP. We will characterize the death assemblage composition and the postmortem modifications observed in the bones and carcasses. Similarities and differences among the sampled habitats will be described in terms of the species composition, degree of articulation, ontogenetic age, number and type of fractures, degree of completeness, degree of burial, weathering stage, abrasion stage, and type and quantity of trampling and chewing marks. Our final aim is to increase our understanding of the early postmortem processes that affect the information present in modern death assemblages, and eventually in the fossil record, and that affect our ability to reconstruct past environments and biotas.



<sup>&</sup>lt;sup>°</sup> Speaker

### The Korbach fissure fill – a unique window into late Permian terrestrial vertebrate ecosystems of central Europe

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The Korbach locality in central Germany represents the only tetrapod-bearing fissure fill from the Late Permian and one of the few terrestrial tetrapod sites at low latitudes during this time. It formed in a marine carbonate of the Zechstein Sea during a stratigraphically constrained, local regression in the Changhsingian. The fissure is highly fossiliferous, but thus far, only the otherwise African and Russian basal cynodont Procynosuchus has been definitively reported from this fauna. Recent preparation of the extensive collections recovered from Korbach during the 1990s has allowed recognition of a distinctive, very diverse Late Permian continental tetrapod assemblage. In addition to Procynosuchus, which represents by far the most abundant taxon at this locality, new fossil identifications include representatives of the major therapsid clades Gorgonopsia, Dicynodontia, and Therocephalia, mostly based on isolated teeth and dentigerous jaw elements. In addition, the fossil assemblage comprises remains of pareiasaurian and lanthanosuchoid parareptiles as well as those of a Protorosaurus -like archosauromorph and two captorhinid eureptiles. The latter include a diagnostic maxilla and additional bones referable to the Middlelate Permian Chinese genus Gansurhinus, as well as a yet unidentified single-tooth-rowed taxon. Finally, new records of Late Permian tetrapods from the Korbach locality include a new taxon of bystrowianid chroniosuchian. This member of the enigmatic Laurasian reptiliomorph clade is documented by an isolated distinct dorsal osteoderm, which is diagnosed by concave lateral margins and subrectangular accessory processes. The discovery of Gansurhinus as well as the new chroniosuchian anamniote and lanthanosuchoid parareptile in Korbach provide strong evidence of tetrapod faunal connections between Western Europe and Eastern Europe and East Asia during the Permian. However, the presence of these Laurasian faunal elements as well as the otherwise mainly Gondwanan Procynosuchus in the Korbach locality indicates a complex biogeographic pattern among late Permian tetrapods, not reflected in higherlatitude Late Permian faunas.



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<sup>&</sup>lt;sup>\*</sup> Speaker

# A morphometric approach to the diversity of marginocephalian dinosaurs including ontogenetic data

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For the past decade, palaeontologists studying dinosaurs have been heavily debating whether certain morphotypes originally described as separate species are in fact only different ontogenetic stages of the same species. Most prominent examples are the thick-headed dinosaurs – Pachycephalosauria – Pachycephalosaurus wyomingensis vs. Dracorex hogwartsia and Stygimoloch spinifer, or the horned-face dinosaurs - Ceratopsia - Triceratops horridus vs. the species of Torosaurus. In the latter case, characters indicating the identity as ontogenetic stages of the same species occur on the frill of T. horridus, which seems to be developing into a more elongated shape, with thinner inner regions, and on the horns, which progressively curve forwards during ontogeny, in the largest specimens closely resembling specimens classically identified as Torosaurus. Comparable aspects can be observed in the horns and domes of D. hogwartsia and S. spinifer which may be interpreted as the earlier and later immature stages of P. wyomingensis. Which interpretation is preferred has a significant influence on the species diversity of dinosaurs in the late Cretaceous. Here we use geometric morphometrics, for comparing the skulls of selected marginocephalian dinosaurs (Marginocephalia = Ceratopsia + Pachycephalosauria) to shed further light on the true diversity in the late Cretaceous. We test the hypothesis whether multiple different described species of marginocephalian dinosaurs may actually only represent different ontogenetic stages of a single species, by projecting the skull shapes into a growth pattern. This pattern is compared to that of known ontogenetic patterns of other marginocephalians. If the patterns match, the "same species hypothesis" cannot be rejected. If the patterns do not match, the hypothesis is rejected. A possible alternative explanation for the thinning of the frill and the forward curving of the horns during development in ceratopsians might be that it is actually a shared trait among a larger ingroup of Ceratopsia and not a species specific trait. The species-or-stage problem is in fact a widespread phenomenon in different groups of animals. Developing and refining tools for identifying cases are therefore an important task. Marginocephalian dinosaurs are not only a good test group for such methods, but also an ideal case to popularise this rather general scientific problem.



S43 // Oral

Speaker

### Evolution of the dental eruption sequence in Cetartiodactyla (Mammalia) and phylogenetic insight: new evidence from fossils

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Dental ontogenetic parameters, such as the relative timing of dental eruption, were shown to provide clues to better understand the evolution and biology of mammals in their phylogenetical context. Among mammals, Cetartiodactyla, currently encompassing ruminants, tylopods, suines, hippos and cetaceans, display phylogenetic relationships that were the subject of longstanding debates. It has been recently demonstrated that in extant species of artiodactyls the eruption sequence of cheek teeth strongly varies from one clade to another. Here, we choose to investigate the origin of these dental ontogenetic changes and variations, as well as their phylogenetic interest by integrating early diverging cetartiodactyls (i.e. Paleogene species) to the picture. A special focus is made on Hippopotamoidea (i.e. "Anthracotheriidae" + Hippopotamidae), the putative sister clade of Cetacea according to molecular data. Our results show that the use of this source of dental character is reliable to characterize extinct and extant cetartiodactyl families. Interestingly, the reconstructed ancestral sequence based on fossils differs from the previous reconstruction based on extant species only, with the last molar erupting well before the last permanent premolar in most early diverging taxa. If this dental ontogenetic state is also observed in archaeocetes, it is not the case for Hippopotamoidea, in which molars erupt later. This difference might be explained by different growth rates and ecological traits possibly related to their distinct modes of adaptation to aquatic life

Speaker

### A 'double whammy' for dinosaurs and ammonoids: fake news or the real deal?

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66 million years ago, dinosaurs and ammonoids faced a nearly instant death in the aftermath of the impact of a 10-km asteroid or comet near Chicxulub (Mexico). Several hundreds of thousands years before and after, voluminous lava flows in the Deccan (India) upped climate change, possibly weakening biota and community structures before and delaying recovery afterwards. This 'double whammy' may have accounted to the massive scale of the 5th episode of mass-extinction on planet Earth, altering many evolutionary pathways across the 'Tree of Life'. Although that this 'double whammy' theory may sound sturdy, there is not so much evidence to support it. At least not for the two most iconic fossils of all time.

For the possibility that lava flows would alter diversity and spread of dinosaurs on the continents, there is simply very little evidence. In only one spot, the Hell Creek Formation, dinosaur remains are common in a sedimentary trajectory from within the ultimate 1 myr of the Cretaceous. Nearly all other sites only delivered bits and pieces on which it is difficult to evidence change throughout time (cf. type Maastrichtian), and for those sites with abundant skeletal remains, there are still a lot of timing issues (cf. only datable to the Maastrichtian or Upper Maastrichtian in a whole, and not with certitude within the Deccan outflow times). These two pitfalls make it nearly impossible to evaluate the impact of Deccan on dinosaur evolution, at least if based on real fossils.

For ammonoids in the marine realm, the resolution is much better, but still with a lot of blind spots, in particular in the vicinity of Deccan. Scouring through the literature, one can find a number of small to larger scale changes in ammonoid faunas that at least for their timing may correlate to the warming and cooling phases ascribed to Deccan volcanism, but also here, much more study is necessary.

To conclude, at present, it seems inappropriate to state that Deccan volcanism had a major effect on the composition of dinosaur and ammonoid faunas prior to the Chicxulub impact. Only more study and more field data are necessary to further explore this possibility.



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### Crocodylomorph teeth paleobiodiversity from a new locality in the Lourinhã Formation, Portugal (Late Jurassic)

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Five crocodylomorph species have been recovered from the Upper Jurassic of Portugal: the Teleosauridae *Machimosaurus hugii*, the Goniopholididae *Goniopholis baryglyphaeus*, the Atoposauridae *Knoetschkesuchus guimarotae*, and the mesoeucrocodylians *Lisboasaurus estesi* and *Lusitanisuchus mitracostatus*. All have been identified in the Guimarota site, and M. hugii and L. mitracostatus have been also recovered from the Lourinhã Fm..

Few studies on microfossil vertebrate assemblages have been carried on the Lourinhã Fm. (Late Kimmeridgian/Tithonian) of the Lusitanian Basin in Portugal, located 65 km north to Lisbon. As a part of systematic sampling of the microfauna of this formation, this study focuses on 95 crocodylomorph teeth, recovered in Valmitão (Ribamar, Lourinhã), split in four different morphotypes.

Teeth from morphotype 1 (n=44) are conical, lingually curved, withovoid to subcircular crosssections, well-marked carinae and enamel covered by vertical and parallel striations in both lingual and labial surfaces. These teeth morphologies characterize crocodylomorphs with generalist feeding habits, which may correspond to Goniopholididae. Teeth from morphotype 2 (n=11) are sub-conical, lingually and distally curved, with lenticular cross-sections, ziphodonts (with serrated carinae), and with smooth enamel. This kind of teeth is present in several crocodylomorph clades, thus we assign them to Mesoeucrocodylia indet. Teeth from morphotype 3 (n=15) are molariform to conical shaped, with bulky and low crowns, reniform to subcircular cross-sections, and enamel covered by vertical and parallel striations. These features characterized durophagous crocodylomorphs, belonging probably to Bernissartiidae. Teeth from morphotype 4 (n=25) are broad leaf-shaped, lanceolate to conical in shape with a hook-shaped apex, labiolingually compressed and elliptical to subcircular cross-sections, with mesiodistal carinae, and striated enamel with fan-shaped distribution. These features are typical of Atoposauridae.

The Valmitão crocodylomorph assemblage is congruent with those observed in other European localities from Late Jurassic and Early Cretaceous, with crocodylomorph faunas resembling to Atoposauridae, Bernissartiidae, and Goniopholididae. Similar associations have been recognized in other Portuguese Late Jurassic localities, but the studied sample differs by the absence of the marine *M. hugii*, which would suggest that Valmitão was deposited in a more continental environment.



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# An actualistic study of the taxonomic significance of skeleton and otolith morphology in *Gobius* and *Pomatoschistus* (Teleostei: Gobiiformes)

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The Gobiidae and Oxudercidae account for a significant fraction of the benthic component of the present-day ichthyofauna in the Mediterranean Sea, the North Sea and the NE Atlantic. The most speciose genera of the European Gobiidae and Oxudercidae are Gobius and Pomatoschistus, respectively, making them a particularly attractive model for the study of present – and past – species diversity. Both families have a fossil record based on skeletal material and isolated otoliths ("ear stones") that reaches back to the Oligocene. As whole skeletons are seldom preserved, while otoliths are much more abundant, many fossil species of Gobius and Pomatoschistus have been described exclusively on the basis of otoliths. However, the identification of fossil skeletons and of otoliths requires comprehensive knowledge of the taxonomic significance of their respective characters in modern species, which is currently not available for either Gobius or Pomatoschistus. Consequently, their 'true' species diversity in the fossil record has most probably not been fully recognized. Here we present an actualistic study of 14 extant species of Gobius and six species of Pomatoschistus, each represented by 5-10 individuals. We compiled four data sets comprising (i) meristic data (counts of vertebrae, fin spines, rays, pterygiophore formulae), (ii) linear measurements for morphometric characterisation, (iii) otolith shape indices based on linear, perimeter and area measurements, and (iv) Fourier analysis of otolith outlines. Each of the data sets was investigated using uniand multivariate statistical approaches. The results indicate that, while the two genera can be distinguished by any one of the four methods, only multivariate analysis of the Fourier otolith outline data could reliably separate almost all of the studied species of Gobius and Pomatoschistus from their congeners. Our findings thus provide a significantly improved framework for the taxonomic interpretation of fossil otoliths of Gobius and Pomatoschistus at the genus and species level. Nonetheless, species identification based on skeletons requires more characters than those studied here, and further assessment of the range of osteological variation between (and within) the extant species of Gobius and Pomatoschistus will be required to fully appreciate their species diversity in the past.



### Morphometric analyses of *Thecidellina* (Brachiopoda) from the upper Cenozoic of Curaçao: A record of attachment and modified shape

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The cideid brachiopods are less well-known components of the Modern Evolutionary Fauna, ranging in age from Triassic to Recent, and occupying cryptic habitats that are commonly overlooked; the shells are generally cemented to varied substrates which can modify the external morphology of the attached ventral valve. Although well known in cryptic, encrusting communities of Jurassic and Cretaceous age, they have received less attention in Cenozoic environments. Morphometric analysis of two samples of *Thecidellina* from the Pliocene Seroe Domi Formation and the overlying Pleistocene terraces on the Caribbean island of Curaçao shows that they have a high degree of morphological similarity and are probably the same species. The asymmetric form of this genus, however, shows no strong preference for any particular pattern of asymmetry suggesting that these shapes are not controlled by genetic factors. Rather the asymmetry appears to be determined by the size and shape of preferred attachment sites associated with a varied benthos and substrate, preferably coral and coralline algae.

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### Thinking outside the boxes, or why fossils are so important for improving our ways of biological categorisation

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We as humans like to think in boxes. It seems that this specific strategy of organising what we see in the world is accepted as being written deep down in the structures of our brains. Let us assume that this is correct for the moment being. Yet, the way how we form these boxes, logical classes or categories can follow various different strategies. Some of them are more effective than others in terms of necessary complexity. Speaking in an evolutionary-ecological manner there are strategies with a good cost-benefit ratio and some in which costs are unnecessarily high. I will present examples in which fossils can be used to identify cost-intensive categorisation strategies. Based on a limited view from modern-day biology the costs of these cases may seem low at a first glance. Often intensive comparison of extant forms can demonstrate that this is in fact not the case. Yet, their true ineffectiveness can be demonstrated more easily by bringing fossils into the picture. Examples to be discussed include classical Linnean ranks, species concepts, but also subdivision of individual development such as larval-juvenile distinctions. Fossils can help to identify cases where common strategies of categorisation will either lead to an ineffective high number of supposed categories or an indistinguishable continuum. In both cases the modern-day categories fail to properly include fossils. This discussion of how we identify categories has wide reaching implications. All metaanalyses in a biological context are highly dependent on the quality of the a priori categorisation. If the categorisation fails to properly represent the actual biological condition, the meta-analysis will be unable to provide a reliable result. In the times of modern biodiversity research, conservation biology and climate change we have to sharpen our tools. Fossils may prove to be the right sharpening steel.



Speaker

### Diversity and palaeoecology of tropical marine softbottom assemblages from the Late Triassic (Cassian Formation, northern Italy)

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Two fossil assemblages from the Late Triassic Cassian Formation (northern Italy, Dolomites) were investigated regarding palaeoecology and diversity. Both stem from landslide sites situated in the vicinity of Misurina and Lago Antorno. They consist of surface collections and bulk samples, which were washed and wet-sieved with a mesh size of around 0.5 mm. Both fossil assemblages are characterised by a similar set of species, dominated by molluscs, especially gastropods with respect to species richness and abundance. More than 600 specimens were found in the bulk samples from Misurina landslide and c. 250 specimens in those from Lago Antorno. Approximately 40 species were retrieved from Misurina landslide in comparison to c. 30 species from Lago Antorno. The surface collections from Misurina landslide contained 26 species and 116 specimens. At Lago Antorno, 17 species and 152 specimens were found in the surface samples. The gastropods Prostylifer paludinaris, Coelostylina conica and Ampezzopleura hybridopsis belong to the most abundant species. Nuculid bivalves and echinoderm ossicles are also characteristic fossil components. In addition, foraminifers are highly abundant, especially members of the genus Glomospira, as well as trace fossils representing coproliths in most cases. Less common are scaphopods. Sponges, ammonoids, and ostracods were only found with one or two specimens each. Diversity indices suggest that diversity of both assemblages is moderate. Both sampling types, bulk and surface sampling, differ regarding speciesabundance distributions, since smallsized species are overlooked in most cases during surface sampling. Nevertheless, rarefaction curves are similar between both sampling types pointing to a similar diversity regardless of the used sampling technique. Rarefaction analyses also show that evenness and species richness are low in comparison to other fossil assemblages from the Cassian Formation stemming from reefal or lagoonal settings. The palaeoenvironment of the assemblages from Misurina landslide and Lago Antorno can be interpreted as a basinal soft-bottom habitat of unknown water depth but probably considerably deeper than the nearby carbonate platforms. The presence of mostly articulated bivalve shells in addition to the lack of typical shallow water indicators, for example ooids, indicate an autochthonous origin of the invertebrate assemblages.



Speaker

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## A new narrow-gauge sauropod trackway from the Candeleros Formation (Upper Cretaceous, Patagonia, Argentina): a singular case for the Cenomanian sauropod track record

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Whereas theropod and ornithisquian dinosaur tracks are abundant in the Cenomanian rocks worldwide, sauropod tracks are relatively scarce. Hitherto, Cenomanian sauropod tracks are only known from Croatia, Morocco and Argentina. The Candeleros Formation (Neuquén Basin, Patagonia, Argentina) comprises a multiplicity of continental paleoenvironments. Its fluvial deposits exhibit the richest Cenomanian sauropod track record in the world, including the medium-gauge ichnotaxon Sauropodichnus giganteu s and a new sauropod trackway reported herein. This new finding is preserved in an alluvial plain paleoenvironment and is composed of five manus-pes track sets of a narrow-gauge trackway. Both manus and pes tracks are large in size and include conspicuous rims with very well-preserved symmetrical ripples on the top that are unprecedented in the track record. Such ripples suggest shallow waters previous to the track record and desiccation cracks all around in the surface indicate subaerial exposure after the tracks were produced. In the islet of Fenoliga (southern Istria, Croatia), wide-gauge and medium-gauge sauropod trackways have been related to the ichnotaxon Brontopodus. In the Kem Kem Beds (Morocco), two isolated and undetermined sauropod tracks have been reported. In the three occurrences, the tracks are preserved as concave epirelief, but it is not usually clarified if they are true tracks or undertracks, an important distinction for the gauge analysis. While wide-gauge trackways are dominant throughout the Cretaceous record and have been mainly attributed to titanosauriforms, narrow-gauge trackways, practically absent in Late Cretaceous deposits, have been referred to diplodocoids. The gauge in the Croatian trackways and in previous Argentinian records point to titanosauriforms as trackmakers. This new Argentinian record presented here is a narrow-gauge trackway. The trackmaker is attributed to diplodocoids, which in the Cenomanian are only represented by rebbachisaurids. This record represents the first sauropod narrowgauge trackway for the Cenomanian (and possibly for all the Upper Cretaceous) worldwide.

Speaker

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# The Quaternary deposits of the South Caspian and the adjacent areas on ostracoda fauna

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The South Caspian is one of the largest oil-producing regions within the Caspian Sea. Most of the offshore fields are focused here along with the main geologic oil and gas reserves of Azerbaijan. The development of the discovered fields as well as prospecting and exploration of new ones require detailed study of the Quaternary deposits: their material composition, stratigraphy, thicknesses and other properties. It is necessary to study these issues not only to improve the efficiency and provide safe geological prospecting and exploration but also to solve engineering and geological tasks related to the planned development of discovered oil and gas fields.

Study of fauna and stratigraphy of the Quaternary deposits in the South Caspian is important to learn the Quaternary history of the Caspian Sea. The Quaternary time interval is known for its frequent and abrupt fluctuations in climate, ocean and sea levels, considerable changes in topography, fauna, flora and other natural components of the Earth. The large-scale stratigraphic test drilling in the South Caspian water area provided multiple well sections and ostracod fauna, stratigraphy and lithofacies features of the Quaternary deposits in the region were studied in detail on this data.

We investigated the systematic composition and distribution of ostracod fauna from the Quaternary deposits over the vast South Caspian territory, the stratigraphic significance of the fauna and correlation of the data with the coastal area. Multiple well sections and their enclosed micro- and macrofauna were the study target. When well sections and natural outcrops were analyzed and correlated, other methods were also used (lithological, macrofaunistic, radiometric, electric logging, seismic logging, etc.). Based on the performed study, for the first time, a detailed stratigraphical sectional plane was designed for the Quaternary deposits of the South Caspian with their subdivision into suprahorizons, horizons and index species. Index species were identified on the successive change of zonal complexes. All these subdivisions play a regional role and correlate well with the ones from the adjacent areas of the Caspian region.

The paleontological processing of individual ostracod contingents, including multiple representatives of the genera *Leptocythere, Amniocythere, Euxinocythere, Caspiocypris, Cyprideis* and others, allowed species-specific features to have been identified appropriate for new ostracod species.

In the publication, we also highlighted the issues of stratigraphy, facies analysis and thicknesses of the Quaternary deposits in the South Caspian. The analysis of facies, thicknesses and fauna distribution shows that in the Quaternary time interval in the South Caspian region was characterized by rather dynamic paleogeographic settings: along with the active change of the sea bottom topography, salinity and temperature varied considerably and often, as well as the sea level.

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### The first skull of a Neogene Vermilinguan (Xenarthra, *Pilosa*) from the Inter-tropical Americas: Evolutionary significance

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The South American anteaters (Vermilingua) are part of Xenarthra, one of the four largest branches of the placental mammal evolutionary tree and one of the most characteristic terrestrial mammal groups throughout the Cenozoic of the Americas. Vermilingua includes highly specialized extant forms with remarkable anatomical modifications related to their myrmecophagic diets and a disparate range of locomotor modes, from mostly terrestrial to fully arboreal species. However, we know little about the evolutionary history that gave rise to these fascinating xenarthrans, largely due to their poor, fragmentary, and geographically-biased fossil record. Here we describe preliminarily the first fossil skull of a vermilinguan from the Intertropical Americas, specifically from the late Middle Miocene (Serravalian) of La Venta area (La Victoria Formation), Colombia. The new specimen (VPPLT 975) consist of the pre-parietal portion of a skull, without jugals. Based on the similar skull architecture and measurements of Tamandua, the estimated total skull length and possibly body size is slightly lower in the new specimen than those in that extant genus. The skull VPPLT 975 has a combination of distinctive features, including: (1) relatively short and thick rostrum (more than those of Myrmecophaga tridactyla and Neotamandua conspicua, slightly less than in Tamandua); (2) lateral suture lines of nasals tend to converge anteriorly with each other; (3) the lacrimal is relatively small and has a largely triangular outline; (4) jugals are inserted anteriorly respect to the position of nasals (more than those in Tamandua), which is a feature associated to the relative reduction of the posterolateral process of maxillary; (5) the maxillary is not part of the orbit. We also provide a phylogenetic hypothesis on the evolutionary affinities of this specimen and its respective taxonomic allocation. According to our analysis, this skull from La Venta represents a new genus and species of Myrmecophaginae with a basal position respect to the node Tamandua +Neotamandua +Myrmecophaga and probably more derived than Protamandua, from the early Miocene of Argentina. We suggest the existence of two recognizable taxa of extinct vermilinguans in La Victoria Formation of La Venta area, including the larger Neotamandua borealis. However, we call to caution about the weak support for the hypothesis that this latter species does belong to Neotamandua.



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### The ecology of brachiopods in ancient methaneseep environments

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Brachiopods were thought to have dominated deep-sea hydrothermal vents and hydrocarbon seeps for most of the Paleozoic and Mesozoic, and were believed to have been outcompeted and replaced by chemosymbiotic bivalves during the late Cretaceous. But recent findings of bivalve-rich seep deposits of Paleozoic and Mesozoic age have questioned this paradigm. By tabulating the generic diversity of the dominant brachiopod and bivalve clades from hydrocarbon seeps through the Phanerozoic, we show that their evolutionary trajectories are largely unrelated to one another, indicating that they have not been competing for the same resources. Whereas chemosymbiotic bivalves mostly rely on sulfide-oxidizing symbionts for nutrition, for the brachiopods bacterial aerobic oxidation of methane likely played a more prominent role. The availability of hydrogen sulfide and methane at seeps is governed by geochemical gradients and marine sulfate concentrations. Low sulfate concentrations result in low rates of sulfatedriven anaerobic oxidation of methane and consequently more methane is available to aerobic oxidation. Assuming lower marine sulfate concentrations during the Mesozoic compared to the Cenozoic, and consequently higher methane concentrations above the sediment surface at seeps, Mesozoic seeps facilitated colonization by epifaunal brachiopods. Thus rather than competition, geochemical gradients and ocean chemistry are put forward to have controlled the distribution and diversity of brachiopods and bivalves at hydrocarbon seeps through the Phanerozoic

Speaker

### New tetrapod specimens and chronostratigraphy of the Late Triassic Ischigualasto Formation at Cerro Las Lajas (La Rioja Province), northwestern Argentina

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The early diversification of most modern amniote clades, such as testudinatans, lepidosauromorphs, archosauromorphs, and mammaliaforms, started during the Early–Middle Triassic, and by the Late Triassic most of them were abundant and diverse. The Ischigualasto Formation of northwestern Argentina (late Carnian-early Norian), mainly explored at the Hoyada de Ischigualasto (San Juan Province), is one of the continental units that has best documented this transition. Recent fieldwork on the Ischigualsto Formation at Hoyada del Cerro Las Lajas (La Rioja Province) allowed us to considerably improve the knowledge of the fossil record of this unit. Only three archosaur taxa based on three specimens were previously reported from Cerro Las Lajas by José Bonaparte in the 70's: the holotypes of the ornithosuchid Venaticosuchus rusconii and the dinosauromorph Pisanosaurus mertii, as well as a specimen recently referred to the crocodylomorph Trialestes romeri. Here, we report additional fossil remains from the lower third (70m to 200m) of the Ischigualasto Formation at Cerro Las Lajas that includes: skeletons of four different species of hyperodapedontine rhynchosaurs (two of which are new), few partial skeletons of the traversodontid Exaeretodon sp., plus incomplete skeletons of an aetosaur, a proterochampsid archosauriform (Proterochampsa sp.), a non-shuvosaurid poposauroid, and a probainognathian cynodont (cf. Ecteninion). These taxa, except for three of the rhynchosaur species and probably the poposauroid, were previously reported from the two lowermost members of the Ischigualasto Formation at Hoyada de Ischigualasto. Our new high-precision U- Pb geochronology by the CA-ID-TIMS method suggests that the Cerro Las Lajas captures a near-complete succession of the Ischigualasto Formation and that the faunal assemblage presented here allows an assignment to the Scaphonyx -Exaeretodon -Herrerasaurus biozone of the Ischigualasto Formation at Hoyada de Ischigualasto. However, no diagnostic fossil remain has yet been discovered from the upper two-thirds of the unit at Cerro Las Lajas to be able to compare to the entire faunal assemblage of the Ischigualasto Formation in San Juan.



<sup>\*</sup> Speaker

#### Saurischia, Ornithoscelida, and the first dinosaurs

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Recent studies have challenged the traditional classification that splits dinosaurs into Saurischia (including theropods and sauropodomorphs) and Ornithischia, suggesting instead that theropods and ornithischians form a clade - Ornithoscelida - to the exclusion of Sauropodomorpha. These same studies have also argued for an older origin for dinosaurs, possibly in the northern part of Pangaea. We have reevaluated the main morphological dataset underpinning this proposal and, after rescoring each taxon based on first-hand observations of the fossils (thus providing an additional control check on scoring), a parsimony analysis recovered the traditional Saurischia/Ornithischia scheme, with theropods and sauropodomorphs united as Saurischia. However, this arrangement is not a significantly better explanation of the data in hand than either Ornithoscelida or the long-forgotten Phytodinosauria (Sauropodomorpha plus Ornithischia), showing that there is significant uncertainties about early dinosaur relationships and the basic structure of the dinosaur family tree. Our results also demonstrate that most alleged ornithoscelidan synapomorphies can be easily conceived as dinosaur symplesiomorphies, or as convergences between theropods and ornithischians, stressing the need for careful consideration of primary homologies during the framing and coding of character hypotheses. The Early-Middle Triassic timing of dinosaur origins has been suggested based on the putative deep nesting of the Middle Triassic Nyasasaurus parringtoni within dinosaur phylogeny. However, the incompleteness and questionable association of these fossils renders this hypothesis very weakly supported. Although there is some evidence for a Middle Triassic origin of dinosaurs, this is not substantiated by any uncontroversial record of the group in rocks dating to this age. Additionally, multiple palaeobiogeographical analytical tools, including numerical estimates of ancestral states, categorically supports the commonly suggested scenario of a southern Pangaea ancestral area for dinosaurs across a series of simulated iterations of the dinosauromorph evolutionary tree. This demonstrates that it is imperative to employ appropriate computational analytical tools before making biogeographical claims. In sum, we do not find substantive evidence for discarding the southern Pangaean model for the origin for dinosaur, nor the classical division of the group into Saurischia and Ornithischia.

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### A new chondrichthyan fauna from the Zhuganpo Member of the Falang Formation at Nimaigu section, Guizhou, China

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The Middle-late Triassic succession of the Nimaigu Section (Wusha area, Xingyi City, Guizhou Province, South China) has yielded two exceptionally well-preserved marine vertebrate faunas, i.e. the middle Late Ladinian Xingyi Fauna and the overlying younger Carnian Guanling Biota, of which the former moreover shows turnover of marine reptiles from coastal to oceanic environments. Herein, we report on a newly discovered chondrichthyan fauna from Nimaigu section, ranging from bed 135 to bed 153 of the Zhuganpo Member of the Falang Formation, near/within the Ladinian-Carnian boundary. This chondrichthyan assemblage consists of isolated teeth of three non-neoselachian shark genera (Hybodus, Lissodus and Prolatodon), one neoselachian shark genera (Mucrovenator) and front clasper denticles of a holocephalan (Arctacanthus). Hybodus and Lissodus are common components of Middle Triassic shark faunas in Europe, the former genus is also distributed in North America, Thailand, and Zuodeng of Guangxi province, China, and the latter also appears in South Africa, southwestern Kyrgyzstan, Central Asia. Prolatodon is a newly established genera based on 'Polyacrodus' bucheri and 'Polyacrodus' contrarius, which is known previously from British Columbia, North America, Guanling of Guizhou Province, China and Iberian Range, Spain during the Middle-late Triassic. Mucrovenator is a neoselachian shark genera only reported from Middle Triassic in Nevada, USA. Arctacanthus originated in the Permian and persists until the Carnian, its record can be found in Greenland, USA, Japan and Guanling of Guizhou Province, China. A further study of the fauna, associated with the Ladinian Xingyi Fauna and the Carnian Guanling Biota, possibly not only traces the survival of Palaeozoic chondrichthyan lineages into the Triassic but also enriches the ecosystem around the Ladinian/Carnian boundary.



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Speaker

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### Behavioural leads in evolution: New data on the evolution of Proboscidea (elephants and their relatives) through the Neogene to Quaternary of Africa

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Behaviour is a crucial element in morphological evolution among animals, for it is the means by which morphological adaptation is applied to the environment. While standard accounts of evolution explain the origin of adaptation by natural selection, they generally sidestep the question of the order in which a change in environment, change in behaviour, and change in form, take place. The potential importance of behaviour as an initiator of adaptive change has long been posited but little-investigated, and palaeontological time-series can in principle provide valuable case-studies to test for this mechanism. Following environmental change, a behavioural shift may allow the species immediately to survive the changed conditions while the slower process of morphological adaptation catches up. The nature of the behavioural accommodation may also influence the morphological changes that follow. Testing for this process in the fossil record requires us to break the circularity of deducing behaviour from morphology; it depends on proxies for behaviour independent of morphology itself. We have examined the morphological adaptive response of proboscidean feeding organs (teeth) to major shifts in climate and vegetation in the African Neogene to Quaternary. Using stable isotopes as proxies for habitat and diet, we previously found a 'lag' of several million years between a feeding shift (from C3 to C4 plants) in several lineages, and the morphological change in their teeth to better withstand abrasion. In our recent work we have used dental mesowear to more precisely identify a shift from browsing to grazing, and have also considered another potential driver of the adaptive change, an increase in environmental dust and grit, using dust records from adjacent marine cores. The results confirm a behavioural shift from browsing to grazing at a time of palaeovegetation change, but that dental evolution was a later, more immediate response to increased abrasion by dust and grit. These data illustrate the complex interaction of environmental change, behaviour and evolution, and highlight the requirements for cases-studies appropriate to test for the behavioural contribution to evolution in the fossil record.



<sup>&</sup>lt;sup>°</sup> Speaker

### New findings from the Naobaogou Formation (Lopingian, Permian) of Nei Mongol, China and their faunal implications

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The late Permian Naobaogou Formation of the Dagingshan Mountain produced the first vertebrate fossils in 1982 and although the discovered specimens represented different groups of amniotes, only the dicynodont Dagingshanodon limbus was formally described. Our recent survey of this geologic unit highlights that the Naobaogou fauna is dominated by dicynodonts. Thus, more than half of the discovered specimens are member of the Dicynodontia and a preliminary survey suggests the presence of seven or more dicynodont species in the fauna. The second more diverse group is Therocephalia, represented by three specimens documenting three different species. Two species are basal Akidnognathidae and the third appears to be related with the basal eutherocephalian Scylacosuchus from Russia. These therocephalian findings are important as they suggest that the early evolution of eutherocephalians as well as that of akidnognathids were a Laurasian phenomenon. Pareiasaurians are also represented in the Naobaogou fauna by at least two taxa. One can be referred to *Elginia*, only known from Scotland and its record in China indicates that there were no geographic barriers for tetrapods between Europe and China during the late Permian. What controlled the diversity of dicynodonts? One key factor is the diversity of plants they fed on. Different plants have been proposed as food for dicynodonts, including ferns and sphenophytes. The ferns and sphenophytes are diverse in Cathaysian flora, which distributed in the Permian of the Ordos Basin. Our work shows that the dicyndonts are also diverse in this area, and that their diversity might have been controlled by the diverse of ferns and sphenophytes.



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### Conodont biostratigraphy and age of the Early Triassic Fish-bearing-nodule levels in the Lower Yangtze Region of South China

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The Early Triassic Fish-bearing-nodule levels contain abundant, well preserved and diversified fish fossils, which presented a typical peri-Pangean distribution, recorded in East Greenland, East Spitsbergen, Northwest Madagascar and South China. The study of the Early Triassic fish faunas preserved in these nodular levels will help to understand the early evolutionary history of actinopterygians and the trophic recovery of the ecosystems after the end-Permian mass extinction. Outside South China, the richest fossil assemblages of those Fish-bearing-nodule levels are potentially synchronous, mainly concentrated around the Dienerian/Smithian boundary, with the exception of East Greenland that has a Griensbachian (early Induan) fish record. In South China, the fish-bearing-nodule levels preserved abundant perleidids, parasemionotids, coelacanths and other undescribed taxa, and have been found at Chaohu of Anhui Province, Longtan and Jurong of Jiangsu Province and also perhaps in Zhejiang Province located in the Lower Yangtze Region. The age and correlation of these Chinese fish-bearing-nodule levels are still unclear. We herein improve the knowledge of the age constrains for Early Triassic fish-bearing-nodule levels in the Lower Yangze Region of South China, based on conodont biostratigraphic data. A total of 101 samples were collected at Longtan (LT) section of Zhenjiang County and Qingshan (QS) section of Jurong County, Jiangsu Province, South China. Three conodont zones were recognized in the two sections, in ascending order as Scythogondolella milleri Zone, Novispathodus pingdingshanensis Zone, Triassospathodus aff. homeri Zone, among which the Scythogondolella milleri Zone is globally considered as the uppermost conodont zone of the Smithian and the base of the Novispathodus pingdingshanensis Zone is even proposed as the marker of the Smithian-Spathian boundary. The results of our study indicates that the Fish-bearing-nodule layers of Longtan and Jurong in Jiangsu Province are within the conodont Scythogondolella milleri Zone, correlating with the upper part of the Novispathodus waageni Zone of Chaohu in Anhui Province where fish-bearingnodule level lies, which confirms the Early Triassic fish-bearing-nodule levels in the Lower Yangtze region are precisely coeval, with an end-Smithian in age.



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# Evolution and diversification of dormice: first phylogenetic analysis

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Gliridae, the family of dormice, comprises today 9 genera and 29 species distributed in the old world. They are widely spread from temperate to tropical climates and from humid forest to open dry landscapes. The first occurrence in the fossil record is know from the Early Eocene in France (Eogliravus wildi), but the family has undergone a rapid diversification during the Oligocene and Miocene. For instance about 30 genera and nearly a hundred species are known in the Miocene-Pliocene of Europe. The reasons of this fast diversification and later drastic decrease of diversity remain poorly understood. Previous palaeontological studies are based on a classification separating Gliridae into five subfamilies: Gliravinae, Glirinae, Dryomyinae, Myomiminae and Bransatoglirinae. Subsequent works follow this classification, but still, the referral of some genera to a subfamily remains questionable and palaeoecological inferences of the different subfamilies remain difficult. Here, for the first time, a phylogeny of the family is proposed, including both extant and fossil taxa. Our first results partly support this classification but also illustrate an evolutionary history more complex than expected. A complementary analysis using molar enamel thickness (based on CT-scans) shows that glirid taxa can be divided in two groups with different ecological features. The group with small sizeand generally low thickness values (group 1) includes Eogliravus, Glamys, Glirudinus, Microdyromys, Paraglirulus, Eomuscardinus and Butseloglis, whereas the other one with larger sizeand thicker enamel (group 2) includes Glis, Bransatoglis, Myoglis, Miodyromys and Pseudodryomys. Group 2 shows significant negative correlation (Spearman, p =0,045) between enamel thickness (based on the root mean square of thickness values) and size (based on molar size), which is interpreted as a mechanical adaptation to accommodate different morphologies from buno-lophodont to lophodont. This ecological diversification starting during the Late Oligocene might have enabled the strong Early Miocene diversification, at a time when both groups co-exist. In turn, the decrease of the diversity from the Pliocene onward might be linked to the almost disappearance of group 1.



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### The first unambiguous skeletal record for the skates (Batomorphii, Rajiformes) from the early Miocene of Upper Austria

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The order Rajiformes, whose representatives are also known as skates, is a diverse and welldefined monophyletic group within the Batoidea which includes almost half of all living batoid fishes, and consisting of about 290 living species arranged in 38 genera. Skates are worldwide distributed and occur mainly on continental and insular shelves, from coastal to abyssal depths, and from temperate to cold waters. Skates are benthic batoids characterized by a series of morphological traits, including oviparous development, alar and malar thorns in adult males, weak electric organs on tail, pelvic fins expanded laterally and usually divided into two lobes, branchial copula with forked anterior expansions, suprascapulae fused to the median crest of the synarcual forming the pectoral arch, secondary hemiaulacorhizid root type, and other unique features of the clasper morphology. Although divergence time estimates predict that skates should have been already present in the Jurassic, unambiguous fossil occurrences are known only from the Late Cretaceous. However, since all fossil taxa are represented by isolated teeth only, which are phylogenetically poorly informative, very little is known about the evolutionary history of this group. Some complete and articulated skeletal remains from the Late Cretaceous deposits of Lebanon have been traditionally assigned to skates, but their placement within the group requires further deep investigation since they lack most of the diagnostic features of the skates. Although in the Cenozoic articulated batoids have been recovered from Palaeogene marine sediments of the Bolca Lagerstätte and Grube Unterfeld, freshwater deposits of Green River Formation, and from the Neogene of SE Asia, no skeletal material referred to skates has been recognized so far. Here we report the first unambiguous holomorphic skate in the fossil record represented by a single articulated skeleton collected from the early Miocene fish-bearing strata of Upper Austria, and today housed in the Natural History Museum of Vienna. This specimen exhibits a unique combination of skeletal and dental features that clearly support its assignment to a new genus of the order Rajiformes. The phylogenetic analyses revealed its derived position within the family Rajidae, which includes genera like Amblyraja, Leucoraja, Rajella and Raja. The comparison between this Miocene specimen and the holomorphic Late Cretaceous batoids from Lebanon traditionally assigned to skates, concurs to suggest that this Neogene occurrence from Austria represents unquestionably the first known skeletal record for the group. Finally, the morphological and phylogenetic affinities of the specimen with the living skates suggest a close association of this taxon with the temperate-cold water environments hypothesized for the Central Paratethys during the early Miocene.

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## Use of convolutional neural networks to automatically identify holes in brachiopod fossil using pictures

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In the study of fossil brachiopod valves, a feature of interest is the presence of holes. Such features can indicate possible ecological interactions, that otherwise would not be observable in the fossil record. Depending on the number, morphology and position of the holes they can be interpreted as predatory, opportunistic or even parasitic in origin. Other studies also point to holes made by severe transportation, in the case of robust valves.

A growing area of research in machine learning is the automatic identification of features in images. Applications such as identifying presence of people or particular animals, differenting animals such as separating dogs from wolves are successfully solved using the technique of convolutional neural networks. Two of the main advantages of the technique are: an end to end learning system, namely that the machine needs nearly no information or pre-processing in order to identify a pattern in a picture apart from a labeled dataset giving the presence of the desired feature; and the fact that is open to tell apart abstract features no easily specified using mathematical and geometrical parameters or even logical statements.

It is proposed to train a convolutional neural network using images from the literature and images collected as research work in order to achieve an automatic system for classifying and locating holes in brachiopod fossils.

Such a system represents a first step towards applications of machine learning in paleontology as an automated tool to aid paleontological researches. The fossils used in this study are from the Paraná Basin Devonian. Among 6,000 samples containing lingulid valves, only 25 valves showed the occurrence of holes. This project now aims to automate the recognition of these features on the photographs of this material.



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#### X-ray fluorescence as a tool for interpreting pigmentary colours in fossil insects

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Many insects exhibit striking colour patterns on their cuticle, which are produced primarily by pigments such as melanins, carotenoids and pterins. Fossil specimens can exhibit similar patterns, but the origins of this fossil patterning and the nature of the pigments responsible are unknown. We resolve these issues using synchrotron X-ray fluorescence to characterize the spatial distribution of trace elements in the cuticles of fossil and extant insects. We mapped the concentrations of 11 elements in cuticle regions known to possess specific pigments in extant insects. Linear Discriminant Analysis (LDA) of the concentration data reveals a strong taxonomic signal whereby members of the same family show similar chemical signatures. Within families, cuticle regions containing different pigments have distinct trace element chemistries, demonstrating that the broad taxonomic trends in chemistry are overprinted by a strong pigment-specific signal. The trace element chemistry of fossil insect cuticle differs to that of the modern analogues, indicating diagenetic overprinting, and is controlled by both depositional context and taxonomy. These data will aid the interpretation of pigmentary colour patterning in fossil insects, thus informing models of the functional evolution of colour in insects through deep time.

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# Evolution of Foraminifera reflected in their geological record

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Foraminifera is a unique group with the most full geological record since Cm. The presence of their five classes is documented in this record at different times: Astrorhizata and Spirillinata since Cm, Nodosariata and Miliolata (including fusulinoids – Mikhalevich, 2009, 2013) – since O, Rotaliata – since upper D, mostly C (classification after Mikhalevich 1980 – 2013, Saidova, 1981 based on phylogenetic and morphologic analysis and supported by later molecular studies (Pawlowski et al. // 2013). Their shell wall developed from the organic and agglutinated to different calcareous types at different times: in Spirillinata - Late D, Nodosariata – Early D, in Miliolata - C, but including fusulinoids – much earlier, Rotaliata – in Upper Tr. Foraminiferal shells developed from unilocular and pseudochambered (Astrorhizata and early representatives of Spirillinata, Miliolata, Nodosariata (this class having also highly specialized unilocular line-lagenids) to multichambered (Spirillinata, Miliolata, Nodosariata, Rotaliata) and supermultichambered in Miliolata and Rotaliata in the process of polymerization. In some advanced lines the differentiation of chambers at the morphological and even functional level took place (embryonic, floating, brood chambers - Spirillinata, Miliolata, Rotaliata). The integrative systems within the shells developed from foramina to additional systems such as stolons, tunnels, apertural integrative systems up to the systems of canals unique at the unicellular level and comparable in its function with the blood system of higher animals. The aperture turns its position from terminal in all the multichambered classes except Rotaliata, where it is initially basal. The multiplication of the apertures and the complications of their inner and outer structure took place in all the classes. In their cytological development the polymerization of the nuclei occurred (Spirillinata, Miliolata, Rotaliata) and their further differentiation (Miliolata, Rotaliata) as well as the presence of some special organelles in planctonic forms (subclass Globigerinana of the class Rotaliata) – such as microvilli, wide cytoplasmic layer around the shell or cytoplasmic capsula (in Hastigerina). The evolutionary advancements were going independently and in parallel in each of the phyletic lines (classes) having in each of them their special characters and resulting in the morphological complexity of the Foraminifera striking for the unicellular level of organization.



<sup>&</sup>lt;sup>'</sup> Speaker

#### Estimating a growth rate and habitat of the late Cretaceous *Eutrephoceras* (Nautilidae, Cephalopoda) with stable isotope records

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Cephalopods, a group of molluscs, which arose in the Cambrian, have been well diversified through the almost entire interval of the Phanerozoic. Although, besides external morphology, their mode of life and longevity have potentially been modified through this evolutional history, many aspects of these issues are still not fully understood. For instance, since they are assumed to have maintained neutral buoyancy within a water column, precise depth of habitat is difficult to estimate only from shell morphology. For tackling these issues, stable carbon and oxygen isotopic analyses have been conducted on both extant and extinct cephalopods. Oxygen isotopic temperatures recorded on shell materials of modern Nautilus (Nautilidae) have revealed the depth of habitat of an individual analyzed, when they were compared with the thermal structure of a water column. In this study, we show stable carbon and oxygen isotopic records of the late Cretaceous Eutrephoceras (Nautilidae), which is the direct ancestor of modern Nautilus, to understand evolution of mode of life of nautilids. Bivalves (Crassatellites vadosus), Eutrephoceras dekayi, and a variety of microfossils utilized in this study were recovered from the Coon Creek Formation, Tennessee, U.S. Oxygen isotopic temperatures obtained from shell materials of E. dekayi are comparable to those of benthic foraminifers and ostracods, and significantly cooler than those of planktic foraminifers, indicating that E. dekayi analyzed inhabited on or very close to the bottom of the ocean. We also assessed seasonal variability of physical and chemical properties of the water column from sclerochronological and isotopic analyses of bivalve shells. Seasonal cycles in carbon and oxygen isotopes identified in bivalve shells are compared with the sigmoidal patterns in isotope records on E. dekayi to estimate a growth rate. The estimated growth rate of E. dekayi is comparable to those of modern Nautilus, implying that the depth of habitat and growth rate are conservative propertied in Nutilidae.



Speaker

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# Evolutionary history of higher gastropods - fossil milestones

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The gastropod subclasses Caenogastropoda and Heterobranchia are the most diverse groups of living gastropods. They are sister-groups according to recent phylogenetic analyses and form the informal clade 'higher gastropods'. Both subclasses can be separated from each other by their protoconch morphology. Marine caenogastropods have orthostrophic, multi-whorled protoconchs if formed by plankton-feeding larvae; larval shell and teleoconch have the same coiling direction (orthostrophic). By contrast, Heterobranchia undergo a change in shell coiling direction during ontogeny (larval heterostrophy). However, protoconch preservation is rare, especially in the Palaeozoic. The minimum age of caenogastropod/heterobranch divergence is probably Devonian and certainly Early Carboniferous. The oldest possible caenogastropods with preserved orthostrophic larval shells have been reported from the Devonian - clear caenogastropods are as old as Early Carboniferous. High-spired slit-bearing gastropods (Murchisonia -like) from the Carboniferous have a larval shell resembling that of some modern cerithioids and a crossed lamellar shell structure which suggest that they are caenogastropods. The oldest member of the extant superfamily Cerithioidea combining a siphonal canal with a carinate larval shell has a Middle Permian age. The oldest Stromboidea are known from the Early Jurassic and belong to Aporrhaidae. The oldest possible neogastropod (Maturifusidae) has an Early Jurassic age. Cypraeidae appear in the Late Jurassic and very diverse parasitic caenogastropod families such as Triphoroidea originate in the Late Cretaceous. The oldest gastropods showing possible heterostrophy have been reported from the Devonian but clearly heterostrophic gastropods are present since the Carboniferous with the families Donaldinidae and Streptacididae. They closely resemble living 'lower Heterobranchia' (Ebalidae and Murchisonellidae). In the earliest Triassic, the first architectibranchs (formerly 'opisthobranchs') and Mathildoidea occur suggesting a major turnover in Heterobranchia after the end-Permian mass extinction. Ringiculoidea date back to the Middle Jurassic and are the shell-bearing sister-group of the shell-less Nudibranchia. These fossil milestones of gastropod evolution may mark true originations as well as the age of exceptional preservational windows i.e. formations which have yielded gastropod with preserved protoconchs and thus such data must be used with caution.



Speaker

#### Evolution of the molecular characteristics of feathers: evidence from feathered dinosaur and bird fossils from China

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Discoveries in the past twenty years of dinosaurs with feathers or feather-like integumentary structures have not only provided compelling evidence in support of the dinosaurian origin of birds, but also greatly increased our insight into the origin and evolution of feathers. Despite the significant progress made toward understanding the morphological evolution of early feathers, far less is known about their molecular characteristics. The biochemistry and molecular composition of feathers in living birds is well defined, but the molecular composition of the fossil feathers is debated. Modern biophysical studies on feathers suggested that the molecular structure of feathers contributes directly to its biophysical capabilities, specifically, the feather  $\beta$ -keratin.

Hypotheses regarding the role of  $\beta$  -keratin evolution and its relationship to both feathers structure and flight can be only best resolved through direct testing of the molecular evidence from fossil record. To accomplish this, we selected five samples of feathered dinosaur and bird fossils from Middle-late Jurassic, Early Cretaceous and Oligocene of China for analyses. We employed multiple high-resolution analytical methods, e.g. SEM, TEM, ChemiSTEM elemental mapping, and in situ immunohistochemistry, to show convincingly that the preservation of endogenous  $\beta$ -keratin in Mesozoic and Cenozoic feathers are morphologically, structurally and chemically consistent with  $\beta$ -keratin in extant feathers. Then we capitalized on the homology and variations of the molecular structure of  $\beta$  -keratin, to generate polyclonal antisera against two synthetic peptides that specifically recognize only the feather-type (feather and feather-like)  $\beta$ -keratins.

Results show that the  $\beta$ -keratin epitopes specific to feather-type  $\beta$ -keratins are preserved in all studied five fossil feathers, in patterns consistent with those seen in extant feathers. While another two fossil samples (the claw of an oviraptorid dinosaur and the fiber of Shuvuuia), previously showed to contain  $\mathbb{P}$ -keratins, here they lacked the feather-type  $\beta$ -keratins. When these data are considered in context of the geologic age, and based upon the well-established phylogenetic framework of the avian and closely-related groups, feather-type  $\beta$ -keratins arose in the feathers before the divergence between non-avian dinosaurs and birds, and thus preceded the origin of powered flight of birds.

Our work provides a case study of using molecular evidence from fossils to test hypotheses on evolution of major clades and biological innovations, and highlights the importance of integrating morphological, developmental, past and present molecular data for discussing broad evolutionary issues.

Furthermore, from a molecular structure level, has high preservation potential, low potential sources of contamination, but phylogenetically informative, which plays a key role in the study on the origin of new integumentary structures and morphological complexity of vertebrates. So  $\beta$  -keratins are excellent targets for molecular studies on deep time fossils.

\* Speaker



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#### The oldest record (pre-Callovian) of thyreophoran dinosaur tracks in the Southern Hemisphere: ichnological and geological implications

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The track record of thyreophorans is well known in the Jurassic, but it is restricted to the Northern Hemisphere. Only in the Cretaceous it is documented around the world. Some ichnogenera attributed to thyreophorans are well documented in the Jurassic of Europe, North America and also in Northern Africa. Conversely, in the Southern Hemisphere, the oldest documented thyreophoran tracks were described in the Jurassic-Cretaceous boundary, particularly in South America; but the stegosaurian or ankylosaurian affinity of some trackways remains debatable. These groups only present unequivocal tracks in the Upper Cretaceous. In this work, an isolated track from the Middle Jurassic of the Neuquén Basin in Patagonia of Argentina is reported. It is a well preserved pes documented on the top of a 3D fluvial dune. It is subtriangular to subrounded distally, with a well impressed heel, and three very short digit impressions of similar length which are not rotated. The track is slightly longer than wide, with an L/W ratio in agreement with the ichnogenus Deltapodus. However, since it is an isolated track and differs in the digit morphology from the holotype, the assignment to this ichnogenus remains tentative. The continental deposits containing the track belong to the Lajas Formation (Aalenian to Callovian). This unit have been traditionally interpreted like marine or marginal marine (deltaic) in outcrops. It constitutes the regressive phase of the first full paleopacific transgression in the Neuquén Basin. The lower boundary of the unit is transitional while the upper one is an unconformity intra-Callovian in age. The track is recorded in the lowermost part of the unit possibly overlying the intra-Bajocian unconformity in the Covunco area, and documents the first documented subaerial exposition for the unit. The thyreophoran affinity is supported osteologically for an almost complete skull discovered in the underlying Los Molles Formation (mainly Toarcian), but the material is under review and it could be assignable to stegosaurians, which were already documented in outcrops of the Early Cretaceous La Amarga Formation (post-Hauterivian). The track constitutes the oldest dinosaur record in the basin, but also the oldest track with thyreophoran affinity in the Southern Hemisphere. Other dinosaur tracks recorded in the basin are dominantly Cretaceous and correspond to theropods and sauropods.



Speaker

#### The Tahag Rhino, Atakor, Southern Algeria

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During the 1960's mentions were made in several publications of the discovery of vertebrate fossils at Tahag, Hoggar, southern Algeria. The small basin from which the fossils were collected has been localised using Google Earth based on the maps in the thesis of Pierre Rognon. It lies at 23°24'18.0"N 05°34'53.1"E at an altitude of ca 1780 m. The specimens which formed the basis of the reports were never described, although allusion was made to a lower incisor of a rhinoceros, and some proboscidean and crocodile remains, as well as coprolites, some of which reportedly contained rodent remains, on the basis of which a Lower Villafranchian or Pliocene age was estimated for the Tahag deposits. The Tahag collection has resurfaced in the Muséum National d'Histoire Naturelle in Paris, having been stored in drawers that have been inaccessible since the mid-1960's. This presentation discusses the rhino fossils from which it is concluded that they are likely to be Middle Miocene or older, the lower incisor agreeing in dimensions and morphology to specimens from Maboko (Middle Miocene) and Karungu (Early Miocene) in Kenya. Detailed description and comparisons of the fossils are envisaged, because, if the new correlation is valid, it opens a new chapter on the biogeography and biochronology of a part of Africa which has not previously yielded Middle Miocene fossil mammals.

Speaker

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### Laser-Stimulated Fluorescence: soft tissue and skeletal detail revealed in micro and macro fossils

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Laser-Stimulated Fluorescence or LSF uses laser light to stimulate the fluorescence of fossil skeletons as well as the chemical signatures and morphologies of preserved soft tissues. This includes fluorescing specimens that are dark under UV light, backlighting carbon films, detecting unseen body outlines, revealing fake or composite fossils and detecting geochemical differences at the parts per million level.

Since 2015, the use of LSF has produced many new and exciting discoveries. LSF clarified the countershading camouflage of the early horned dinosaur *Psittacosaurus*. It showed the wing configurations and footpads of the basal bird *Anchiornis* and the early short-tailed bird *Confuciusornis*. LSF images of *Archaeopteryx* specimens revealed the hidden quill of the first feather fossil and contributed to significant revisions of their phylogenetic codings. Among pterosaurs, LSF showed the shoulder bulk and hinted at the vasculature of the wings. It showed structural details of a fish eye that corroborate the lagerstaetten taphonomic model of the fossil deposit. LSF has been used to differentiate the parts making up composite specimens, helping to ensure their proper study. Rare specimens of egg shell have even been found on anthills by using LSF at night.

Currently, new uses are being developed for histology to complement traditional white light and cross-polarised light microscopy as well as the potential to reveal 'hidden' soft tissues in the earliest life. In presenting past uses and results as well as on-going work, we intend to provide a platform for further methodological development and its popular utility by the palaeontological community.



Speaker

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#### The significance of wing base in Palaeodictyoptera (Insecta: *Pterygota*): a case study of *Dunbaria* Tillyard

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The articulation of insect wings has been studied for more than a century. Currently the structure of the wing base is particularly useful for resolving higher phylogeny of various groups even on ordinal or supraordinal levels. However, the correct interpretation of wing bases and the identification of homologous structures among the main clades of Pterygota as Ephemeropterida, Odonatoptera, and Neoptera remains a difficult issue of morphology. The Late Paleozoic Palaeodictyopterida is a major clade to help clarifying the early divergence of Pterygota and shed light on this problem.

The present study uncovers new evidence of wing base structures in the genus *Dunbaria* and provides broader comparison among Spilapteridae and other Palaeodictyoptera. In contrast to previous works these newly obtained results reveal the homologous architecture between Palaeodictyoptera and extant Ephemeroptera, Odonata and Neoptera.

This study is a contribution to the project of the GrantAgency of the Czech Republic (No. 18-03118S).



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Speaker

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### Late Paleogene xenarthrans from Quebrada Fiera (west-central Argentina): implication for the paleogeography of cingulates (armadillos and glyptodontids) and the basal condition in megatherioid and mylodontid sloths

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Late Oligocene vertebrate faunas are uncommon in South America. The Argentinean locality of Quebrada Fiera was first noted by Gorroño and colleagues during the 1980s. Recently, more than a dozen field expeditions have revealed an abundant and diverse mammalian fauna, mainly composed of notoungulates but also with representation of marsupials, rodents, and xenarthrans. A lizard and a giant carnivorous bird complete the vertebrate assemblage. Here we present its highly diversified armored xenarthrans and one of the oldest sloth assemblages of America.

Hundreds of isolated scutes reveal the existence of eleven cingulates. Dasypodid armadillos are represented by *Stenotatus ornatus* and two species of *Meteutatus (M. lagenaformis* and a new species), and a new genus of Euphractini. Peltephilids are represented by two species of *Peltephilus (P. undulatus* and a new species). Giant Glyptodontidae are represented by *Glyptatelus* cf. *tatusinus* and cf. *Clypeotherium*, a taxon of uncertain affinities, a Propalehoplophorinae, and the palaeopeltid *Palaeopeltis inornatus*.

Cranial and post cranial remains suggest the presence of three sloths, two species of the mylodontid *Octodontotherium* (*O.* cf. *grande* and a smaller species), and a small sized megatherioid Megalonychidae. *Octodontotherium* teeth are constituted by a thin peripheral wall of cementum, a thick orthodentine layer, and a reduced central core of vasodentine. Lumbar vertebrae of *Octodontotherium* preserve the oldest evidence of xenarthry in the order, with supplementary intervertebral joints, reduced anapophyses, and short diapophyses. Its hind limb is markedly curved and the knee joint includes an ossified meniscus and a cyamo-fabella, which contribute to the characteristic locomotion of "ground sloths." The second mylodontid referred to *Octodontherium* is represented by a short, bulky humerus with a massive deltopectoral shelf, a deep entepicondylar foramen, and a gigantic entepicondyle. The small megatherioid possesses a reduced lower caniniform followed by a diastema and a *Hapalops* -like astragalus but with fused ectal and sustentacular facets.

The mammalian assemblage of Quebrada Fiera is now well known with about thirty taxa, principally native ungulates and endemic xenarthrans, and almost all groups of mammals present at that time in South America are represented. Its composition, clearly Deseadan in age, reveals a mix of taxa represented only in this locality or reflecting a strong austral influence.



<sup>&</sup>lt;sup>\*</sup> Speaker

#### New Pleistocene mylodontid ground sloths from the Quaternary of Brazil

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Xenarthra is a characteristic group of the endemic South American mammalian fauna. Most knowledge of the evolution of South American mammals is closely tied to austral areas, whereas tropical regions have been largely neglected. Several expeditions carried out by one of us (C.C.) over several decades in some 400 caves in Minas Gerais and Bahia (Brazil) have uncovered five extensive mammalian assemblages including ground sloths. Following the recent descriptions of the megalonychids *Ahytherium aureum* and *Australonyx aquae*, we are currently focusing our efforts on mylodontid taxa.

Preliminary revisions of *Glossotherium* have allowed us to validate at least *G. robustum*, and *G. tropicorum*. The latter is characterized, among other features, by an elongated and slender skull, nearly linearly arranged tooth rows, and a medial humeral margin extending distally beyond the deltopectoral shelf.

Thereafter, we were able to recognize a new Quaternary *Glossotherium* species from the Brazilian cave of Toca dos Ossos (Bahia), represented by several skulls and nearly complete postcranial remains. It is characterized by a gently convex dorsal skull margin over frontoparietal region, short predental region, upper tooth row length nearly twice width across the C1s, M1 with mesial wear, humerus similar to that of *G. robustum* but with a less prominent deltopectoral shelf, and radius with a maximal distal width one third its total length. Preliminary phylogenetic analysis based on craniodental characters, suggests the monophyly of (*Glossotherium* + *Pleurolestodon*), whereas *G. tropicorum* and *Glossotherium*. *sp.* nov. are sister taxa.

Finally, *Ocnotherium* was erected by Lund in 1839 based on three isolated teeth from Lagoa Santa. New specimens from Toca dos Ossos cave, including a nearly complete skull and a partial skeleton, allow us to describe more completely this very poorly known gigantic sloth. *Ocnotherium* is characterized by a skull equivalent in size with *Lestodon* but post-cranial elements slightly smaller than in the latter, two upper caniniform teeth separated from the third upper tooth by a prominent diastema, first upper molariform with characteristic mesial and occlusal wear, broad and rounded mandibular symphysis, and manus and pes with the same general conformation as those of *Lestodon*. The description of *Ocnotherium giganteum* will permit evaluation of its phylogenetic position among Mylodontidae and testing of the monophyly of Lestodontinae.



Speaker

#### A new cladistic insight at the comparative anatomy, phylogeny and systematics of rudists (Bivalvia, Hippuritida)

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The rudists (order Hippuritida) are a taxon of bivalve animals that are now extinct, characterized by a pachyodont hinge composed of three thick teeth. Appearing in the Jurassic (Oxfordian, 164 Ma), the diversification of rudists occurs in warm shallow seas, on the carbonate platforms of the Tethys and Atlantic, until they completely disappear during the Cretaceous/Palaeogen crisis (66 Ma). The history of rudists spreads over nearly 97 Ma and counts more than 2000 species. The phylogeny of the rudists is however very poorly known, as only one complete cladistic analysis has been produced to reconstruct the kinship relationships between families. The problematic of our work has been to bring new elements to the understanding of the history of rudists by applying new approaches and developing new methods of phylogenetic analysis. The phylogenetic method used here is three-taxon analysis. The use of triplets (three-taxon statements) has also allowed us to develop a new metric, the nodal retention index, which we use to describe evolutionnary trees. We propose a new phylogeny, based on 40 arborescent characters. The evolutionnary scenario of the rise of pallial canals is completely reviewed and involves now nine derived states, compared to two in the previous analysis. This new phylogeny completely overhauls relations between the rudists families. For example, the large Hippuritidae family is found as sister group of the Radiolitidae, a kinship relationship which had never been proposed before. Of the thirteen rudist families, only four are found monophyletic, and both of the two superfamilies are found polyphyletic. Two major episodes of diversification are found, respectively during the Hauterivian and Albian. These initial results are a starting point for addressing other issues, such as whether these radiations are adaptive or linked to episodes of maximal extension of carbonate platforms.



Speaker

### Beta diversity in Triassic and modern marine communities

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To uncover changes in diversity patterns through time, it is useful to analyze faunas with minimal preservational bias from different time periods. Due to the wealth of well-preserved fossils from different habitats, the Middle to Upper Triassic Cassian Formation is very well suited to test hypotheses on the principles of diversity assembly and to provide a baseline for the evolution of community diversity over time. Biodiversity is very high in the tropical reef-related setting, not only for a Triassic assemblage, but also compared to similar Recent environments. Over 1000 species have been described from the Cassian Formation. Based on a quantitative analysis of 44 samples, the total gamma diversity measured as Shannon entropy ( $\gamma$ ) is 4.26 (based on all taxa, a large majority being molluscs). Mean Jaccard dissimilarity among fossil sites ( $\beta_{JAC}$ ) is 0.94. What is the origin of such a high diversity?

Two Recent molluscan death assemblages from shallow-water shelf areas are analyzed for comparison: Bulk samples collected from the Gulf of Trieste, Northern Adriatic Sea ( $\gamma = 3.55$ ;  $\beta_{JAC} = 0.67$ ), and bulk samples from the Northern Bay of Safaga, Red Sea ( $\gamma = 4.40$ ;  $\beta_{JAC} = 0.83$ ).

To help discern the patterns of between-assemblage diversity, we partitioned beta diversity into its spatial turnover and nestedness components. With a multiple-site Simpson dissimilarity of  $\beta_{SIM} = 0.94$ , we find that beta diversity in the Cassian Formation is ascribed almost completely to species turnover. The nestedness component is very low ( $\beta_{NES} = 0.03$ ). The Safaga Bay fauna exhibits a similarly low nestedness component ( $\beta_{NES} = 0.05$ ) and lower species turnover ( $\beta_{SIM} = 0.82$ ) than the Cassian fauna. The results reveal a much lower species turnover in the Adriatic Sea fauna ( $\beta_{SIM} = 0.53$ ) and a larger nestedness component ( $\beta_{NES} = 0.19$ ). Comparing the results with several other fossil datasets (Jurassic, Eocene, Pleistocene), all with a species richness of the same order of magnitude, we find a similarly low nestedness component as in the Cassian fauna (only the Adriatic fauna shows higher nestedness values). This implies that species replacement, not species loss, is at the root of the high dissimilarities among the faunal assemblages in the Cassian Formation, as well as in the other tested datasets. This leads us to postulate that speciation took place in separate areas in this heterogeneous reef environment, yielding very high gamma and beta diversity.

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#### Taxonomic studies of fossil bovids from the Lower Siwalik Hills of District Chakwal, Punjab, Pakistan

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The Dhok Bun Ameer Khatoon (DBAK) is an important site in the lower Siwalik deposits of Chakwal district, Punjab, Pakistan, containing a highly diverse fossil fauna. Several field tours were conducted to collect fossil specimens. The collection indicates that Bovids are dominant in this locality. We have collected the fossil remains of an important genus *Gazella* (family Bovidae) for thorough investigation which had previously been recorded from Middle Siwaliks. The samples have been identified as *Gazella lyddekeri* on the basis of mandibles and isolated upper and lower molars. Different aspects like biogeographic distribution, evolution and taxonomy have been discussed and compared with European fauna. This species was a mixed feeder- indicating the presence grass and bushy vegetation in DBAK.



Speaker

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#### New fossil remains of even toed mammals from the Late Miocene of Pakistan: evolution, systematics and biogeography

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The Siwalik formations of northern Pakistan consist of ancient river deposits that accumulated from the early Miocene to late Pliocene. The Siwalik sequences have been recognized for their rich terrestrial vertebrate fossil record. The Miocene-Pliocene strata have traditionally been divided into the Kamlial, Chinji, Nagri and Dhok Pathan formations. The ridges are formed by laterally extensive channels, sandstones and the valleys. The floodplain mudstones and siltstone eroded more rapidly and crop out between the ridges, providing ideal conditions for controlled sampling within well-defined stratigraphic intervals. Fossil sites of the Late Miocene Dhok Bun Ameer Khatoon (DBAK) and Lava have yielded a significant quantity of mammalian assemblage including families Suidae, Tragulidae, Giraffidae, and Bovidae. These sites have well exposed Chinji Formation dated approximately 14.2-9.5 Mya. The extended span of time accounts for the high diversity of mammalian genera which are important palaeoecologically, palaeogeographically and palaeoclimatologically. A detailed study was carried out in these localities of the Siwaliks and isolated upper, lower teeth and fragments of mandibular rami were recovered. The studied specimens belong to Giraffokeryx punjabiensis, Listriodon pentapotamiae, Dorcatherium majus, Gazella sp. and Selenoportax Vexillarius. Palaeoenvironmental data indicates that the Miocene climate of Pakistan was most likely to be monsoonal as it is at present. The diets and distribution of all these animals suggest the presence of abundant forests, herbaceous, grassy and bushy vegetation.

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Speaker

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#### The Gray Fossil Site of Tennessee: a unique record of mammalian life in the early Pliocene of eastern North America

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The Gray Fossil Site (GFS) of northeastern Tennessee has well-preserved and diverse flora and fauna, representing one of only a few late Neogene fossil sites in eastern North America. The fauna unearthed so far includes fish, amphibians, non-avian reptiles, birds, and mammals, and is unlike others of similar age. Tapir (Tapirus polkensis), rhino (Teleoceras), Alligator, and turtles are common, while an ailurid (Pristinailurus bristoli) and tremarctine bear (Plionarctos) are present. Both macro- and microfossils of plants from the site indicate a forested environment, which was dominated by oak, hickory, and pine. Ongoing excavations and extensive screen-washing efforts in recent years have yielded thousands of specimens, including remains of many new mammals. Rodents include two castorids (Castor and Dipoides), six cricetids (Antecalomys, Neotoma, Postcopemys, Repomys, Symmetrodontomys, and an unidentified species), a dipodid (Sicista), and five sciurids (Eutamias, Glaucomys, Miopetaurista, and two Sciurini). Leporids include Notolagus and Alilepus. Talpids are Parascalops, Mioscalops, Quyania, and a new stem desman. Additional carnivorans include a new species of wolverine (Gulo), a mephitid (Buisnictis), and a ringtail procyonid (Bassariscus). The dromomerycid Pediomeryx is the first ruminant recognized from the site. Multiple skeletons of an unusual large, longirostine mammutid are currently being excavated. A number of these new taxa support previous environmental interpretations based on fauna, flora, and isotope records. Tree squirrels, flying squirrels, and a ringtail at the site support the forested interpretation, as does the absence of burrowing rodents. The presence of two beaver species and a desman support the presence of year-round water. In sum, the combination of flora and fauna at GFS are unique among North American biotas, and have potential to greatly improve our understanding of the origin of modern ecosystems in the Appalachian region of eastern North America. Stratigraphic ranges of newly recognized taxa are consistent with an early Pliocene age-constraint for the site and provide a substantially narrower range than previous estimates. The site lacks any taxa restricted to the Miocene or Hemphillian NALMA and has multiple taxa characteristic of the Blancan NALMA. In sum, biostratigraphy based on the mammal fauna suggests the site ranges from 4.9 to 4.5 Ma.



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### The evolution of shark, ray and catfish diversity on Tropical America and the closure of the Central American Seaway – a palaeontological and molecular examination

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New palaeontological discoveries in northern South America serve to characterize faunas of terrestrial mammals just before and during the closure of the Central American Seaway (CAS). The presence of migrants from North American mammals in early Pliocene and early Pleistocene sites is minimal, being larger in younger deposits that document major landscape changes. The Neogene record of northern South America records migrants from North America (carnivorans and camelids) only in Pliocene and early Pleistocene localities. But fossils of two marine groups do speak for an earlier closure of the Central American Seaway than classically assumed. We analyzed new and published data on fossil sharks and rays from 67 geological units in 17 countries, from both shallow and deep-water habitats, across five timeclusters from the Miocene to the Pleistocene. Fossils from the Western Atlantic (WA) and the Eastern Pacific (EP) include 63 and 44 genera, respectively. The Neogene extirpation/extinction patterns include 27 genera (22 of sharks and 5 of rays) having been affected. The highest faunal similarity between the assemblages from the Eastern pacific and the Western Atlantic regions is at the early Miocene, with subsequent faunal differentiation within each of those regions, probably related with the increasing closure of the CAS and thus the formation of a barrier. Using Bayesian divergence-time estimation with genomewide single-nucleotide polymorphism data of sea catfishes, we identify a series of divergences between groups of Caribbean and Pacific sea catfishes around 10 Ma, indicating that processes related to the emergence of the isthmus led to vicariant speciation millions of years before the final isthmus closure. Our molecular estimates are based on calibrations from three critical fossil otoliths of uncontested allocation and on a new method that avoids the problems presented by the use of few molecular markers or by concatenation of genome-wide sequence data. The differential timing of diversification in terrestrial and marine groups in the northern neotropics relates more to ecological preference than to dispersal abilities.



Speaker

#### Submerged caves of the Yucatán reveal Late Cenozoic biodiversity and faunal interchange in middle America

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Tropical regions are notorious for poor fossil preservation, leading to significant gaps in the fossil record, and therefore in our understanding of paleobiology, evolution, and temporal biodiversity of vast areas. In the Americas, these tropical environments extend from southern North America, through Central America, and into northern South America. Caves in tropical Middle America provide important windows into this otherwise depauperate record, but preservation is often meager. Recent exploration of submerged cave systems by technical divers in the Yucatan Peninsula of Mexico is now revealing a diverse record of well-preserved late Pleistocene and early Holocene mammals.

This presentation focuses on Outland Cave, near Tulum, Mexico. While skeletal remains have been found throughout this cave, most attention has centered on Hoyo Negro (HN), a natural trap collapse chamber now under 45 m of water. Mammals entered the cave through horizontal passages when sea level was lower during the late Pleistocene, and many fell to their deaths in HN. Expeditions to the site require innovative technology to document and retrieve specimens. Underwater photogrammetry is used to record fossils *in situ* prior to removal. The fauna includes opossum, bat, rodent, tapir, peccary, an elephant-like gomphothere, at least three types of giant ground sloth, sabertooth cat, puma, ocelot, coati, short-faced bear, canid, and a human. The human skeleton is the oldest and most complete of early *Homo sapiens* in the Americas.

Recovery and analysis of sloth, bear, and canid remains provided biogeographic and evolutionary surprises. A megalonychid sloth is a new genus and species that may be endemic to Middle America. The bear, *Arctotherium* ("South American" short-faced bear), is the first record of this genus outside South America. The relative abundance of *Arctotherium* individuals in the deposit, and pristine condition of their remains, makes this the most complete and abundant short-faced bear material from any locality. A terminal Pleistocene radiocarbon date indicates the bear co-occurred with early humans in the Yucatán. A canid represents another "South American" genus, *Protocyon*, previously unknown outside that continent. While the sloths may be part of earlier stages of the Great American Biotic Interchange, we hypothesize that the bear and canid expanded their distributions out of South America during the late Pleistocene.

\* Speaker



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## Bryozoan strategies for neutralizing evolution within their colonies

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Bryozoan colonies often contain many generations of zooids. This sets up an evolutionary tension between the zooid and the colony levels, because evolutionary change may accumulate among zooids as the colony they are a part of expands or dies in response to intense biotic interactions involved in the competition for space. This within-colony evolution may thwart evolution that occurs among colonies (caused by differential sexual reproduction among colonies). In order for bryozoans to be evolutionary successful, this tension between levels of organization must be resolved somehow. Here I present three strategies that bryozoans have for resolving this tension in favor of the colonial level of evolution. Big colonies, such as the coral-dwelling cheilostome genus Stylopoma, neutralizes evolution within its colonies by eliminating the heritability of phenotypes between clonal zooids. This results in no evolutionary accumulation of phenotypes even across many generations of zooids in colonies that grow in response to intense ecological interactions. Wilbertopora, a Cretaceous cheilostome, and the first genus to evolve avicularia, takes a different strategy. The phenotypic traits of zooids of Wilbertopora are highly heritablesimilar to phenotypic traits of solitary animals like humans, cows, and fruit flies. Nevertheless, the variation among a generation of zooids in the multiserial Wilbertopora is structured spatially such that adjacent zooids are sufficiently different from each other to neutralize the accumulation of evolutionary change due to differential growth of the colony. We propose that multiserial growth and the zone of autogenetic change are both colony-level adaptations that act to neutralize zooid-level evolution by maximizing variability among zooids in all spatial directions. A third strategy is taken by bryozoans that have colonies formed by uniserial growth. These small weedy colonies have low numbers of generations and so never experience a high enough growth rate to permit selection differentials to arise within their colonies. For these small uniserial species, their low growth rates (in terms of numbers of generations) shields them from the evolutionary tension between the zooid-level and the colony-level. Bryozoan growth forms are therefore evolutionary as well as ecological strategies.

Speaker

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#### Bryozoan diversity and palaeoecology in the historical type Campanian (Upper Cretaceous) of Charente, SW France

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Bryozoans are among the most abundant and diverse macrofossils in Henri Coquand's historical type region of the Campanian between Aubeterre-sur-Dronne (Charente) and the coast near Royan (Charente-Maritime). Nevertheless, these benthic suspension feeders have been severely neglected: the only significant study since Alcide d'Orbigny's Terrains Crétacés (1851-1854) is the Université Bordeaux doctoral thesis of Janine Ducasse (1957). New research, initiated in conjunction with the writing of a guidebook to the Campanian stratotype, has aimed to compile an inventory of all species present and their stratigraphical distributions. Research is also being undertaken on the critical evolutionary turnover from cyclostome- to cheilostome-dominated assemblages, and the palaeoecology of bryozoan-rich sclerobiont communities on shells of the bivalve Pycnodonte vesiculare. Much basic taxonomic research remains to be done but preliminary results show the presence of well over 100 species. Most of the bryozoans grew as erect colonies, some are encrusters, but free-living colonies (lunulitiforms) are rare. Cyclostomes constitute the majority of the robust, visually conspicuous erect species, whereas cheilostomes tend to have gracile erect colonies, with the exception of some broad, foliose onychocellids. All of the encrusting cheilostomes possess sheet-like colonies, often covering significant areas of substrate. In contrast, cyclostomes can develop as sheets or have diffuse runner-like or small spot-like colonies. The abundance and species richness of encrusting colonies in both groups increases through the upper Campanian from the Biron to the Barbezieux and Aubeterre formations. Faunal lists for bryozoans of all colony-forms show an overall increase through time in the proportion of cheilostome species to cyclostome species, with ascophorans appearing in increasing numbers at higher stratigraphical levels. This is paralleled by a proportional increase in cheilostome relative to cyclostome biomass as estimated from the weights of the two groups in bulk samples.



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Speaker

#### Body mass predicts diet-bioapatite $\delta^{13}$ C isotope enrichment in herbivorous mammals

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Carbon isotopic signatures recorded in vertebrate tissues reflect ecologies and ecosystems because carbon in animal body tissues derives from ingested food. But for almost two decades most carbon isotopebased ecological interpretations of extant and extinct herbivorous mammals have used a single dietbioapatite enrichment value (14). This 14 value has been systematically but uncritically applied in virtually all dietary and environmental interpretations of fossil and extant mammalian herbivores, regardless of body size, phylogenetic affinities, or other life history traits. Assuming that this single value pertains across all herbivorous mammals, from tiny monkeys to giant elephants, overlooks potential effects of distinct physiological and metabolic processes on carbon fractionation. By analyzing a never before assessed herbivore group spanning a broad range of body masses- sloths-we discovered considerable variation in diet-bioapatite d13C enrichment among mammals. Statistical tests (OLS, quantile, robust regressions, and AICc model tests) document independence from phylogeny, and a previously unrecognized strong and significant correlation with body mass. These analyses permit development of a size-dependent prediction of this value for herbivores across Mammalia, spanning body sizes ranging over > 5 orders of magnitude. Furthermore, because the correlation between body mass and diet-bioapatite enrichment is even stronger if mammals are separated by digestive system type (foregut vs hindgut fermentation), our proposed regression models may also predict type of digestive physiology for fossil mammals. Thus, our results suggest that ground sloths, the largest mammals that ever existed in South America would be, together with modern hippos, the largest known non-ruminant foregut fermenters. Sloths challenge previously proposed ideas of constraints imposed by large body sizes on foregut fermentation showing an unparalleled combination of morphological variability and physiological traits likely responsible for their extremely wide ecological diversification in the Americas.



#### Morphometric analysis of Cenozoic cassids (Mollusca: Gastropoda) from Florida

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Predatory cassid snails feed on echinoids, creating distinct drill holes in prey tests. Cassid predation on present day echinoids is well documented and drill holes are increasingly used to study predator-prey interactions between cassids and echinoids archived in the fossil record. The ongoing Echinoid Associated Traces (EAT) project targets drill holes on post-Paleozoic echinoids to investigate predation by cassids and parasitism by eulimid snails. Trace data are compiled in the associated EAT Database to better understand the evolutionary history of biotic interactions. Although drill holes resembling those made by cassids are common in the fossil record, cassids are an underexplored group and their taxonomy is poorly resolved for many taxa, regions, and time intervals.

Here we report pilot results of a morphometric analysis using common cassid morphotaxa reposited in the Invertebrate Paleontology Division, Florida Museum of Natural History. Our aim is to delineate morphotaxa using a combination of linear and semi-qualitative character variables. Seven linear measurements and four ordinal variables were collected for 55 specimens representing five qualitatively defined morphotaxa: (1-3) three morphotypes of Eocene cassids, (4) *Semicassis aldrichi* from the lower Miocene Chipola Formation, and (5) *Semicassis granulata* from the Pleistocene Caloosahatchee and Bermont Formations.

Principal component analysis (PCA) using seven continuous linear variables failed to fully differentiate the five morphotaxa. However, ordination plots suggested that notable differences in morphological variability (disparity) and body size exist among morphotaxa and/or through time. In contrast, an expanded analysis including discrete morphometric variables (Non-metric multidimensional scaling; NMDS) successfully delineated all five qualitative morphotypes and, consistent with PCA, also suggested variable disparity across morphotaxa and body size trends through time. The results suggest that integration of continuous ratio variables and ordinal variables can enhance our ability to rigorously delineate morphogroups in the ordination space. Future analyses, based on an expanded specimen-level dataset should help us to (1) delineate the different cassid morphospecies; (2) improve the taxonomic resolution of Cenozoic data compiled in the EAT Database; and (3) assess more reliably intriguing preliminary patterns suggestive of taxon/time specific trends in disparity and body size.



Speaker

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### Molluscan assemblage shift in a littoral setting at the base of the Neogene

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Marine diversity during the Oligocene and early Miocene has been the scope of various studies that focused on fossil molluscan material from the Eastern Atlantic or the Paratethys Sea where fossiliferous locations are abundant and preservation is good. Less is known from the Proto-Mediterranean area (Spain through Turkey and the Eastern Mediterranean) where the fossils are not as well preserved and the fossiliferous localities are scarcer. In order to fill this gap, molluscs from a section of earliest Miocene age (Aquitanian) of the Mesohellenic Basin (NW Greece) are presently studied.

Twelve 5-litre bulk samples were taken from a small section of the Mesohellenic Basin (Grevena area) from which the  $250\mu$ m sieved fragment was used for retrieving molluscs. Thus, a multitude of juveniles and micromorphic specimens (< 1cm) were recovered. This newly-described material includes species from the Eastern Atlantic and the Paratethys that are reported for the first time in Greece, including 27 micromorphic species, and 5 new species. Including micromorphic species in a palaeoenvironmental analysis helps yield reliable results due to the higher taxonomic diversity. In the present case this is very important since medium-sized species are not abundant or poorly preserved.

For the palaeoenvironmental analysis, the molluscan composition of each sample was analysed. Two assemblages were determined, a brackish with low taxonomic diversity (including

12 species, dominated by *Granulolabium plicatum* and *Mesohalina margaritacea*) and a shallow marine with a high diversity (including 46 species, dominated by *Bittium larieyense*). No transitional fauna was observed, which leads to the conclusion that any environmental change was relatively rapid. In order to illustrate this abrupt shift in molluscan taxonomic composition and environment, clustering and ordination methods were used. The clustering results clearly separate the brackish from the marine assemblages. Ordination methods included a principal component analysis (PCA), principal coordinates analysis (PCO) and non-metric multidimensional scaling (NMDS), for which both taxonomic composition and environmental factors were used. The results show close affinities of the 3 marine assemblage samples but indicate some differences within the 5 samples from the brackish assemblage. This hints towards more instable brackish environments ranging from littoral mudflats (suggested by the presence of *Melongena lainei*) to mangrovial environments (with the presence of *Granulolabium plicatum, Mesohalina margaritacea* and *Terebralia lignitarum*).

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### Towards a reconciliation of the commonality of long-term stasis in the fossil record and rare stabilizing selection in extant biota

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Rapid evolutionary changes are common in many extant species, whereas fossil species regularly display morphological stasis for millions of years. Hence, evolutionary biologists from different disciplines can carry drastically different expectations on rates of evolutionary change and the prevalence of stabilizing selection in nature. Here I dissect these apparent discrepancies in expectations by examining morphological change in a fossil species lineage that displayed stasis in all examined traits for over 5,000 years, and that was sampled at a resolution bridging ecological and evolutionary timescales. I first fit time-series models to the data and subsequently relate observed rates and magnitudes of morphological change to trait change expected under various micro-evolutionary processes (genetic drift, directional and stabilizing selection). Time- series analysis indicates that the observed stasis relates best to models that allow for changes in the adaptive optimum within narrow bounds, as could be expected under weak stabilizing selection. On ecological timescales the expected rates and magnitudes of trait change are very similar for all examined micro-evolutionary processes, and the observed changes in the fossil species lineage fall largely, but not exclusively, within the range of genetic drift. On evolutionary timescales, however, change is more constrained than expected under neutral evolution. In short, the absence of evidence for stabilizing selection from studies of morphological change over ecological periods even applies to high-resolution studies of evolutionary stasis and it does not imply that the process is rare in extant natural populations.



Speaker

### Morphological diversity of calmanostracan crustaceans in time: ontogeny and palaeontology

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Tadpole shrimps have become famous for two aspects: first, as a kind of "toy" which can easily be bred at home, and second, as being evolutionarily stable, hence representing "living fossils". Yet, Calmanostraca (Branchiopoda, Eucrustacea), the group including tadpole shrimps (Notostraca) and some stranger appearing exclusively fossil relatives (Kazacharthra), exhibits indeed quite some morphological diversity.

We present here calmanostracan crustaceans from the Upper Triassic of southern Germany (Keuper, 237-227 million years) generally referred to as Triops cancriformis minor. Based on numerous specimens, we reconstructed the ontogenetic sequence and compared it to the ontogeny of the modernday Triops cancriformis, focusing on shield and trunk morphology. Both forms, the fossil and the extant one, show an elongation of the shield in the course of their ontogeny. However, there are differences in the starting point of the developmental processes, with fossil forms starting out with a more rounded shield, which becomes more elliptical during ontogeny, while extant forms already start with a more elliptical shield shape. Differences were also found when comparing shield to trunk ratios. All these ontogenetic differences cast severe doubt on the interpretation that the morphology of *T. cancriformis* has been static for 237 million years. Expanding this approach, we compared shield and trunk morphology to that of other extant and fossil calmanostracan representatives. A morphospace with size-corrected measurements was used to compare the different morphologies. Results indicate a high diversity in shield and trunk morphology within Calmanostraca, ranging from broad and rather short shields, mainly within Kazacharthra, to elongated and rather narrow shields within the modern group Lepidurus. This approach also allowed us to recognise new morphologically distinct specimens most likely representing separate species. Similar to modern molecular methods our results indicate a so far largely unrecognised diversity within Calmanostraca.



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#### New data of the Paleogene stratigraphy and mammalian palaeontology in the Erlian Basin, Inner Mongolia, China and its implications to the asian Paleogene biochronology

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The well-known Erlian Basin in Inner Mongolia, China has played an important role in establishing the Paleogene Asian Land Mammal Ages (ALMAs). The investigations to the Paleogene in the Erlian Basin in over a decade have clarified a number of long-standing basic stratigraphic confusions. The terrestrial Paleogene in the Erlian Basin comprises seven formations, the Nomogen Fm, the Ashanto Fm, the Irdin Manha Fm, the Shara Murun Fm, the Ulan Gochu Fm, the Xianaogangdai Fm, and the Shangnaogangdai Fm in ascending order, corresponding to the late Paleocene Gashatan through early Oligocene Hsandagolian ALMAs. The Gashatan mammals include Lambdopsalis, Sphenopsalis, Tribosphenomys, Bayanulanius, Hyracolestes, Subengius, Pastoralodon, Prodinoceras, Palaeostylops, and Dissacus serratus, etc. The Bumbanian mammals consist of Anatolostylops zhaii, Gomphos elkema, Rhombomylus turfanensis, Chenomys, Yuanomys, Advenimus hupeiensis, Baataromomys, Pataecops parvus, and Minchenoletes, etc. The Arshantan mammals consists of Archetypomys, Erlianomys, Advenimus ulungurensis, Dawsonolagus, Mongolonyx dolichognathus, Mesonyx, Gobiatherium, Schlosseria, Litolophus, Teleolophus primaries, Heptodon minimus, and Pappaceras, etc. The Irdinmanhan mammals include Asiomys dawsoni, Pappocricetodon neimongolensis, Yuomys, Lophialetes, Protitan grangeri, Triplopus, Forstercooperia, Teilhardia, Gobiohyus, Propterodon, Tarkops, Harpagolestes, and Andrewsarchus, etc. The Sharamurunian mammals is represented by Archaeomeryx, Pterodon, Gobiolagus tolmachovi, Rhinotitan, Deperetella cristata, Lushiamynodon sharamurunensis, Juxia sharamurunensis, etc. The Ulangochuian mammals include Amynodontopsis parvidens, Embolotherium grangeri, Teleolophus magnum, Anagale gobiensis, Ardynomys olsoni, and Gobiolagus andrewsi, etc. The Erigilian mammals include Heosminthus nomogenesis, Allosminthus ernos, A. diconjugatus, Eucricetodon wangae, Pappocricetodon siziwanggiensis, Embolotherium andrewsi, Parabrontops gobiensis, Zaisanamynodon borisovi, Ardynia praecox, Proeggysodon giui, and Urtinotherium, etc. The Hsandagolian mammals include Tsaganomys altaicus, Cyclomylus intermedius, Paraceratherium transouralicum, Ardynia kazachstanensis, and Entelodon gobiensis. Paleomagnetic result suggests that the Paleogene deposits span from the Chron C12r through C26r of GTS. The P-E boundary is in the upper part of the Nomogen Fm, and the E-O boundary is in the upper part of the Xianaogangdai Fm.



<sup>\*</sup> Speaker

#### Investigation of the Middle Miocene ichthyofauna of Cyprus Island (Lemesos, eastern Mediterranean) and palaeoenvironmental reconstruction

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A new fish fauna is described from the Serravallian sediments of Alassa section (Limassol, Cyprus). Five samples, weighting approximately 30 Kg each, were collected along the section. They were wet-sieved through a 250-µm diameter mesh sieve, and otoliths and foraminifers were handpicked under a stereoscope. The palaeobathymetric estimation method of Nolf & Brzobohaty (1994) was applied and the assemblages were further analyzed based on ecological information from the closest living relative of the identified taxa. To reinforce our palaeobathymetric estimations, a micropalaeontological analysis was performed, based on the collected foraminifers. More specifically, the oceanity index (Gibson 1989) was used to define palaeodepth. The 879 studied otolith specimens belong to the following eleven (11) taxa: A) Myctophiformes: Diaphus befralai Brzobohaty and Nolf, 2000, Diaphus cavallonis Brzobohaty and Nolf, 2000, Ceratoscopelus maderensis (Lowe, 1839), Benthosema suborbitale (Gilbert, 1913), Myctophum cf. fitchi Schwarzhans, 1979, Diaphus austriacus (Koken 1891), Diaphus sp.1 and Diaphus sp.2. B) Gadiformes: Bregmaceros albyi (Sauvage, 1880) and Bregmaceros sp. 1, C) Stomiiformes: Phosichthyidae and D) Perciformes: Aphia sp. Risso, 1827. From the stratigraphic range of the associated Foraminifera, the age of the studied samples is estimated as early-middle Serravallian. The fish assemblages consist mainly of pelagic and mesopelagic taxa; thus, they can be considered typical of a continental slope environment with depths > 500 m, which generally agrees with the 550 m estimation provided by the palaeodepth analysis using the Oceanity Index. Bregmaceros albyi (97.15%) is the most abundant species in the Alassa section. The existence of such tropical species, not found in the Mediterranean Sea today, indicates the prevalence of a warmer climate during the Middle Miocene in the eastern Mediterranean.



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### Late Miocene mesopelagic fish size distribution in the Mediterranean

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Was the mesopelagic fish size affected by the environmental changes toward the onset of the Messinian salinity crisis (MSC; 5.97–5.33 Ma) in the Mediterranean? During the late Miocene, the Mediterranean went through significant oceanographic changes, due to the gradual restriction of its connection with the Atlantic Ocean that led to the MSC, which ended with a massive flood of the basin and the re-establishment of normal marine conditions at the beginning of the Pliocene. The marine gateway restriction commenced with the closure of the Betic corridors at the Tortonian–Messinian boundary, followed by the Rifian corridors gradual closure, certainly by 6.0 Ma. The Messinian stage in the Mediterranean therefore is characterized by progressive salinity increase and water-column stratification. In order to test the hypothesis that these changes affected Mediterranean mesopelagic fish biomass, we compare the fish otolith length distributions of the species *Ceratoscopelus maderensis, Diaphus* spp., *Hygophum* spp. and *Myctophum* spp. between Tortonian, pre-MSC Messinian, post-MSC Messinian, and Zanclean assemblages across the Mediterranean. Acknowledgements.

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Speaker

#### The benthic foraminifera, bio-indicators of paleoenvironments and extreme events during the Quaternary of Rabat-Temara (Moroccan Atlantic Coast)

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This study deals with Quaternary storm deposits in the Rabat-Temara region (Moroccan Atlantic coast). The objective is to describe, characterize and identify these deposits generated by storms and to deduce the mechanisms involved in their formations and the factors that control their preservation. In the Atlantic coastal area of Rabat-Témara, we have based on the regional stratigraphic and palaeogeographic context through which we studied the paleoenvironmental significance of quaternary littoral land tempests. The approach adopted is based mainly on palaeontological content (foraminifers, ostracods, gastropods, bryozoans, sponges and echinoderms) and sedimentological characteristics of deposits. In our approach, the microfauna studied is essentially represented by benthic foraminifers, which are identified and determined for the first time in the coastal area of Rabat-Témara. These marine microfauna of the Quaternary are abundant and very diversified; it is represented by several taxa that prove to be excellent bioindicators of shallow marine environments. Ammonia supports coastal environments with high salinity. Milioles (Quingueloculina, Q. seminulum, and Spiroloculina, etc.) and Elphidium (Elphidium advenum, E. crispum, and E. macellum, etc.) constitute a coastal assemblage comprising characteristic species of shallow warm-water marine environments and less salty. Discorbis and Cibicides characterize relatively deep marine environments. By their spatial distribution and their adaptation to preferential environmental environments, these species are good indicators of environments with particular climatic conditions linked to a very strong hydrodynamism due to extreme extreme events (floods / storms / tsunamis).



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### A revision of the Late Triassic "*Metoposaurus*" *azerouali* from the Argana Basin (Morocco) and a preliminary phylogenetic analysis of the Metoposauridae (Amphibia, Temnospondyli)

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The Argana Basin (Western High Atlas, Morocco) provides an important series of continental deposits spanning from the Middle-late Permian to the Early Jurassic. Since the 1960's, this basin has yielded numerous vertebrates including the metoposaurid amphibians Dutuitosaurus ouazzoui (Dutuit, 1976), Arganasaurus lyazidi (Dutuit, 1976) and Metoposaurus azerouali Dutuit, 1976. The latter is problematic because its status is controversial: according to some authors, it has been considered as a nomen dubium. The Metoposauridae is a group of temnospondyl amphibians which occupied freshwater predatory niches during the Upper Triassic (Lower Carnian to Middle Norian). Their fossils are found in low palaeolatitude deposits in North America, Africa, Europe, presumably France and Algeria, but also in India and presumably Madagascar. Phylogenetic analyses involving the Moroccan metoposaurids have already been published but no global analysis of the whole family Metoposauridae has been done so far. To fill this important gap, this study provides a revision of Metoposaurus azerouali and a preliminary phylogenetic analysis of the group. Our results suggest that "Metoposaurus" azerouali is sister-taxon to the Moroccan Arganasaurus lyazidi and then needs a new generic attribution to keep the European genus Metoposaurus monophyletic. These results also show that Dutuitosaurus is a basal metoposaurid as suggested by previous studies and that the genus Koskinonodon is paraphyletic. Combined with the stratigraphic and geographic occurrences of the taxa, our phylogenetic analysis proposes a chronological and biogeographical framework explaining the origin and evolution of metoposaurids and highlights important paleoenvironmental and paleoclimatic implications on this evolution.



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#### New radiocarbon AMS ages on mollusks from the Sopas Formation (Pleistocene, Uruguay) and a new continental Holocene record for Uruguay

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The Sopas Formation is a Late Pleistocene sedimentary unit from Uruguay, mostly known for its typical South American fossil mammal assemblage, but also containing fossil traces, wood, and continental mollusks. Up to date, Radiocarbon AMS ages have been obtained from some outcrops of Tacuarembó, Artigas and Salto departments. They indicate a Late Pleistocene age, ranging from  $33,560 \pm 700$  years B.P. (cal36,089 – 39,426 years) to 39,900 ± 1,100 (cal 42,025 – 45,389 years). Besides, there are some TL/OSL ages, ranging from  $27,400 \pm 3,300$  to  $71,400 \pm 11,000$  years. These last ages suggest a relationship with Marine Isotopic Stage 3 (MIS-3) for the Sopas Formation. During an ongoing study using the mollusks assemblages as environmental indicators, AMS ages for four new localities were obtained: three did not have a previous numeric age, and for the other one (Arapey Chico River, Buey Negro), a new bed was chosen (overlying the typical Sopas Formation brown sediments). The new radiocarbon ages are: Arerunguá River (Paso del Potrero) 42,100 ±1,500 years BP (49090 calBP to 43229 calBP, 95%) (sample: Cyanocyclas limosa); Itapebí Grande River (left side of Rout 31 northbound) 37,600 ± 870 years BP (43324 calBP to 40440 calBP, 95%) (sample: Cyanocyclas limosa); Itapebí Grande River (right sideof Rout 31 northbound) 41,900 ± 1,500 years BP (48944 calBP to 43067 calBP, 95%) (sample: Cyanocyclas limosa), and Arapey Chico River (Buey Negro) (black sediments) 5,869 ± 23 years BP (6733 calBP to 6540 calBP, 95%) (sample: Cyanocyclas limosa). All data confirm a late Pleistocene age for the Sopas Fm. falling into the interval related to the MIS-3, except Arapey Chico River (Buey Negro) that indicates a Holocene age. It should be noted that in this last locality the sediments bearing the mollusks are quite different from the other outcrops, so perhaps this level should not be included within the Sopas Fm. This level of mollusks indicates a new record for the continental Holocene of Uruguay. There are no significant differences between the freshwater mollusk assemblages of the Sopas Fm. and of this new level. This suggest that both were deposited under similar taphonomic and paleoecological conditions.

Contribution to F. Cabrera's doctoral thesis, PEDECIBA



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#### A new chirotheriid tetrapod track site from the Solling Formation (Olenekian/Anisian) of Lower Franconia (Hohenroth, Southern Germany)

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A new chirotheriid track site from the Lower/Middle Triassic boundary of Northern Bavaria, Southern Germany is presented. Two partial chirotheriid footprints, as well as several scratch and claw marks, all preserved in convex hyporelief, were discovered on the lower bedding planes of two sandstone blocks in an abandoned quarry near the municipality of Hohenroth (district of Rhoen-Grabfeld, Bavaria). The sandstone blocks, which had been mined in the quarry but remained on-site belong lithostratigraphically to the Solling Formation of the uppermost middle Buntsandstein and thus represent the Olenekian/Anisian boundary interval. On the lower surface of a ca. 60 cm thick block (B1) of yellowish gray, medium-grained sandstone exhibiting weak planar cross-beding, a 16.2 cm long and 11.3 cm wide right pes imprint (T1) with three well-defined digits and claw impressions is preserved. In addition, possible scratch marks can be identified (T3-T6) on the beding plane. On the lower surface of a second, yellowish gray, medium-grained sandstone block (B2) of ca. 40 cm thickness, a further tridactyl pes imprint (T2) with a length of 14.6 cm and a width of 14.1 cm was preserved, which could be identified as an undertrack. Observation of two generations of desiccation cracks on the lower bedding planes of the sandstone beds indicate several drying-up phases of the former sedimentary surface before lithification. The morphology of the studied footprints allows their tentative assignment to the ichnogenus Brachychirotherium. Due to the size, stratigraphic position and geographic provenience of the finds, a "rauisuchian" archosaur is assumed to be the most likely producer of the chirotheriid tracks. The discovery of this chirotheriid track site closes a ca. 60 km wide biogeographic gap between other chirotheriid localities of the same age, such as the famous track sites at Hildburghausen and Harras in southern Thuringia and Chirotherium -localities near Euerdorf in northwestern Bavaria. The newly identified tracks are further indication of the cosmopolitan occurrence of large archosaurs in the Germanic Basin of Central Germany during the Early/Middle Triassic transition.

Speaker

### On the preservational pattern of terrestrial Archosaurs of the Bauru Basin (Late Cretaceous, Brazil) and the possible role of thermoregulation in crocodylomorphs

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The Late Cretaceous Bauru Basin of Brazil is known for its rich Crocodylomorph fossil record, comprised of taxa such as baurusuchids, peirosaurids and sphagesaurids, among others. The Bauru Basin also exhibits an abundant record of fossil dinosaurs, including sauropod and less abundant theropod remains. It is not clear whether the taphocenosis of the Bauru Basin reflects or not the real biocenosis of the environment in which the basin was deposited. Some works advocate that the taphocenosis reflects the biocenosis and that the baurusuchid crocodylomorphs compensated for the absence of theropods through their terrestriality and hypercarnivorous feeding habit. Others, however, argue that the taphocenosis is a result of a taphonomical bias that favoured the preservation of crocodylomorphs but not that of theropods. Regardless of which approach may turn out to be valid, this work brings a hypothesis absent in previous studies. The possibility is that the good preservation pattern seen in the crocodylomorphs of the Bauru Basin is the result of the thermoregulatory needs of those animals that made them spend time in aquatic environment, regardless of the fact that many of those taxa were terrestrial forms. Previous works have attested that extant crocodylians achieve thermoregulation through behavioural rather than through physiological means. Especifically, they regulate their body temperature through exchanging between spending time predominantely either in the water or on the land during the day or the night according to their thermic physiological demands, with water being preferred during the day in the summer and during the night in the winter given the characteristics of the specific heat capacity of the water. The environment of the Bauru Basin is described as arid, dry and hot. A previous work suggested that the crocodylomorphs of the Basin inhabited areas near aquatic environments, but this work proposes that they had to spend considerable times in water bodies especifically due to thermoregulatory needs, which would be true even for the more terrestrial forms such as baurusuchids and peirosaurids. As living near aquatic environments facilitates the preservation of fossil vertebrates, this would explain why even the terrestrial crocodylomorphs have such a good preservational pattern in the Bauru Basin. The reasons for the preservation pattern of sauropods and especially theropods, however, still need to be thoroughly addressed by further works.



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#### A rare Osmylidae species (Insecta, Neuroptera) in Baltic amber displaying a critical character state for understanding hind wing evolution in the family

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Among insects, representatives of Neuroptera (antlions, lacewings, and their kin) exhibit an unusually high diversity of wing venation patterns, suggestive of an accumulation of differentiations during the 275 million years of the group evolution. As a consequence, the establishment of robust conjectures of topological homology (THC) can prove challenging. In some Osmylidae, recent studies based on extant material documented the acquisition of a fusion involving two particular veins, MP2 and CuA, in the forewings. Contrasting fore- and hind wing patterns, the same fusion was assumed in hind wings, but without direct evidence, and necessitating a counter-intuitive basal fusion of CuA with MP. Following this THC, the genus *Osmylus* would exhibit veins MP2 and CuA distinct (i.e. the assumed plesiomorphic condition).

We gathered microtomography data on two specimens from Eocene Baltic amber (ca. 45 Ma) which can be confidently assigned to the Osmylidae owing to diagnostic features of the head and genitalia structures. The specimens probably belong to *Protosmylus pictus*, known from a single specimen (also from Baltic amber), incompletely described and probably lost. Both specimens display a very unique hind wing venation pattern, best interpreted as possessing (i) a short basal fusion of CuA and MP, near the wing base and (ii) a distal fusion of MP2 with CuA. Thus, it represents a putative intermediate condition between 'CuA fully distinct from MP', as in *Osmylus*, and 'long MP + CuA fusion', as in the remaining Osmylidae.

The phylogenetic relationships of the species among Osmylidae are unclear. Referring to recent molecular-based phylogeny, the subfamily Osmylinae is not the sister-group of the remaining Osmylidae. Thus, a long MP2+CuA fusion would have appeared several times within the family. In summary, this new fossil material represents a key taxon in Osmylidae hind wing evolution, showing that a MP2+CuA fusion likely occurred in this family.



Speaker

#### Crocodylomorph coprolites from the Adamantina Formation (Bauru Group, Upper Cretaceous), São Paulo, Brazil

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The fluvial deposits of the Adamantina Formation (Bauru Group, Upper Cretaceous, Brazil) have a rich record of fossils, including vertebrates such as fish, turtles, and dinosaurs. The crocodylomorphs, however, are the most expressive both in terms of diversity and in quantity of material. Here we discuss some features of coprolites found with remains of crocodylomorphs from the Adamantina Formation in Jales and Fernandópolis, São Paulo State. In Jales, so far, besides the coprolites, only Baurusuchidae remains and crocodylomorph eggs were found. In Fernandópolis, the remains of Baurusuchidae and Sphagesauridae were found, being the crocodylomorph eggs less common. A total of 41 coprolites collected in these two areas were analyzed, ranging from broken remains to complete ones. Several features commonly present in coprolites were evaluated, like: fractures, perforations, desiccation cracks, and wear. They vary from 1.09 to 5.54 cm (mean 2.26  $\pm$  0.9 cm) in length and 0.58 to 2.81 cm (mean 1.6  $\pm 0.5$  cm) in width. In terms of morphology, 31.71% are cylindrical (n = 13), 17,07% liquefied (n = 7), and 51,22% undetermined (n = 21). Some coprolites have structural deformation due to the plasticity of the feces when expelled, causing terminal deformation (sample FUP-000153), longitudinal curvature (sample FUP-000156), and structural deformation and surface marks (sample FUP-000160). In some samples bone fragments (up to 1 cm in size) can be found (e.g. FUP-000151), indicating carnivory/scavenging. Bone fragments were also found in thin sections (FUP-000183). SEM-EDS analysis showed that some coprolites are mostly composed by P and Ca (including that ones with bone fragments), while some coprolites found in Fernandópolis have Ca, Si, Mg, Al, P, S, and Fe in their composition. One of the samples has two cylindrical perforations (less than 0.5 cm in diameter) filled with sediment, possibly made by some coprophagous invertebrate. Desiccation cracks were found in some samples, suggesting a subaerial exposure period before burial. In the thin section of the sample FUP-000183, small submillimetric cavities produced by gases are present. The characteristics suggest that at least some of these coprolites have been produced by Baurusuchidae. However, additional analyses are required to verify if some of the samples from Fernandópolis were produced by Sphagesauridae, since the presence of heterodonty and tooth wearing facets strongly suggests they fed on distinct types of food.

<sup>\*</sup> Speaker

#### The Molteno Formation (South Africa), a testimony of the diversity of Odonata (Insecta) during the Triassic

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Extant odonates (damsel and dragonflies) represent only a small subset of the historical biodiversity of the group. Compared to most other insect orders, its fossil record is rich. Many of the successive fossil sister-groups of crown-Odonata have been documented and classified, essentially based on wing venation, which is very elaborate and disparate in these insects. Yet, some periods and geographical areas are not well documented, such as the Triassic in the Southern Hemisphere.

We studied new material from the Molteno Formation (Karoo Basin, South Africa), dated from the early Carnian (Late Triassic). We described and identified the various species based on their fossilized wings. Different taxa are represented, such as a new genus of Triadophlebiomorpha and a new species of Triadotypomorpha, both clades previously known from several localities in the Northern Hemisphere. Several species of Protomyrmeleontidae, a group essentially known from Northern Hemisphere localities, also occur. New material of a known Triassolestidae species was also examined, leading us to reconsider some aspects of wing venation homologies in this group. The new specimens further demonstrate that the corresponding odonate groups had a worldwide distribution by the Triassic, and that odonates were very diverse at that time. Groups which flourished during the Permian, such as the Archizygoptera, co-existed with odonates more closely related to extant ones, such as the Triassolestidae. The phylogenetic position of the Triadophlebiomorpha and Triadotypomorpha, only represented in the Triassic, remain enigmatic, even though we had the opportunity to study well-preserved material.



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### The Late Cretaceous enchodontids (Enchodontidae: Aulopiformes) fishes from Mexico: New light into the evolution of *Enchodontidae*

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Enchodontids are a well-diversified fish group known from Cenomanian to Paleocene shallow marine deposits around the world. Enchodontids range in size from a few centimeters to more than one and half meter and are characterized by a middle longitudinal thickening bar in the opercle; their almost nude trunk bearing a series of large predorsal scutes, and in most cases the typical large fang-like single palatal tooth. Enchodontid fishes have been studied since the beginning of the 20th century in Europe, Northern Africa, Middle-East and United States; previous studies suggest that this group was originated in the Middle-East. In Mexico, the Enchodontidae fossil record had been scarce until today that different Late Cretaceous paleontological sites where these fish have been found. So far only two Mexican species have been formally described, Enchodus zimapanensis (from Albian-Cenomanian deposits of the Muhi quarry, Hidalgo, Central Mexico) and Unicachichthys multidentata (from the El Chango quarry, Chiapas, southeastern Mexico); however, the enchodontids of this country have begun to reveal an unexpected diversity that glimpse different phylogeny and biogeography stories. The Cenomanian deposits of the El Chango, El Espinal, and Ochuxhjob quarries, Chiapas, southern Mexico bear a rich enchodontid assemblage including longirostrine specimens like Saurorhamphus and typical short-snout Enchodus -like fishes. Additional Enchodus -like specimens have been collected in many Late Cretaceous deposits of Muźquiz-Piedras Negras area, Coahuila, northern Mexico; in Las Bocas quarry, Guerrero, southern Mexico, San José de Gracia quarry, Puebla, and Xilitla quarry, San Luis Potosi, central Mexico. The Mexican fossils represent the largest assemblage of enchodontid fishes so far found in the America, which despite having been found only recently, already begins to rival with the diversity of this family found in Europe and the Middle East. The last phylogenetic analysis locates U. multidentata, a peculiar enchodontid with a palatine patch of multiple teeth, at the base of the enchodontids suggesting that the origin of the group is the southern end of North America. Today, authors are working on the description of a Enchodus -like fish from El Chango quarry too, which differs from other enchodontid taxa because of its palatine bone bears nor many teeth or a single tooth, this has two palatine teeth. This new finding supports the previous idea about the origin and early diversification of enchodontids in America.

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### Radiological study of a complete dental ontogeny sequence of *Hipparion* sp.

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Hipparionine horses constitute a group of great prominence in the evolutionary history of equids as their remains were very abundant and they were represented by numerous species during the Late Miocene and Pliocene of Eurasia, Africa and North America.

Complete sequences of dental ontogeny are rare in the fossil record but provide valuable information on the patterns of mineralization, eruption and replacement of the teeth and on aspects of the life history of extinct species. Also, the study of the dentition ontogeny allows us to infer the age at death of the individuals from a fossil site and, by analysing the age-frequency distribution, the causes behind the death and the mode of formation of a taphocoenosis can be inferred.

Only paleontological sites with exceptionally rich and well-preserved fossil assemblages provide an adequate number of specimens to describe dental ontogenetic series. This is the case of Cerro de los Batallones fossil sites (Madrid Basin, Spain), which are known for containing diverse and extremely abundant mammalian fossils. Among the many species represented at the Cerro de los Batallones sites, *Hipparion* sp. (*= Hippotherium* sp.) from the site of Batallones-10 stands out as it is represented by one of the largest and best-preserved assemblages for the Hipparionini tribe not only in Spain but also in Europe and is constituted by a large sample of skulls and mandibles with their dentition in place. The goal of this study is to describe for the first time with radiological techniques (X ray and CT scan) the postcanine dentition ontogeny (mineralization, eruption and replacement patterns) of hipparionine horses.

We have defined 7 age classes for Batallones-10 *Hipparion* sp. and determined that the sequence of mineralization and eruption of hipparionine horses is: m1, m2, (p2, p3), p4, m3. The number of individuals at groups with the highest risk of natural mortality (infants and yearlings dependent on their mothers, as well as pregnant females) are predominant at Batallones-10, so we considered that this accumulation was the result of a gradual, attritional mortality. The death of weak individuals gathered around a water body during drought periods constitutes a plausible hypothesis for the accumulation of hipparionine individuals at Batallones-10.



<sup>&</sup>lt;sup>°</sup> Speaker

### A new theropod footprint site in the Upper Cretaceous El Molino Formation, Torotoro National Park, Bolivia

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Footprints and trackways of sauropods, theropods and ornithopods are common in exposures of Upper Cretaceous rocks of the El Molino Formation within the Torotoro National Park, the Cal Orcko paleontological site near Sucre, the Maragua syncline, and other sites in Bolivia. A new site is reported here located at 18° 9' 11.17"S, 65° 46' 13.68"W, in the south limb of the Torotoro syncline, southwest of the town of Torotoro along the trail to Siete Vueltas. The footprints assemblage consists of three small epichnial theoropod footprints in a nearly vertical layer of fine sandstone, 30 cm thick. The footprints (SV1, SV2 and SV3) are preserved as relief and have the same dimensions, which are 18 cm in length and 13 cm in width. They are oriented in three different directions and do not form a trackway. SV1 and SV2 occur next to each other, with the digits oriented 90 degrees to each other; SV1 and SV3 are separated by 62 cm (from tip of digit III of SV1 to the distal end of the talus of SV2). Footprint SV1 is a right pes with digit III projecting the farthest anteriorly, followed by digits II and IV, both with similar length. The digit III exhibits a slight sinusoidal pattern, with its tip inclined distally. The marks of the three claws are sharp, especially for digits II and III, and the talus is well marked. Footprint SV2 is also a right pes and shows well marked digits II and III, with digit IV very tenuous, claw of digit III marked, and the rim of the talus absent. Footprint SV3 shows digits II and III well marked, whereas digit IV is absent, and the rim of the talus is very shallow. Marks of claws of digits II and III are well marked. The footprints are preserved in carbonate-cemented fine- grained sandstone, which in the study area is highly burrowed, with ripple marks and without desiccation cracks. The footprints do not show evidence of bioturbation, desiccation or cracking on their surface, and the burrowing of the sediment occurred prior to the formation of the footprints. The stratigraphic succession in the area indicates pulses of deepening (transgression) and shallowing (regression), though the overall sequence records a gradual shallowing upward trend. The sedimentological texture and the preservation degree of the footprints suggest that they formed in an intertidal foreshore that was rapidly covered by the overlying sandstone layer.



<sup>&</sup>lt;sup>°</sup> Speaker

### Comparative anatomy and systematics of forcipulatacean sea stars: new insights from three "forgotten" Jurassic species

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Asteroidea (also called sea stars or starfish) is a class comprised of about 2 000 extant and 600 extinct species. It is generally accepted that all extant orders emerged during the Jurassic period, and then had about 200 million years of independent evolutionary history. The study of Jurassic fossils is therefore essential to understanding the initial diversification of all extant sea stars. The clade Forcipulatacea, comprised of about 400 extant species, is morphologically well-defined. However, its fossil record is relatively sparse with all representatives being assigned to two extant families; the Asteriidae and; Zoroasteridae, or erected as exclusively extinct families. Most have not been re-studied since their original description, and so we here reappraise three such "forgotten" Jurassic Forcipulatacea species: Asterias gaveyi Forbes 1850, Compsaster spiniger Wright 1880 and Ophidiaster davidsoni de Loriol and Pellat 1874. Extensive new descriptions of each species, including key details of the abactinal skeleton, ossicle spination and, where present, pedicellariae are made. This, combined with detailed comparative anatomical studies of extant taxa, and comparison with recent molecular based phylogenetic hypotheses for the Forcipulatacea, suggest all 3 fossil species need re-assignation. A. gaveyi has a compact abactinal skeleton and lacks crossed pedicellariae and so is removed from the Asteriidae. C. spiniger possess crossed pedicellariae but lacks the wreath organ (concentration of crossed pedicellariae around one spine) typical of the Asteriidae and is thus removed. The arm ossicles of Ophidiaster davidsoni clearly follow the Forcipulatid Plating Rule and thus belongs to the Forcipulatacea, but its family affinities are currently uncertain. In the future, the characters derived from these new descriptions will be used to infer their phylogenetic position inside the Forcipulatacea. The reanalysis of these taxa demonstrates that the early diversity of the Forcipulatacea was greater than previously thought and challenges existing perceptions of the evolutional history of this major modern order.



Speaker

### Locomotion of carnivorous mammals (Mammalia: Carnivora and Creodonta) at the transition of the "Grande Coupure": paleoecological and phylogenetic contribution

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Fossil mammals are rarely known by complete or partial skeletons. Compared to the dental material, the postcranial skeleton is neglected when found disconnected from cranium elements. At a first glance, one actually thinks that the systematic attribution of the isolated postcranial elements is complicated or even impossible. As a result, the systematics and ecology of the extinct species are often based only on dental features. For instance, the locomotion of the mammals that lived in Europe around the Eocene-Oligocene transition ("Grande Coupure") is poorly known. This is mainly due to the fact that the postcranial elements of these animals housed in European collections are mainly from karst fillings located in the Quercy phosphorites (France). They thus have been found separated from the dental elements, which hinders their determination. Moreover, most of the collections from Quercy phosphorites correspond to mix of localities that recorded different periods (i.e., late Eocene, early Oligocene, and late Oligocene).

The aim of our present study is to characterize the locomotion of the predatory mammals of the "Grande Coupure", a critical period marked by a profound modification of the ecosystem (i.e., reduction of forest cover in Europe, establishment of the ice cap at the North Pole) and mammalian fauna. This period is crucial for the history of the carnivorous mammals because it corresponds to the radiation of the carnivorans – at the opposite we noticed a decline of the Hyaenodonta – and the settlement in Europe of the large groups known today (Felidae, Mustelidae, Ursidae, etc.).

The first step was to sort and to assign the postcranial material from the karst fillings of Quercy (about MP 19 to MP 30) to several predatory morphotypes known from this era. In order to assign the tarsal bones to known taxa by their dental remains, we used criteria of general morphology (morphometric analyzes), size and relative abundance; these data were analyzed in comparison with those from dental remains. Identifying the tarsal bones of several groups of carnivorans allowed to reconstruct the locomotion of these animals and, therefore, to improve our knowledge of their respective ecology. In order to test their impact on the phylogenetic relationships, we also completed the existing character-taxon matrices by coding the postcranial characteristics of the Quercy taxa. We hope that they will clarify some relationships that are still obscure, particularly at the base of Feliformia and Caniformia.

<sup>\*</sup> Speaker

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### The giant ground sloth *Eremotherium* (Xenarthra, Megatherinae) from the Pleistocene of Colombia: morphometric description and biomechanical analysis of to the locomotor system

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The Xenarthra constitute one of the representative groups of extinct land mammals in South America, but were also present in Central and North America. They have been documented from the Eocene to the Late Pleistocene and their fossil record suggests a particularly wide distribution and considerable diversity, referred to four major clades (Megatheriidae, Megalonychidae, Nothrotheriidae and Mylodontidae) with arboreal, semi-aquatic and terrestrial forms of medium to large size, reaching up to 4000 kg in weight (Megatherium and Eremotherium). Eremotherium is an extinct genus of Pleistocene giant ground sloths, whose northernmost fossil record corresponds to remains found in New Jersey (United States) and the southernmost to material from the state of Rio Grande in southern Brazil. In Colombia there are several reports of Pleistocene fauna in which reference is made to giant sloth remains, such as the material excavated in 1945 in Las Lajas stream in Villavieja-Huila, and in 1961 referred to Eremotherium rusconii, which is the subject of this contribution. This fossil is the most complete specimen of a giant ground sloth found in Colombia, consisting of an almost complete skeleton, only missing parts of the skull; the specimen is currently exhibited in the Geological Museum José Royo y Gómez, Colombian Geological Survey, Bogotá, Colombia. This work provides a thorough morphometric description of the Villavieja specimen, information on taxonomic position, and helps to resolve the discrepancies for the proposed species within the genus *Eremotherium*, which are a matter of current debate.

A biomechanical analysis is undertaken on one of the most striking characteristics of these animals, the locomotor system. The legs in ground sloths are morphologically different from the rest of mammals, as most of the weight of the animal is supported by the calcaneus and the fifth metatarsal.



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### The sub-fossil fauna of BEL XXII (Belobaka, Northwest of Madagascar)

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Belobaka (catalogue prefix BEL) is located 10 km east of the city of Mahajanga, northwestern Madagascar. In 1911 and 1912, this site yielded sub-fossil remains of Pachylemur insignis (a lemur) and other material. Between 2003 and 2012, new surveys and excavations were undertaken by a French-Malagasy MAPPM team (Mission Archéologique et Paléontologique dans la Province de Mahajanga), which led to the discovery of previously unknown karst infillings. In 2007, BEL XVII yielded the remains of a hippopotamus (H. laloumena) dated circa 20,000 years BP. In addition, a right maxilla of a small species of "sloth lemur" was discovered at BEL XIX, and became the type specimen for Palaeopropithecus kelyus Gommery et al. //2009. This genus is also represented by Palaeopropithecus maximus Standing, 1903 and Palaeopropithecus ingens Grandidier, 1899. Two lower molars of Palaeopropithecus have also been reported from Ambongonambakoa. In 2009, some breccia with microfauna was discovered at BEL XXII. The excavation began in 2010. Important discoveries were made in 2011 and 2012 with the help of students of the University of Mahajanga during field school. This locality yielded many remains of P. kelyus and other faunal remains (chelonian, carnivores, lemurs, rodents and bats). But, the collection of P. kelyus is the most important, best represented by teeth (especially partial mandibles and anterior teeth). The excavation exposed cave deposits; part of which were unfortunately destroyed in the 1980's during quarrying. The proximity of BEL XXII and BEL XIX suggests that the two localities belong to the same karstic network

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Speaker

### The primates from BPB (Bolt's Farm Cave System, South Africa)

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Beginning with the research of Robert Broom in 1936, the Bolt's Farm Cave System (BFCS) has yielded remarkable fossils of non-human primates. BFCS is situated in the Sterkfontein Valley in the Cradle of Humankind, recognised as a World Heritage Site by UNESCO in 1999. BFCS has several localities with deposits dated biochronologically between 0.9 and 4.5 Ma. Brad Pit B or BPB was discovered in November 2010 by the French-South African HRU team, associated with the HOPE (Hominid Origins and Past Environments) Research Unit. BPB is located on the Klinkert's property of BFCS and was excavated for the first time in November

2013. As in the case of many sites in the Cradle of Humankind, BPB is an eroded deroofed cave deposit which was fortunately not severely affected by lime-mining activities about 80 years ago. Three major areas of *in situ* breccia are recognized. Samples of breccia were carefully prepared with 5% acetic acid at the Ditsong Preparation Laboratory in Pretoria. This method facilitates good control of the preparation of fragile fossils, as in the case of the BPB material. The *in situ* breccia of "*Parapapio* Spot" was dated biochronologically (with rodents) between Waypoint

160 (Klinkert property, Bolt's Farm area, between 4.0 to 4.5 Ma) and the oldest deposits of Makapansgat (between 2.58 and 3.03 Ma). This breccia seems to be Mid-Pliocene in age. BPB has yielded two taxa of Cercopithecoidea (*Cercopithecoides* and *Parapapio*) commonly found in the terminal Late Pliocene and Early Pleistocene in South Africa, and from the Pliocene to the Early Pleistocene in East Africa. These fossils could represent one of the oldest co-occurrences of these two genera in Southern Africa, corresponding also to a similar association at Sterkfontein (Member 2) dated at 3.67 Ma. The BPB fossils were compared to specimens from Makapansgat, Sterkfontein and the Bolt's Farm area. They display many similarities with *Pp. broomi* and *C. williamsi*. The BPB *Pp. broomi* specimens indicate a great age for this taxon in South Africa. *C. williamsi* has a wide geographical distribution: at Koobi Fora in Kenya, it occurs in younger deposits (2.5-1.5 Ma) except for an isolated M3dated at around 3.5 Ma. Other primate remains have been discovered elsewhere at BFCS which is now recognised as being especially important for understanding the diversity of primates in the Cradle of Humankind World Heritage Site in South Africa.



Speaker

### Raptorial appendages of fossil and extant euarthropods: a prime example of convergent evolution

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Euarthropods – insects, myriapods, eucrustaceans and chelicerates – have evolved various different life styles and therefore dominate our modern ecosystems. Many different euarthropods of numerous lineages became highly specialised predators. This mode of feeding and the structures required for it evolved independently in the different lineages, starting from non-raptorial ancestors, hence represent cases of convergent evolution. All euarthropods do whatever they do with their appendages; this is also true for catching prey. Due to the specific mechanical requirements of a predator several different lineages have evolved very similar solutions and consequently extremely similar-appearing morphologies of raptorial appendages. Euarthropod joints are in principle very simple. Unlike in tetrapods, ball-and-socket joints or similarly complex joints are not found in euarthropods; instead only hinge joints appear to be feasible. Due to these strong constraints and the apparent presence of cases of independent evolution of very similar-appearing morphologies, euarthropod lineages are a perfect "natural experimental setup" for deepening our understanding of convergent and also parallel evolution and functional constraints. For a precise reconstruction of the character evolution of such lineages with presumable convergent similarities, fossils offer an invaluable source of information. Only with these fossils small intermediate evolutionary steps can be revealed. A better understanding of the functional constraints is also strongly beneficial for palaeo-ecological reconstructions of individual species. Such cases allow a more reliable reconstruction of life habits of now fully extinct lineages. I will discuss different lineages of raptorial euarthropods which appear to show such convergent patterns of character evolution and in which fossils play a major role in reconstructing these.



Speaker

## Super-size me – the fossil record of giant larval forms of arthropods

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Many organisms have a post-embryonic development including distinct phases in which they morphologically and ecologically differ from their later or earlier phases. In such developmental patterns the earlier phases are generally termed larvae. Depending in which groups of animals we look for larvae we expect different properties of them. I will concentrate here on fossil representatives of arthropods (insects, myriapods, other crustaceans and chelicerates). The fossil record of arthropod larvae is in fact not too bad, although larvae are less often given attention. Therefore, I focus here on cases that we should pay attention to, unusually large- sized larval beings that fool our recognition, i.e. we tend to misidentify these forms as adults, as we somehow assume that larvae are always small. Yet, among arthropods very largesized larval forms can be found, large in comparison to their adults or large in comparison to larvae of closely related forms. Palaeopteran, plecopteran and holometabolan insects throughout have very large and long living larvae. Still recognising fossil representatives as such is not easy. More tricky are the larval forms of marine crustaceans; here the average larva is small, below a millimetre in many lineages, but even in species with large sized adults, larvae of 5 mm are the common theme. Yet, in few lineages real giant larvae are known that have also left their traces, among them giant larvae of mantis shrimps, the deep water inhabiting polychelid decapods, spiny lobsters and slipper lobsters, but also candidates of giant larvae of false sand crabs or related forms have been found. All these reach far into the centimetre range, some being even up to 150 mm long. In modern seas, giant larvae seem to represent a large share of the zoo-plankton; in terrestrial habitats, insect larvae are also a major part of the biomass. Similarly, in the past large arthropod larvae seem to have played a major role in the food webs. Reconstructing extinct ecosystems will significantly benefit from giving some additional attention to the large larval forms.



Speaker

### Exploring deep-water methane-seep faunas in the Oligocene of northern Peru

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Deep-sea biogeography based on the fossil record provides direct evidence on evolution of deepsea metazoans throughout geological time. During the Cenozoic the Earth has undergone major climatic and oceanographic changes which have affected global CO2-levels. Deep-sea cold seeps are an important source of the greenhouse gas methane and fossil seep deposits can be identified in the field by the presence of fossilized remains of chemosymbiotic animals that used methane and hydrogen sulfide as energy source.

The Oligocene of northern Peru is characterized by expanding or transgressing seas and consists of marine and non-marine deposits of the Màncora Formation that is underlain by an unconformity and followed by the Heath Formation, as first described by Axel A. Olsson in the 1930s. The Heath Formation consists of shales containing a concretion zone from which mollusks of the so-called '*Pleurophopsis* fauna', now known from chemosynthetic environments, have been reported. The topmost layers of the Heath Formation have been recognized as "heath shales" and are described as limy with wide belts of thinbedded yellow limestone, indicative for seep carbonates. However, rapid shifts in sedimentation, intense block faulting, and insufficient geological mapping in this part of northern Peru makes the recovering of these seep carbonates difficult.

Here we present results of our recent field survey and a preliminary list of species recovered from seep carbonates from the Heath Formation in coastal northern Peru, as a first step to assess the origin of these methane-seep communities, their biogeographic relationships, and their implications for faunal exchange between the Atlantic and Pacific Oceans.



Speaker

### Rhinocerotidae (Mammalia, Perissodactyla) remains from the new Pleistocene locality of Richea (Laconia, Greece)

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In the present study, rhinoceros fossils are described from the new locality of Richea (Eastern Laconia, Greece) for the first time. The fossils were discovered in bone-bearing calcified breccia inside the limestone fissures of the Tripolis geotectonic zone, and were deposited in the collections of the Museum of Palaeontology and Geology of Athens (AMPG). The studied material consists of six isolated teeth and five postcranial elements. The limited number of specimens and their overall poor state of preservation made the identification of the species difficult. The material was compared with the four common Pleistocene Stephanorhinus species of Southern Europe: *S. etruscus, S. hundsheimensis, S. hemitoechus* and *S. kirchbergensis*. The specimens from Richea show clear differences from the last two species. Among the other two species, the morphology of the Richea specimens is closer to *S. etruscus*, which suggests an Early Pleistocene age for the locality. This is the southernmost occurrence of a representative of the genus *Stephanorhinus* in the Balkan Peninsula, thereby providing new insights about its palaeogeographical distribution in Europe.



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### A new "triplearmoured" clupeomorph (Actinopterygii) from the continental Kem Kem beds (Cenomanian, Southeastern Morocco)

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Clupeomorpha (herrings, anchovies and relatives) are formed by twomain clades, Clupeiformes, the only one with Recent representatives and Ellimmichthyiformes. Ellimmichthyiformes are known from the Early Cretaceous to Eocene, in both continental and marine palaeoenvironments. One of their main synapomorphies is the presence of a predorsalseries of scutes, in addition to the ventral series characterizingclupeomorphs. They were especially well diversified during the Late Cretaceous, with mostly marine occurrences. In Morocco, ellimmichthyiforms are known from the marine Cenomano-Turonian localities of Jbel Tselfat and Gara Sbaa, but they have also been reported from the continental Cenomanian Jbel Oum Tkout locality.

Jbel Oum Tkout(OT1) is a small clayey lens outcropping in the second unitof the continental Kem Kem beds, in Southeastern Morocco. It is reconstructed as a quiet freshwater environment, like the dead arm of a riveror a small pond. The fishfauna comprises the polypterid *Serenoichthys*, the acanthomorph *Spinocaudichthys*, the incertae sedis actinopterygian *Diplospondichthys* and at least twelve other taxa which are still unpublished. This taxonomic assemblage is very different from that of the surrounding detritic Kem Kem beds levels, or from other contemporaneous continental or marine localities. Two clupeomorphs are present, the one described herein belonging to ellimmichthyiforms.

This new taxon is known by seven specimensof small size (i.e., less than 5 cm in standard length). This high bodied fish exhibits various features of Clupeomorpha (ventralseries of scutes, hypural 2 fused with the first ural centrum), Ellimmichthyiformes (predorsal series of scutes) and Paraclupeidae (predorsal scutes increasing in size posteriorly, and postpelvic abdominal scutes bearing prominent and strong ventral spine). It shares with other "triplearmoured" ellimmichthyiforms (i.e., *Triplomystus* and *Scutatoclupea* ) the presence of a third post-dorsalseries of scutes. It is unique among ellimmichthyiforms in having a peculiar anvil-shaped keel on some of its predorsal and ventral scutes. Its description enhances the clupeomorph fossil record by providing one of the few continental occurrences of an ellimmichthyiform during the early Late Cretaceous. It also enlarges the palaeogeographic distribution of "triplearmoured" clupeomorphs, previously known only from Lebanon and Mexico.

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#### A Miocene rodent with exceptional preservation of soft tissues

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Diatomites are renowned amongst palaeontologists due to their high potential for preserving exceptional fossils. Remains of fragile organisms, or parts thereof, are frequently found in diatomites: examples include leaves, insects, and vertebrate soft tissues. As such, diatomites often form Konservatlagerstätten. Unfortunately, diatomites are globally rare; whilst the oldest are Cretaceous in age, all significant fossil-bearing deposits are Cenozoic. Because these units were deposited in marine or lacustrine environments, the vertebrates they yield are primarily fishes and amphibians. Fully terrestrial vertebrates are rare. In Spain, there are two Late Miocene diatom sites, Tresjuncos (Province of Cuenca) and Cenajo-1 (Province of Albacete), which have produced exceptionally preserved vertebrate fossils. We present a rodent from Cenajo-1 (circa 7-8 Ma), about 20 km East of the village of Elche de la Sierra. The specimen comprises an articulated and almost complete skeleton missing only the hands, a hemimandible, and the rostral part of the skull. The specimen is further remarkable for its preserved soft tissue structures, which stand out well from the chalk-white matrix. These include integument (hairs and skin) but, more importantly, also non-integumentary regions of the body, such as parts of the digestive tract (e.g., caecum). Preliminary study of this specimen in the 1970s suggested that it belonged to the genus Paraethomys. However, recent re-examination of the lower dentition suggests that both the size (below the range shown by the species of Paraethomys) and morphology (anteroconid almost symmetrical, first molar cuspid c1 not laterally compressed) are more consistent with the specimen representing Occitanomys. The skeleton has been µCT-scanned and digitally visualised in three dimensions. Synchrotron X-ray fluorescence and absorption spectroscopy, as well as infrared spectroscopy, has been used to assess the fossil's chemistry. These analyses confirm the identification of coloured residues as remnants of soft tissues in the body with a high concentration of Cu, Zn and S in both the mandible and gut areas. The presence of organic sulphur species, disulphide plus cysteine, evidences the preservation of structural protein residue, most likely derived from original keratin.



<sup>&</sup>lt;sup>°</sup> Speaker

### Invasive species, a natural experiment in actualistic taphonomy

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We present the first results of an ongoing research project which objective is to characterize and compare the taphonomic attributes of the valves of two species that invaded the Rio de la Plata in the last decades. These are the gastropod Rapana venosa and the bivalve Corbicula fluminea. The chronology concerning these invasions has been precisely established, being known that they are in the area since two and three decades respectively. This time lapse is adequate to fill in a natural way a (negative) taphonomic window that exists in actualistic taphonomy: the time between the experimental taphonomy (comprising weeks or months), and the study of the present, time averaged, death assemblages, that comprise hundreds or thousands of years. The taphonomic attributes and their different states are being quantitavely analysed. The effect of the granulometry of the substrate, and also of the elemental composition of the shells and their microstructure (by EDS and SEM respectively) is being evaluated. This use of invader species as a model to improve our knowledge about short-term taphonomy is new, and we give here the first, preliminary results. We analyzed a sample of Rapana venosa from a beach in Gorriti Island, Uruguay, collected in the austral summer of 2017. This beach concentrates shells and gravel when severe storms occur, and abrasion is not common in between. Rapana venosa has established populations in the area since around 2009, so the maximum time available for the action of taphonomic agents has been ca. 10 years. Up to now, we studied a sample of 110 specimens (shells or fragments larger than 3 cm), considering fragmentation, colour, bioerosion, bioencrustation, and corrosion, each one quantified in three cathegories, according to the intensity of the respective process. Fragmentation is very frequent. Remains comprising less than 30% of the whole shell predominate. Colour is lost in about half of the specimens, and in only about 20% is minimally altered. Bioerosion affected about three-quarters of the specimens, mostly in a moderate degree. Bioencrustation is scarcely present and corrosion is moderate to high. This preliminary results show that for an epifaunal medium sized gastropod in a beach environment, taphonomic destructive processes take place in a very short lapse.

Contribution to project FCE 1 2017 1 135699.

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Speaker

# Bounded by depth: The marine habitat of the enigmatic Miocene fossil mammals *Desmostylus* and *Paleoparadoxia*

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The extinct marine mammals *Desmostylus* and *Paleoparadoxia* are classified within Desmostylia (?Afrotheria) and lived between the early Oligocene and the late Miocene. All known fossils of these taxa are found in marine strata along the coasts of the North Pacific Ocean. Although *Desmostylus* and *Paleoparadoxia* are similar to each other in body form, their paleoecologies, including habitat preferences, are thought to have been distinct because of differences in their cranial and tooth structures as well as the fact that they are known from separate localities.

One approach to clarifying the habitats of extinct animals is to analyze the sedimentary environments of fossil-bearing strata. This is important because the environments in which animal fossils are found to some extent reflect their habitats during life. Animal fossils include remains deposited within life habitats (autochthomous) as well as those that have been moved and re-deposited within this preservational environment by post-mortem transportation (allochthonous). It is also noteworthy that the bodies of animals are often more or less destroyed by the time that the fossilization process reaches its midpoint; for this reason, numerous studies on the degradation of vertebrate remains during this process have been performed, leading to a range of conclusions. The nature of vertebrate fossils that have been largely influenced by post-mortem burial following transport can therefore be determined approximately on the basis of preservation and the condition of fossil-bearing strata.

We estimated the depositional depths of 45 desmostylian fossil occurrences in this study using the associated mollusk fauna and benthic foraminiferal assemblages. In addition we only considered data for complete or partial skeletal specimens in order to exclude cases of reworking and the pre-burial drift of carcasses that might have confounded our analysis.

The results of this study indicate that the depositional environment of *Desmostylus* specimens was restricted to the inner sub-littoral zone shallower than 30 m in depth whereas *Paleoparadoxia* specimens are found within the inner sub-littoral (down to depths of 50 m) and upper bathyal zones (between 150 m and 500 m). Results also suggest that *Desmostylus* lived in nearshore waters while *Paleoparadoxia* foraged in relatively deep, offshore waters. The depositional segregation observed between these two genera most likely reflects their different foraging habitat preferences.



<sup>&</sup>lt;sup>°</sup> Speaker

## Stable isotopes studies in Late Pleistocene horses from Uruguay

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The first isotope data of horses belonging to a Late Pleistocene mammalian assemblage of northern Uruguay (Sopas Formation) is provided to document their dietary preferences and paleoenvironmental implications. Radiocarbon and OSL ages of the Sopas Formation encompass mostly the interval 60-30 kyr BP, correlated to the last interstadial (MIS-3). It has been used  $\delta^{13}$ C preserved in fossil tooth enamel of Equus (Amerhippus) neogaeus (n: 17) and Hippidion principale (n: 6), collected from the same sedimentary context, suggesting sympatry. Specimens belong to the Paleontological collections of the Facultad de Ciencias (FC-DPV) and Museo Nacional de Historia Natural (MNHN) of Montevideo, Museo Histórico DepartamentalPaleontología of Artigas (MHD-P) and Gizzoni Collection of Salto (C). Pre-treatments and isotopic analyses were performed during an internship at Stable isotopes Laboratory (SIL, University of East Anglia), by one of us, following the protocols previously set. In determining the types of diet, the Feranec-MacFadden model was follow: C3 diet,  $\delta^{13}$ C values from -19 to -8%o; C4 diet,  $\delta^{13}$ C from -2 to 2%o, and C3/C4 diet (mixed diet),  $\delta^{13}$ C from -8 and - 2%o. The  $\delta^{13}$ C average for Hippidion principale is -10.47%o (-12.81 to -9.24 %o), consistent with animals browsing C3 plants in open canopy wooded areas. The  $\delta^{13}$ C result of -7.51% o is not included in the average but was considered in the global study. Meanwhile the  $\delta^{13}$ C average for Equus (A.) neogaeus is -8.33% (-10,15 to -4,55% o), these results would reflect a C3 browser in open canopy wooded areas and a mixed diet (with greater or lesser component of C4 pasture), but not assignable values to C4 grassers. It could explain the co-occurrence of both horses that exhibit in some extent different food strategies. The mammalian assemblage of the Sopas Fm. was characterized as a mixed-fauna, including tropical to temperate taxa associated to arid to semiarid species. The hypothesis of a mosaic of environments, including riparian forest, semi open arboreal context and open plains, is substantiated by the inferred type of diet of both species of horses. The results are discussed in the continental framework including information from late Pleistocene Brazil and Argentina samples. The data obtained suggest a modification of feeding strategies in E. neogaeus probably related to the environmental changes from MIS-3 to last glacial maximum conditions.

Contribution to PhD Proj. Pedeciba (E. Morosi).



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#### Petrosal and bony labyrinth morphology of Choeropotamidae: phylogenetic insights

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Artiodactyls, or even-toed ungulates, encompass a noteworthy diversity of mammals today represented by pigs, ruminants, hippopotamuses, camels and cetaceans. They have a long evolutionary history that goes back to the earliest Eocene (ca. 56 Ma) in Eurasia and North America. In Europe, during the middle and late Eocene (ca. 48 to 34 Ma) artiodactyls went through an outstanding diversification in a context of apparent endemism. Seven families are indeed strictly Europeans. Among them, the Choeropotamidae have been hypothesized to be closely related to the Hippopotamoidea. Historically, the family Choeropotamidae has been defined by Owen in 1845 and included only one genus: Choeropotamus. Then, in the light of successive fossils discoveries, the taxonomic content of Choeropotamidae gathered new taxa and it now comprises up to eleven genera. Thus, Choeropotamidae as defined today, is one of the most successful endemic European artiodactyl families and is retrieved in the fossil record from the early Eocene (MP 8/9) to the early Oligocene (MP22). Today, the taxonomic content of this family reveals to be problematic. Recent phylogenetic analyses find this family polyphyletic and suggest different affinities for Choeropotamus and the other choeropotamid taxa primarily part of Haplobunodontidae. The goal of this work is to test the validity of Choeropotamidae through the first survey of their auditory region based on  $\mu$ CT scan investigations. The study of the petrosal bone and bony labyrinth morphology of four choeropotamids (Choeropotamus, Haplobunodon, Lophiobunodon and Tapirulus) reveals that they exhibit a wide diversity of morphologies with, for instance various promontorium and internal acoustic meatus shapes, and mastoidean and amastoidean taxa. Finally, preliminary phylogenetic analyses based on auditory region characters do not support Choeropotamidae as a valid natural clade.



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#### Quantifying multivariate trait covariation in deep time: issues and some possible solutions

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Trait covariation substantially affects evolutionary patterns and its correct quantification is key to fully understand evolutionary processes in palaeobiology. Geometric morphometrics provides a powerful analytical tool to assess covariation in multivariate traits and in a phylogenetic context. Furthermore, recently developed methods allow for testing differences in the strength of covariation between groups (i.e. clades, ecological guilds, etc). However, the practical application of these methods to real biological problems can be problematic. Here, we evaluate how two different and largely overlooked issues affect shape covariation and we propose possible alternatives for overcoming them. As a case study, we quantified evolutionary shape covariation between the shape of the beak and the shape of the skull in a sample of 437 species of landbirds (Inopinaves) and compared the strength and pattern of covariation between different clades. First, we evaluate how statistical artefacts derived from the Generalized Procrustes Superimposition (GPS, used to extract shape data from raw landmark coordinates) affect covariation. These artefacts (often referred to as Pinocchio effect) emerge after GPS when landmark data exhibits high differences in the variances between different landmark points within the configuration and have been suggested either to solely affect visualization or to substantially spread the variance to the whole configuration of landmarks. We demonstrate that these artefacts do overestimate covariation in a very significant way leading to inaccurate measures of integration. Secondly, we evaluate how heterogeneity in rates of morphological evolution affects covariation. We quantified shape covariation in our sample using both a time-tree and a rate-scaled tree derived from a Variable Rates Model Analysis (VRMA). Our results show that covariation analyses using only the time-tree fail to capture overall covariation with the currently available methods and interpret recent divergent and/or fast evolving taxa as outliers leading also to spurious measures of covariation. We discuss several alternatives to overcome these issues with the available methods.



Speaker

### Dinosaur (Ornithopoda) footprints from the Lower Cretaceous Bata Formation of Colombia, a rare northern South American occurrence

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Dinosaur remains from present-day north-western South America are extremely rare, although tantalizing evidence for the presence of dinosaurs in Colombia has been recovered. Here we report the discovery of a small number of well-preserved dinosaur footprints from the Lower Cretaceous Bata Formation, Departamento de Boyacá, Eastern Cordillera of Colombia, northern South America. The Bata Formation consists of a thick succession (~1000 m) of conglomerates interbedded with sandstones and shales, with the muddy sediments gradually becoming dominant in the upper part. The fining upwards sequence and common presence of wave formed ripples suggests deposition along a tidally influenced palaeoshoreline during a warm, humid climatic regime. The dinosaur footprints come from the upper part of the Bata Formation, where fossiliferous levels rich in tellinid and trigonid bivalves occur. Palynomorph samples previously collected a few metres from the level of the dinosaur footprints indicates a Valangian-Hauterivian age for the Bata Formation. Due to the rise of the northern Andes, the dinosaur footprints are now preserved on a vertical bedding plane, above a deep rock pool, making direct observation problematic, so details of the footprints were obtained from photographs, and the specimens remain in situ. The dinosaur footprints are three-toed, large (approximately 260 mm long from heel to tip of the digit III), show a stride length of 2.2 to 2.4 m, a pace length of 1.1 to 1.3 m, and a pace angulation of 155 degrees. Individual footprint width: length ratio is subequal, and in the best-preserved example the divergence of digits II-IV is 65 degrees. The footprints are therefore very similar to large ornithopod tracks reported from the Lower Cretaceous of Europe and southern South America, and are here attributed to the ichnogenus Iguanodontipus. The Bata Formation footprints from the Eastern Cordillera of Colombia represent the first ornithopod footprints from Colombia, and the first record of Iguanodontipus footprints from South America. These trace fossils are the best-preserved dinosaur tracks thus far reported from the Lower Cretaceous of Colombia.



<sup>\*</sup> Speaker

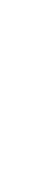
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### Ostracode Distribution in Lakes in the Bahamas as a Response to Sea Level and Climate Change

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Lakes on carbonate platform islands such as the Bahamas display wide variability in morphometry, chemistry, and fauna. These parameters are ultimately driven by climate, sea level, carbonate accumulation and dissolution. A model dividing lakes into either constructional or destructional formational modes has been developed using both qualitative and quantitative data. This model shows that lake formation is influenced by the hydrologic balance associated with climatic conditions that drives karst dissolution as well as the deposition of aeolian dune ridges that isolate basins due to sea-level fluctuations. The lake model was tested as a predictive tool for faunal distribution, using the microcrustacean group Ostracoda. We used an ostracode database comprised of 11 species from the 32 lakes on San Salvador Island. Ostracode counts included at least 400 right valves per lake. Live/dead studies indicate that the death assemblage faithfully records the living community. A non-parametric multi-dimensional scaling model of the ostracodes show that just like the physical and chemical model, blue holes tend to be similar in species composition and the interdunal depressions and cutoff lagoons also have similar assemblages. The two anomalies in the karsted depression are clustered together. These ostracode communities have either low or no Cyprideis americana -a widespread, cosmopolitan species found in almost all lakes. Instead, they are dominated by Peratocytheridea setipunctata, which is an ecological competitor to C. americana and found in almost all lakes but at higher abundances in the blue holes. While many people attribute species distributions to abiotic drivers, this lake model is able to separate physical versus biological variables and in this case, is able to inform us of an important case of competition that would otherwise not have been detected.



### Report on three new ankylosaurine dinosaur skulls from the Bayanshiree Formation (Late Cretaceous) of Eastern Gobi, Mongolia

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During the Korea-Mongolia International Dinosaur Expedition (KID) in 2007, three new ankylosaurine dinosaur skulls (MPC-D 100/1354 and field catalog KID167, KID175) were collected from the Bayanshiree Formation (late Cenomanian - Coniacian to ?early Santonian) at the Bayanshiree type locality of Eastern Gobi, Mongolia. MPC-D 100/1354 is nearly complete except for the damaged right dorsal surface. Both mandibles are missing. KID167 lacks the anterior nasal edge of the skull but preserves one partial left mandible. KID175 also lacks the nasal edge of the skull and no mandibular element is preserved. All specimens are similar in size, 220 - 240 mm in length, and 220 - 315 mm in greatest width. Both KID167 and KID175 show a V-shaped upraised area on the frontals which is a diagnostic feature of the genus Talurus. This feature is absent in the third skull MPC-D 100/1354. MPC-D 100/1354 differs from all known ankylosaurids in the absence of premaxillary sinus, and also differs from all other ankylosaurines, except Pinacosaurus grangeri, in the exoccipital and basioccipital contribution to the formation of the occipital condyle. Furthermore, MPC-D 100/1354 differs from all other known Asian ankylosaurines in a large number of frontonasal cranial ornamentations (more than 30). Therefore, MPC-D 100/1354 represents a new genus and species from the Bayanshiree Formation. We assessed the phylogenetic position of this new taxon by using TNT which placed it as the sister taxon to a clade containing Saichania, Zaraapelta, and Tarchia. Talarurus and Nodocephalosaurus form a polytomy with the clade that includes the four taxa above. Tsagantegia was recovered as the most basal taxon to the clade which includes all Asian ankylosaurines except Pinacosaurus. Our results show that the Asian ankylosaurines had evolved wider skulls and stronger tendency to develop bulbous, pyramidal frontonasal ornamentations through Cretaceous time. The new taxon increases the diversity of ankylosaurs of the Bayanshiree Formation and together with the two new materials of *Talarurus*, strengthens our understanding in the evolution of Asian ankylosaurs.



Speaker

### Bolonia lata Meunier in Lower Cretaceous shallow marine facies from Patagonia: ichnotaxonomic implications

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In this work, Bolonia Meunier specimens are thoroughly described from wave dominated deposits in the Cretaceous of the Neuquén Basin (northern Patagonia). According to the latest amendment of the diagnosis, this monotypic ichnogenus includes horizontal to subhorizontal, epichnial, non-branching, straight, occasionally tapering at the ends, bilobed structures. The outline in cross-section is trapezoidal to heart-shaped. Bolonia lata Meunier has been described from shallow marine paleoenvironments with storm influence. The specimens presented herein are found in sandstone beds with symmetrical ripple lamination covered by massive or horizontally laminated mudstones. These beds are within intervals interpreted as shoreface deposits, probably upper shoreface given the presence of primary current lineation indicating high-energy flow conditions. Even when in the diagnosis of Bolonia these trace fossils are described as having a straight pattern, B. lata was also described as "straight to slightly winding" by the same author. Some of the material now included in Bolonia and previously assigned to Scolicia was also originally described as straight to slightly. The Bolonia specimens reported in the present work bear all the diagnostic characteristics but are straight to curved. Hence, to our understanding the diagnosis of Bolonia should be emended: B. lata should not be restricted to straight structures, since curved patterns are very common in the material presented here and were also described as such by previous authors. Paleozoic records of Bolonia have been found in the Devonian of Spain, the Carboniferous of USA and Ireland, and the Permian of Australia. PostPaleozoic records of B. lata are restricted to the Jurassic of France, Great Britain, Greenland and India, and the Eocene of Spain. Most of these records were originally named differently and later reassigned to Bolonia in the latest revision of the ichnogenus. To our knowledge, the specimens described herein are the only Cretaceous record of this ichnotaxon and its only post-Paleozoic example for the Southern Hemisphere. They also show a greater morphological variety in bedding-plane view than previously reported for Bolonia, and might therefore have future ethological implications for this ichnotaxon whose tracemakers remain uncertain.



Speaker

### Taxonomic analysis of the first ophiuroid remains for the Mesozoic of South America: the youngest record of the extinct genus *Ophiopetra* Hess

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Previous findings of articulated and/or nearly complete brittle stars in South America are restricted to Devonian, Permian and Cenozoic specimens. In this work ophiuroids are described from the Neuquén Basin, Patagonia, Argentina. These are the first remains of ophiuroids for the Mesozoic of South America. The specimens have a disc diameter of 3.5 mm, and five long and slender arms that are 3 times longer than the disc diameter. The stout lateral arm plates exhibited by the specimens are similar to what is found in Ophiodoris Koehler and Ophioplax Lyman, recently included in the family Ophionereididae. However, the disc ornamentation differs from both genera: both sides of the disc are densely covered with granules. We therefore place these specimens in the extinct genus Ophiopetra Hess, also taking into account similarities in the overall shape of the lateral arm plates. The specimens belong to a new species but are poorly preserved. A new name is not introduced, as it would be based on an incomplete diagnosis. At the moment, Ophiopetra is considered an ophiolepidid. In the context of the latest progress in ophiuroid systematics, and thanks to new insights on the spine articulation microstructure of Ophiopetra lithographica found by this study, a transfer of Ophiopetra to the family Ophionereididae within the order Amphilepidida is proposed. This material expands the palaeogeographic record of this genus, since it represents the first remains of Ophiopetra described from the Southern Hemisphere. It is also the first post-Jurassic record of the genus worldwide.



Speaker

### New Iberian Eocene finds of *Leptolophus* (Mammalia, Perissodactyla): first thoughts on its palaeodiet

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The climate cooling that occurred in Europe at the end of the Eocene and mainly during the earliest Oligocene caused environmental changes, which led to important dental pattern changes of the palaeothere equoids. The precocious development of cement on the external wall of premolars and molars, and the reduction of the premolar series combined with heterodont and hypsodont molars series are considered as adaptations to chewing tough plants or more presence of terrigenous in the diet associated with the increasingly more arid conditions. These dental modifications are observed in the western Iberian palaeotheres since the late Middle Eocene and are very pronounced in Leptolophus. This genus is recorded in western Iberia and central Europe from the late Middle Eocene to the Late Eocene; only three species are currently published. The latest excavation campaigns in two localities from western Iberia (Mazaterón, MP 15-16 and Zambrana, MP 18) have provided the best-known fossil collection of this palaeothere. Here we summarize these new discoveries of Leptolophus. The Iberian specimens show more accused development of ribs and styles in the labial side, mainly the mesostyle, the ectoloph with weak "W" shape and lingual inclination of the external wall, and well developed coronary cement in the premolars as well as more hypsodont molars. The largest species from Zambrana exhibits thick coronary cement and a very pronounced hypsodont and heterodont molar series. The analysis of the mesowear pattern of its dentition suggests a more grazer-like palaeodiet in contrast with other Late Eocene palaeotheres. An undergoing study of microwear features of this species and of other palaeotheres will provide more data towards an understanding of the palaeoecological characterization of the environment of western Iberia and its differences with other European areas.

#### Acknowledgements

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#### Early Permian tetrapod footprints from the Central Sudetes (Poland) – new perspectives

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Our knowledge on the Early Permian terrestrial ecosystems of Central Europe remains poor due to the lack of palaeontological exploration and integration in the Pangaean context. Therefore recent intensive fieldworks resulted in a new collection of exceptionally well preserved Early Permian tetrapod tracks (mainly reptiles) from the Intra-Sudetic Basin (more than 60 slabs with various groups of trackways) housed at the Geological and Natural History Museum in the Polish Geological Institute NRI. This collection allows us to complete more precise reconstructions of the highly interesting Early Permian terrestrial ecosystems of Central Europe (located within intra-Variscan sub-basins) and would improve the tetrapod para-taxonomy. New granted paleontological project will start summer this year. This grant will enable us to continue detailed paleontological work and extensive excavation of slabs with tetrapod footprints (mainly in Tlumaczów quarries – Intra-Sudetic Basin), and to continue preliminary research on this Early Permian world class material. The depositional environment of Early Permian red-beds of Tlumaczów flora and fauna is interpreted as palustrine – lacustrine alternately dominated by fluvial inputs. This sedimentary environment is characteristic for semi-arid paleoclimate conditions. Sandstone and mudstone beds were formed as multilateral, stacked sets originated during the rapid and frequent changes of depositional conditions, which made possible the unique and perfect preservations of footprints and tracks of tetrapods and flora inprints. In spite of the tetrapod footprints great abundance in the Late Palaeozoic deposits in Europe, our knowledge of them still remains patchy. Comparative studies between footprints from the Western and Central European Basins (including that of French Early Permian -Autun Basin), allow more precise and exhaustive reconstructions of the terrestrial ecosystems, and integration of palaeogeography and palaeoclimate data in the Pangean perspective.



Speaker

### Preservation of marine mammals in pebble conglomerates, Miocene Pisco Formation, Peru

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Marine mammal fossils are abundant in pebble conglomerates of Cerro Hueco la Zorra and other localities of the Pisco Formation. The layers have an erosional bottom, and are interbedded with thick layers of siltstone. There are three main shapes of clasts: 1) subspherical to spherical, 2) elongate, and 3) flat, with borings. Lithology is predominantly siltstone, though phosphate nodules are also abundant. Grains are very poorly sorted, clast-supported within an uncemented siltstone matrix, or locally cemented in calcite, dolomite or iron oxides. Some flat pebbles have sparse Trypanites borings. Locally, patches of dolomite-cemented hardgrounds with Gastrochaenolites borings occur within the layer.

The skeletons in the pebble layers are mostly disarticulated, with very few articulated bones, mostly consisting of a few attached vertebrae. Bones occur both isolated and in clusters, and include skulls and postcranial bones, with scarce limb bones and very few odontocetes and phocids. Other fossils are rare, and include bivalves (Dosinia), shark teeth, and fish vertebrae.

Bones are randomly oriented. Some of the flat or elongate bones, including ribs, premaxillary and maxillary, and small vertebrae (tail, cervical), are completely or almost completely buried within the pebble layers, whereas thicker bones commonly extend into the overlying siltstone layer. Preservation of bones is uniform in both upper and lower surfaces, small and large bones, and flat and thick bones, with cortical bone only slightly abraded and minimal rounding of edges. Lateral and spinous processes are attached to the centrum of the vertebral body. There is no evidence of macro-bioerosion.

Pebble conglomerates commonly occur within intertidal environments, where storm waves may break the cemented sea floor (hardgrounds) and winnowing waters smooth out and concentrate clasts and skeletal fragments. These processes may have concentrated the whale bones as well. The overall good preservation of the bones suggests little abrasion by pebbles and minimal transport of particles within winnowing waters. The uniform degree of preservation of all the bones and the similar preservation between upper and lower surfaces suggest that the specimens within each pebble layer may be the result of burial of a single mortality event instead of exhumation, concentration and burial of previously buried specimens.

<sup>•</sup> Speaker

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### The continued education of initial years science teachers at Museu da Terra e da Vida (Life and Earth Museum), Mafra municipality, Santa Catarina state, Brazil

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The Museu da Terra e da Vida (Life and Earth Museum – MTV) is the expositive portion of Centro Paleontológico (Paleontological Center – CENPALEO), sustained by Universidade do Contestado (Contestado University – UnC), located in Mafra municipality at Santa Catarina state, Brazil. This study composes a broader research that analyses the potentiality of Museu da Terra e da Vida, integrant of CENPALEO, for the promotion of scientific alphabetization for initial years' students. Aiming the approximation of science teachers to CENPALEO/MTV, pedagogical activities evolving paleontology as theme were developed at the Museum. In the first stage of the research one questionnaire were applied to the teachers of initial years of elementary school of Mafra municipality. The questionnaire aimed to understand the conception of the teachers towards the MTV and to receive purposes of subjects to be approached in the continued education. One course was structured in a pedagogical activity shape, composed by integrated modules, which subjects were the Natural History with emphasis in Paleontology - the main motif of the MTV. Thirteen teachers from elementary school initial series attempt to the course. The modules were planed and developed with the collaboration of CENPALEO/MTV staff, which contributed with the delimitation of subjects, the planning and the development of the activities. The activities were carried out at CENPALEO/MTV during 2017 June and July, in a weekly meeting schedule with two and a half our duration at night. Six integrated modules were developed approaching the fallowing topics: 1 – Knowing about the Museums of Natural History; 2 – Paleontological patrimony; 3 – Earth structure and dynamics; 4 – Rocks and minerals study and its differences; 5 – Fossils and what they say; 6 – Attempting to the museum, what should I know?. The modules involved subjects that privileged the paleontological studies, emphasizing the scientifically based concepts addressed problematizing questions. Practical activities, complementary activities, science literature were applied aiming a broader involvement from participants and the understanding of the possibilities and potentialities that the natural history museums visitation, like MTV, can provide to formal education in a classroom.



Speaker

### The *Diplocynodon* Enigma: Revision of an extremely abundant but poorly understood endemic crocodylian taxon from the Paleogene of Europe

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The Eocene fossil record of Crocodylia in Europe is exceptionally rich and diverse. One of the most commonly found taxa with an extensive fossil record are *Diplocynodon* spp., which are present in many fossil collections in Europe. Literally hundreds of well-preserved articulated specimens exist last but not least from several exceptional Konservat Lagerstätten in Central Europe (e.g., Messel, Geiseltal, etc.). In the past, the extensive fossil record of this group discouraged researchers to work on this material, albeit it is long due for a complete systematic, biogeographic, taxonomic and ecological revision and may add an extremely valuable contribution to our evolutionary understanding of the Palaeogene Crocodylia. This crocodylian group was endemic in Europe from the Paleocene to its extinction in the late Miocene. *Diplocynodon* was the dominant crocodyliform taxon in Europe and one of very few crocodylians surviving until after the Eocene.

Starting with the excellently preserved specimens from the Eocene lignite deposit of Geiseltal, Germany and using modern examination techniques such as digital 3D models based on segmented CT-scans, we tackle the ambitious task of revising the Paleogene record of this taxon with four key questions:

1. Clarifying the phylogenetic position of Diplocynodontinae. *Diplocynodon* is widely regarded as a basal alligatoroid but conflicts between phylogeny, stratigraphic and geographic distribution as well as poor understanding of character evolution at the part of the tree where the major divergences occured within the crown-group put this into question.

2. Is *Diplocynodon* an anagenetic lineage? As an alternative, speciation could have taken place sympatrically as well as allopatrically (=endemic species within Europe) during the evolutionary history of the group. To answer this question, we will need to understand how many Paleogene species are valid.

3. Body size evolution: did sympatric species partitioned the niches by body size? How did climate influence body size evolution of *Diplocynodon* ? Is there a correlation between body size and temperature during the Eocene/Oligocene transition?

4. Ecological disparity and habitat preference: do different species differ in morphological traits (e.g., armor, skull proportions, dentition) that could be potentially related to ecology? In what types of depositional environments are they found most commonly?

All researchers are welcome to contribute to our project!

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#### Extralimital warm water marine molluscs in Late Pleistocene assemblages from Uruguay

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Extralimital marine molluscs, in which past latitudinal range endpoints are far from their present range limits, have been recorded in Pleistocene coastal deposits around the world. Warm extralimitals were reported from interglacial deposits of Pacific and Atlantic islands, the coasts of North America, Greenland, Mediterranean, Australasia and the Atlantic coast of South America. This biogeographic pattern represents confident evidence for the recognition of MIS 5e assemblages in which higher temperatures than today are inferred. Recent research on the Late Pleistocene shell beds from Uruguay (Puerto de Nueva Palmira, Zagarzazú and La Coronilla) resulted in the record of more than 40 warm extralimital molluscs. Their present biogeographic range was established only considering published data. For all taxa the boundaries are located at lower latitudes, in Brazilian warm waters. The species recorded were the chiton Ischnochiton striolatus, the bivalves Abra aequalis, Scapharca chemnitzii, S. brasiliana, Anatina anatina, Anomalocardia brasiliana, Cooperella riosi, Cyclinella tenuis, Cyrtopleura costata, Ervilia concentrica, Gouldia cerina, Laevicardium sp., Limaria sp., Lirophora paphia, Macoma constricta, Chione subrostrata, Pitar cf. P. palmeri, Merisca martinicensis and Eurytellina angulosa, and the gastropods Bacteridium resticulum, Bittiolum varium, Bulla occidentalis, Caecum cf. C. imbricatum, Cerithiopsis fusiformis, Eulimastoma engonium, Fargoa bushiana, Finella dubia, Littoraria flava, Nassarius cf. N. vibex, Odostomella carceralis, Olivella defiorei, Peristichia agria, Philine aff. P. sagra, Seila adamsii, Solariorbis infracarinatus, Turbonilla abrupta, T. arnoldoi, T. brasiliensis, T. deboeri, T. farroupilha, T. penistoni, T. rhabdota and T. turris. The distribution of extralimital species in the assemblages was not uniform. The Puerto de Nueva Palmira included 12 of these species, in Zagarzazú eight of them occurred, and La Coronilla contained 39 extralimitals. The southern boundary of distribution of most of these species is located today at Rio Grande do Sul and Santa Catarina, about 1000 km northwards the Pleistocene localities. However, in La Coronilla the phenomenon is stronger, as taxa reaching Rio de Janeiro or even lower latitudes were recorded. The abundance of extralimital species found clearly supports the presence of warmer waters than today, and a probable MIS 5e age for the Late Pleistocene molluscan assemblages from Uruguay.



Speaker

### Permian-Triassic character evolution in the Trigoniida (Mollusca-Bivalvia): dissecting the 'Myophoriidae-Trigoniidae' transition

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The fossil record of the order Trigoniida dates from the Silurian and was somewhat inconspicuous during most of the Paleozoic. During the Kungurian (Early Permian) the group diversified, but it was strongly affected by the end-Permian extinction event. They recovered fast during the Triassic, showing a great morphological renovation and a main radiation during the Carnian (Late Triassic). It is within Permian-Triassic interval that most of the typical characters of Mesozoic trigoniids (trigonian hinge, strong modular ornamentation pattern, opisthogyrate shell, well developed carina and sulcus) evolved. As a consequence, Paleozoic and post-Triassic genera differ notably. In classic systematic papers, these differences were the basis for the recognition of two main families: Myophoriidae and Trigoniidae. Nowadays, several families are recognized, but the post-Triassic trigoniids are still considered as a monophyletic group with trigonian hinge as synapomorphy.

In this study we define a number of characters and states in order to evaluate their stratigraphical appearance and to analyze the degree of convergence, something usually mentioned for the group but rarely evaluated. This data set may be used as a basis for a cladistic study in future research. Stratigraphic appearance and presence of the different character states on the different genera was established from a comprehensive bibliographic compilation of Permian to lowermost Jurassic bivalve genera.

The primitive stage would be a slightly prosogyrate smooth shell, with schizodian hinge and a rounded marginal edge (genus *Schizodus*). During the Artinskian (Early Permian) commarginal ornamentation pattern (continuous through area and flank) appeared, while radial ornamentation pattern is first recorded during the Kungurian. Marginal carina and antecarinal sulcus appeared associated to the radial ornamentation pattern, but they are absent on commarginally ornamented shells. The myophorian hinge appeared during the Kungurian associated to primitive character states.

During the Triassic those same derived states appeared differently associated, pointing to a convergent origin for many of them. Trigonian hinge appeared for the first time during the Anisian (Middle Triassic), also associated with the first appearance of modular ornamentation and opisthogyrate shell shape. Nevertheless, trigonian hinge is also recorded associated to primitive characters (prosogyrate shell, undifferentiated ornamentation pattern, absence of sulcus and carina) suggesting a convergent origin for this character state too.



<sup>\*</sup> Speaker

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### The Gaâga Campanian-Maastrichtian sediments (North East Algeria): quantitative and qualitative analysis and paleoenvrionmental interpretation

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The upper Cretaceous deposits are characterized by a large extension within the Algerian Eastern Saharan Atlas. A micropaleontological study has allowed us to attribute the Gaâga Mountain to the Campanian-Maastrichtian age. The lithostratigraphic survey and sedimentological analysis has permitted to distinguish three formations (marllimestone, marl, limestone) ranging from middle Campanian to upper Maastrichtian. Microfacies analysis reveals the predominance of three major microfacies types, which occur repeatedly along the series. The identified microfacies types are foraminifera mudstone-wackestone, foraminifera packstone and micritic mudstone microfacies. According to the petrographic study and detailed paleoenvironmental analysis, the counting of microfauna (planktonic and benthic foraminifera and ostracods) and the occurrence of large planktonic foraminifera indicate deep marine pelagic environment, beginning by middle slope in the first formation pointing to 800 m water depth, which is indicated by 70- 87 % planktonic foraminifera with large numbers of keeled specimens. The deep marine hemiplegic environment passes to the (shallower) upper part of the slope zone represented by the second formation pointing to 290 m water depth. This regression trend further develops in the third formation where the depth decreases gradually and the paleoenvironment is represented by middle shelf environment marked by powerful limestone formation.



Speaker

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### The Silurian graptolites of the Co To Islands, Northeast Vietnam

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The lower Palaeozoic graptolite-bearing strata of Vietnam have been noted since the time of the French colonial era, yet most of the assemblages are yet to be illustrated. More recently, Vietnamese and Japanese geologists have examined the Vietnamese lower Palaeozoic succession in detail, including the Co To Formation that crops out over 40 islands and islets of the Co To Archipelago in NE Vietnam. The Co To Formation is more than 1000 m thick and regionally has been considered to be of Late Ordovician and Silurian age, though only strata of Silurian age have been recognised in our study. Newly collected graptolites such as *Spirograptus turriculatus, Torquigraptus proteus, Monograptus priodon, Oktavites spiralis, Oktavites excentricus* and *Monoclimacis subgeinitzi* identify strata that are lower Silurian (Llandovery Series) and further constrain the biostratigraphical age of part of the formation to the *Torquigraptus proteus* Subzone of the *Spirograptus turriculatus* Biozone, and the *Oktavites spiralis* Biozone, both of the Telychian Stage. The material likely includes at least one new graptolite species.



Speaker

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### Isopod diversity in deep time – Assessing the morphological diversity of isopod crustaceans back in the Triassic

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The vernacular name for isopods, woodlice, is highly delusive since the adaption to a life with limited access to water is only one of the many aspects in the adaption of isopods to their environment. Most of the ecological and phylogenetic diversity is represented by the marine relatives of woodlice which also (for example as fish parasites) have a considerable impact on human economy. Although the fossil record of isopods dates back to the Carboniferous, their fossil remains are generally scarce compared to those of other crustacean lineages. Triassic isopods are especially rare. Up to now we could locate only eight published records of Triassic isopods in the literature. Here we present two new species, one from the Triassic of Austria and one from the Netherlands. Resulting from their general body shape most isopod fossils are preserved either from their dorsal or ventral side, but often lack important details. Thus, figuring out the phylogenetic position of the fossil is often challenging as the available characters, such as overall body shape or ornamentation on the tergites, seem to be the results of convergent evolution and hence do not provide reliable phylogenetic information. Here we use a different approach to capture the diversity in deep time. By comparison with extant isopods and fossils from different ages we want to address the question how the morphological range of isopods in the Triassic differs from what we can observe today and in other periods of time. By measuring fossil and extant isopods from a vast amount of literature illustrations we aim at quantifying our findings and possibly correlating them to the affecting circumstances like taphonomy and the restricted sample size.



Speaker

### A new Proterotheriid (Mammalia: Litopterna) from the Salla Beds of Bolivia (Deseadan: Late Oligocene): dental morphology and patellar-pit knee lock

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Our recent survey of fragmentary proterotheriid remains in the Salla collection of the Yale Peabody Museum of Natural History, along with the study of recently discovered remains from Salla housed in the Universidad Autónoma Tomás Frías, illuminate much of the nature of an undescribed diminutive proterotheriid of the Deseadan of Bolivia. Like Lambdaconus suinus (="Deuterotherium distichum") of the Deseadan of Patagonia, the upper molars (M1-2) are distinctive by way of their bunolophodont condition, the conspicuous absence of any trace of a metaconule, and presence of a steep valley that sharply separates the paracone and metacone from the obliquely lined paraconule, protocone, and hypocone. Its molars differ from those of L. suinus and L. lacerum by their lower crown, weaker styles, smaller hypocone and lack of longitudinal concavities on the labial surfaces of the paracone and metacone. The lower molars may be characterized as bunolophodont, having blunter cuspids and cristids than those of Lambdaconus spp. and Anisolophus spp. Trigonid and talonid cristids each appear as a broad crescent, punctuated by a large posterior cuspid: the metaconid forming the terminal cuspid of the trigonid crescent and the entoconid punctuating the talonid crescent. The pes is tridactyl, though functionally monodactyl owing to the diminutive nature of digits II and IV. The distal femur has a deep supratrochlear depression that forms a distinctive patellar "pit", as seen in the late Miocene-early Pliocene Eoauchenia sp. and the Santacrucian (Early Miocene) Thoatherium. The present analysis (Mesquite heuristic search, 9 taxa, 17 characters, with the basal litoptern Protolipterna as outgroup) suggests that the diminutive Salla proterotheriid is the earliest diverging of selected proterotheriids, sister to a monophyletic Lambdaconus clade (L. suinus and L. lacerum) and a clade that includes the remaining proterotheriids sampled. The distinctive suprapatellar fossa of the femur referred to the diminutive Salla proterotheriid is interpreted as a patellar pit knee lock, similar to those of Eoauchenia, some Santacrucian proterotheriids, as well as a number of macraucheniid litopterns.



Speaker

### Palaeoenvironmental implications of trace fossils of the Disang-Barail transition, Priabonian-Rupelian, flysch sediments of Northeast India in the Indo-Myanmar ranges

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The Disang-Barail Transition (DBT) flysch succession of Northeast India in the Indo-Myanmar Ranges (IMR) is approximately 300-400 m thick consisting of intercalations of dark grey shales, silty shales, siltstones and fine sandstones. This transitional succession which lies between the argillaceous Disang Group and arenaceous Barail Group is rich in ichnofossils typical of Teredolites, Glossifungites, Skolithos, Cruziana, Zoophycos and Nereites ichnofacies in association with various sedimentary structures such as sole marks, parallel laminations, massive and structure- less beds, rip-up clasts, current ripples, herringbone structures, hummocky cross stratifications, pot casts and rain prints. The Skolithos-Cruziana mixed ichnofacies is the most common. On the basis of the observations it is likely that the basin in which the Disang-Barail Transition succession accumulated could be related to a tectonically active hyper-extended basin with recurrent change in bathymetry possibly due to pulsatory stretching caused by passive rifting of the then western continental margin of Myanmar. The arkosic nature of the host and infill sediments of the trace fossils suggests a nearby granitic provenance, which consolidates the view that the Disang-Barail sediments were derived from the Myanmar continental landmass rather than the Indian continental landmass. Based on the various parameters discussed, a plausible depositional environment ranging from well oxygenated, high-energy, wave and current dominated marginal marine setting such as tidal flats, shoreface and deltas with sandy facies to the distal fan area in the shelf environment with silty and shaly facies, in general, may be suggested.

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Speaker

# Fossil fish otoliths of the Gobiidae and Oxudercidae (Gobiiformes, Teleostei) from the Pleistocene sedimentary sequence of Sousaki Basin (Eastern Corinth Gulf, Greece)

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Modern Gobiiformes (Teleostei) exhibit exceptionally high species diversity with over 250 genera and about 2000 species. It appears that they constituted a taxonomically complex group also in the Pleistocene fossil record of the Balkan Peninsula. The sedimentary succession of the Sousaki basin (Eastern Corinth Gulf, Greece) consists of marls with intercalations of organic-rich sediments clays and diatomite layers. Upwards, the marly layers alternate with sandy and conglomerate facies. The basement of the basin consists of volcanic rocks dated to 2.8-2.2 Ma age. The studied marly layer has a thickness of 1.70 m and belongs to the lower part of the sedimentary sequence; hence, an early Pleistocene age can be inferred for it. 120 Kg of sediment from three horizons of this layer have been wet-sieved through a 250  $\mu$ m sieve. After drying, otoliths were handpicked using a stereoscope, photographed under the SEM and identified down to the species level wherever possible. In total, approximately 2000 otoliths were collected from each horizon. Over 70% of the collected otoliths from all three horizons belong to the families Gobiidae and Oxudercidae, which are represented by several species. This goby assemblage most likely represents an euryhaline environment. The unusual large number of otoliths and their excellent state of preservation make the study area a hot-spot for otolith studies. Furthermore, the very limited number of Pleistocene terrestrial otolith records in Greece enhances its importance as an otolith lacustrine site from the early Pleistocene.



Speaker

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# Sigmodontine (Rodentia: Cricetidae: Sigmodontinae) diversity from the Holocene of Rio Grande Do Sul, Southern Brazil: The history of an impoverishment

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Sigmodontine rodents constitute a highly diversified clade that occurs mainly in South America. However there is strong evidence pointing for a North American origin of the group. The oldest fossil records of sigmodontines in South America suggest that the group first appeared in the continent in the Early Pliocene. However, the antiquity and origin of the subfamily remain as a controversial matter. In Brazil, the fossil evidence of sigmodontines is scarce and restricted to the Late Pleistocene-Holocene. Recently, sigmodontines from three archaeological sites located in northeast of Rio Grande do Sul, southern Brazil, were studied in order to provide data for paleoenvironmental and paleoclimatic reconstruction of the study area. The studied sites, RS-C-61: Adelar Pilger (29°33'36"S, 51°23'45"W), RS-S-327: Sangão (29°46'2"S, 50°33'4"W) and RS-TQ-58: Afonso Garivaldino Rodrigues (29°34'5"S, 51°38'4"W), are rockshelters which have been occupied by the Umbu Tradition. Radiocarbon dating performed with charcoal from some levels of the stratigraphic column of each site indicates a sequence from the Early Holocene (±9,400 years BP) to Late Holocene (±3,000 years BP). The material, more than 3,500 fragments, is housed at the Archaeological Museum of Rio Grande do Sul; Center for Archaeological Teaching and Research of Santa Cruz do Sul University and at the Archaeology Section of Federal University of Rio Grande do Sul. The Holocene sigmodontine diversity is composed by 22 taxa: Delomys sp., Juliomys sp., Akodon cf. A. azarae, Akodon sp., Bibimys cf. B. labiosus, Brucepattersonius sp., Deltamys sp., Gyldenstolpia sp., Kunsia tomentosus, Necromys lasiurus, N. obscurus, Oxymycterus sp., Scapteromys tumidus, Thaptomys nigrita, Holochilus cf. H. brasiliensis, Nectomys squamipes, Oligoryzomys sp., Pseudoryzomys simplex, Sooretamys angouya, Calomys sp., Reithrodon sp. and Wilfredomys oenax. The record of K. tomentosus is the southernmost record for this taxon, whereas that of *N*. obscurus is the northernmost record for this taxon. These assemblages indicate that faunal changes, such as the regional extinction of Gyldenstolpia sp., K. tomentosus, N. obscurus and P. simplex, happened since Early Holocene in northeastern Rio Grande do Sul. If these changes were triggered by human activity or are related to a climatic trend, must be studied in detail. In any case, it is clear that the recent sigmodontine assemblage in southern Brazil represents a depauperate subset.



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# Game based learning using adaptive virtual field trips to explore the Mesozoic

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Traditional introductory STEM (science, technology, engineering and mathematics) courses often reinforce misconceptions because the large scale of many classes forces a lecture-centric model of teaching that emphasizes delivery of facts rather than exploration, inquiry, and scientific reasoning. This problem is especially acute in teaching about the co-evolution of Earth and life, where classroom learning and textbook teaching are far removed from the immersive and affective aspects of field-based science. Additionally, the challenges of taking large numbers of students into the field make it difficult to expose them to the context of the geologic record. Virtual explorations or Virtual Field Trips (VFTs), allow science teachers to transport students to scientifically significant but inaccessible environments such as the rich paleo-localities associated with the K-Pg and PT mass extinction events. Grounded in the active learning of exploration, users interact non-linearly exploring the evolution of species, the environments, and the key adaptations that occurred along various paths over time. This interactive experience, developed in 360° VR (virtual reality), works in conjunction with an intelligent tutoring system that adapts to the individual student as they interact within the program, making each experience unique to the user. Innovations in immersive interactive technologies are changing the way students explore the evolution of Earth, its environment, and its species, giving them a window into events such as the origin of mammals and the age of dinosaurs. The VFTs utilize state-of-the- art visual tools to capture high-resolution spherical content at field locations such as Mesozoic mass extinction boundary sites. The panoramic footage, giga-pixel imagery of detailed fossil sites, and unique views via drones, combined with advanced software, allows the integration of these field sites into dynamic, game based virtual explorations that utilize adaptive feedback. These experiences allow teachers to give students the opportunity to explore these sites with full pedagogical control over their students' learning. By designing an experience that merges rich paleocontent with intuitive learning courseware, teachers can cater to an individual student's needs and personalize their learning. These visual and scientifically rich experiences surpass conventional online exercises by allowing the student to engage in virtual environments that are more like games than like lectures.



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## Teaching with Trilobites: digital resources to enhance student learning at the Tromsø University Museum

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As libraries of Earth history, museums are essential providers of object-based learning and critical in encouraging students to pursue careers in science, technology, engineering and mathematics (STEM). With shrinking budgets, museums face tremendous challenges in finding novel ways to share scientific processes, practices and discoveries with diverse audiences. Museum education programs that can creatively utilize their exhibits attract more student visitors and facilitate deeper learning. University museums are small and often disadvantaged by space and funding issues; however, they have the unique advantage of close associations with active researchers. New digital teaching resources were developed for the TellUs exhibit at the Tromsø University Museum, Tromsø, Norway. TellUs (Latin for Earth) is a permanent exhibit focusing on Earth history and the evolution of life recorded in the local geology of northern Norway. The e-learning module called *Teaching with Trilobites* uses early Cambrian trilobite and trace fossil discoveries, made by the Digermulen Early Life Research Group, to showcase basic palaeontological concepts. A series of inquirybased lessons were developed in open source and adaptive learning platforms with integrated media including spherical panoramas, soundscapes, videos and 3D objects. Students investigate remote field sites, make observations, develop and test hypotheses on how specific fossils are related. Engaging videos illustrate concepts including the formation of fossils, trilobite morphology and mode of life, and introduce virtual scientists (guides) working in animated museum spaces. The adaptive learning platform provides customized feedback to students based on their individual learning pathway. As part of the module, students can experience audio expeditions and explore immersive soundscapes of palaeontologists at work in the field. When describing a place, sound is often overlooked, but it is a powerful way to connect with natural environments and gives a strong "sense of place". The module is aligned to the Norwegian science curriculum, which emphasizes the importance of understanding both the content and the nature of science. Teaching with Trilobites will help teachers and students connect with the TellUs exhibit by offering engaging online lessons that build digital and STEM skills.

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## Kromdraai, a Plio-Pleistocene cave deposit in the Cradle of Humankind World Heritage Site, South Africa

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Kromdraai is a cave complex situated near Johannesburg in the Cradle of Humankind World Heritage Site, in South Africa. Since 1938, it has yielded early Pleistocene hominins (*Paranthropus* and early *Homo*), and a diversity of fauna (primates, carnivores, bovids, equids, rodents and birds). Palaeomagnetic dating, together with biochronological indicators, has suggested that part of the Kromdraai deposits are dated to at least 1.95 million years ago (mya). The new Kromdraai Research Project (KRP) is a joint French-South African collaboration that has led to the discovery of additional hominin specimens, from deposits which are Late Pliocene in age. The current challenge is to address the question of taxonomy in the context of recent discoveries of specimens attributable to *Paranthropus* and *Homo*, and to assess these specimens in relation to others from sites such as Sterkfontein where both *Australopithecus africanus* and *A. prometheus* ("Little Foot", dated at 3.67 mya) have been discovered.



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# The Plio-Pleistocene cranium of STS 5 ("Mrs Ples") from the Sterkfontein caves in South Africa is probably a small male *Australopithecus africanus*

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Sts 5 ("Mrs Ples") is a Plio-Pleistocene cranium attributed to *Australopithecus africanus*. It was discovered in April 1947 by Robert Broom and John Robinson at Sterkfontein in the Gauteng Province of South Africa, situated in the Cradle of Humankind World Heritage Site. It is thought to be at least 2.1 million years old. Broom considered that the edentulous specimen represented a female (on the basis of canine sockets), but in 1947 he did not have a substantial comparative sample for *A. africanus*. Rak (1983) and Thackeray et al (2002) suggested that Sts 5 was male. Grine et al (2012) contended that it was female. Resolution of this issue is important for an understanding of sexual dimorphism in *A. africanus*. In this study we use measurements of canine socket dimensions published by Broom and his colleagues in 1950 (before damage by acid). We compare these data with measurements published by Grine et al (2012). We show that canine socket dimensions strongly support the hypothesis that "Mrs Ples" represents a small male specimen of *A. africanus* rather than a large female.



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## Theropod footprints from the Enciso Group (Cameros Basin), Lower Cretaceous, La Rioja, Spain

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Cameros Basin is a privileged place to study dinosaur footprints as it is one of the regions with the highest number of footprints in Europe and in the world. In particular, Enciso Group (Barremian- Aptian) which only appears in La Rioja (Spain), stands out because of the huge number of catalogued sites and studied footprints. Among them, theropod footprints are the most abundant with nearly 6000 footprints, which constitute 60% of the total footprints in the area. This type of footprints is known since ancient times and was the core of legends among local towns that identified them as footprints of giant doves or hens. This type of footprints is characterized by being longer than wide, the presence of several pads in a finger and claw marks. The size can range from 12 to 60 cm, but usually they measure between 30 and 50 cm. These footprints are usually tridactyle but exceptionally tetradactyle footprints have been found with hallux impressions. From an ethological point of view, several trackways have been described that show a plantigrade way of walking, limps, abrupt change of direction, running and swimming. Moreover, the presence of parallel theropod trackways in the same site has been related to a gregarious behavior. In particular, theropod footprints in Enciso Group have been associated with several ichnotaxa. Several of them were assigned to ichnogenera Filichnites, Bueckeburgichnus, Irenesauripus and Megalosauripus. A new ichnotaxon has even been defined, Theroplantigrada encisensis. However, several of these ichnotaxa have a dubious ichnotaxonomic value. Therefore, a new revision of the ichnotaxonomy of the theropod footprints in Enciso Group is much needed. This new revision will provide a more real vision about the ichnodiversity of the region and will allow its comparison with ichnofaunas of the same age and the proposal of new ichnotaxa. Also, although the skeletal record of Enciso Group is quite scarce, some remains attributed to Baryonyx and Hipsilophodon have been found. The study in depth of the interaction between the limbs of these specimens and the lacustrine sediments can clarify the identification of the possible trackmakers and reveal the paleoecological interactions between the different components of the biota of Enciso Group.



<sup>&</sup>lt;sup>°</sup> Speaker

## Cenomanian to Coniacian rudist bivalves of Southcentral Pyrenees

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The Upper Cretaceous crops out at the three units of the piggy back thrusting sequence developed in South-central Pyrenees, namely from S to N: Serres Marginals, Montsec and Bóixols. The northern unit started moving southwards in the Late Cretaceous and the southernmost unit stopped moving in the Late Oligocene. Total shortening is estimated in 165 km.

Restitution of the Upper Cretaceous sediments to their original location, depicts, N of the emerged Ebro Massif, a basin deepening from S to N, where it communicated westwards with the former Gulf of Biscay. During Late Cretaceous this basin expanded, covering part of the Ebro Massif, due to the tectonic context but also to the global sea level rise. Approaching the end of the Cretaceous, the basin became almost filled-in with deltaic clastic sediments and, at the end, a general continental regime installed.

Shallow carbonate platforms or mixed (carbonate/siliciclastic), both with the conspicuous presence of rudist bivalves, are developed at most of the depositional sequences that can be distinguished in the basin; that is, rudists occur at different time intervals in different locations of the basin. The Cenomanian to Coniacian rudists reported herein occur in the Montsec and Boixols units, corresponding to the lower four depositional sequences. Three rudist assemblages are recognized in the studied interval; each one is present in different fossil localities which may represent successive rudist horizons within.

CENOMANIAN: Rudists occur in the lower part of the Santa Fe Fm. (Santa Fe 1 and Santa Fe 2 sequences). Caprinids, ichtyosarcolitids and radiolitids have been recorded.

LATE TURONIAN: Rudists identified correspond to Congost Fm. outcrops (Congost A sequence) and include Hippuritids and radiolitids.

CONIACIAN: Rudists have been reported in outcrops from Congost Fm. (Congost B sequence, early Coniacian) and Carreu and Sant Corneli formations and La Cova limestones (Sant Corneli sequence, middle to late Coniacian). Rudists taxa comprise Hippuritids, monopleurids, radiolitids, requieniids and plagioptychids.

Some species represented in the late Turonian are still recorded in the early Coniacian. At the same time, certain species well represented in the Coniacian are recorded sporadically in late Turonian outcrops. Some species occur during most of the Coniacian, while other only locally. The time of greatest taxonomic diversity is in the late Coniacian, when most species of that age are recorded together.



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# New information on tyrannosauroid theropods in the Upper Cretaceous Bayan Shire Formation in Mongolia based on fragmentary specimens

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The fossil record of tyrannosauroid theropods during the early Late Cretaceous (Cenomanian-Santonian) remains extremely poor. The Gobi Desert of Mongolia is not an exception despite a long history of extensive paleontological survey, with only a few specimens having been reported from the Bayn Shire Formation that was deposited during this time period. We here report new, fragmentary specimens of tyrannosauroids found from this formation through the Mongolian- Japanese Joint Paleontological Expeditions. A frontal and an articular were found at the Bayshin Tsav locality whereas a splenial was found at the Hongil Tsav locality. All specimens were found as floats in isolation. The frontal is mediolaterally wide relative to the anteroposterior length, showing a proportion similar to the one referred to Timurlengia euotica from the Bissekty Formation in Uzbekistan. In addition, the specimen shows other derived features including a very little exposure on the orbital margin and the supratemporal fossa occupying a large area, characterizing Tyrannosauroidea or its subclades. Similarly, a large mylohyoid foramen with the long axis inclined posterodorsally on the splenial and the presence of the medial process, as well as a well-developed concavity for the insertion of m. depressor mandibulae, on the articular suggest that these bones are also derived from tyrannosauroids. A tyrannosauroid frontal has previously been reported from another Baynshirenian locality, Tsagaan Teg, characterized by an anteroposteriorly-elongated proportion, quite different from that of the present specimen from Bayshin Tsav. Such difference in morphology between these frontals suggests that divergent lineages of tyrannosauroids may have been present during the early Late Cretaceous in the Gobi region. A frontal belonging to Troodontidae was also found at the Bayshin Tsav locality during the Expeditions, representing the first occurrence of this clade of theropods from the Bayn Shire Formation. Together, these findings demonstrate a large potential of this formation as a rare window into enigmatic time interval of evolution of tyrannosauroids, as well as other theropod dinosaurs.



Speaker

## First fossil record of Chiroptera (Phyllostomidae) from Uruguay (Plio-Pleistocene): a giant desmodontine

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The oldest remains of bats in South America (SA) are Eocene in age. The colonization of this continent by this clade occurred in several dispersal events. Early diversification and subsequent dispersal modelled its diversity in SA. Fossil remains are known from different sites and geological ages of SA (v.g. Brazil, Perú, Colombia, Venezuela, Argentina). Herein it is provided the first record of bats from Uruguay, represented by a complete right humerus (FCDPV-545), housed in the Paleontological Collection, Facultad de Ciencias, Montevideo. It comes from the Raigón Formation, which outcrops in the southwestern area of Uruguay. It has a fluvio-deltaic to fluvial origin, encompassing massive green silty-clayey beds intercalated with fine to mediumgrain sandy levels with parallel and cross-bedding stratification. At the top, paleosoils develop. The mammalian content suggests a Pliocene-middle Pleistocene age. OSL ages of 373 and 218 kyrs for the top of the sequence indicate a middle Pleistocene age. It yields terrestrial mammals, including medium to large ground-sloths, glyptodonts, large notoungulates and rodents (dinomyids), accompanied by large phorusrhacids and large aninghids. The studied humerus belongs to a giant bat referred to the vampire desmodontine group (Phyllostomidae). It was compared with the giant vampire Desmodus draculae (Pleistocene/Holocene of Venezuela, Brazil and Argentina), D. archaeodaptes (late Pliocene/early Pleistocene of NA), D. stocki (late Pleistocene of NA and Mexico), and the extant D. rotundus, and Diaemus youngi desmodontine taxa. The humerus from Uruguay is similar in size to D. draculae, both clearly largest than D. rotundus, D. archaeodaptes, Diaemus youngi and Diphylla ecaudata; is slightly longer than D. stocki but with a clearly wider distal transverse length. Qualitative morphological comparison substantiates the identification of the material into the desmodontine group. Its overall morphology considering the comparative set, more closely relates the material with the extinct D. draculae. Potential prey of this giant vampire bat may have included the giant dinomiyds, medium/large notoungulates and medium/large ground-sloths. Extant vampire bats are mostly distributed in warm to temperate areas of SA and Mexico. The record of this large desmodontine in the Raigón Formation suggests at least a temperate climate at this latitude during the Plio-Pleistocene.

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## A large opossum (Didelphimorphia, Didelphidae) for the Late Pleistocene of Uruguay (Sopas Formation)

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The fossil record of marsupials in the Quaternary of Uruguay not only is scarce but also the previous records have weak stratigraphic information and the material is lost. Here are described the first remains with precise stratigraphic information for the Uruguayan Quaternary (Sopas Formation, Late Pleistocene), assigned to a large opossum of the genus Didelphis. The materials are housed in the Paleontological Collection of the Facultad de Ciencias, Montevideo (FC-DPV) and in the Ghizzoni Collection of Salto (G). The specimens found consist of a partial portion of the skull associated to mandible and some postcranial bones of an adult (FC-DPV 875) (Sopas Creek, Salto department), and both humeri, a complete ulna and part of the other, an incomplete femur, and some vertebrae of an adult/subadult specimen (G 80-1) (Arapey Chico River, Salto department). OSL and radiocarbon ages of the Sopas Formation are mostly related to the interval 60 to 30 kyr BP, correlated with the last interstadial (MIS-3) of the Late Pleistocene. The morphology and dimensions of skull, mandible and postcranial bones (FC-DPV 875) support the assignation to a large opossum. The skull has an elongated and gracile rostral region, in the mandible the angular process is interiorly inflexed and upper and lower dentition, even worm, show the typical metatherian basic sectorial morphology. The humeri and ulnae are robust, large, and very well preserved. Preliminary comparisons of humeri (G 80-1) indicate many similarities with large opossums of Didelphis genus. Body mass estimations based on upper and lower dentition allometric equations for extant marsupials are congruent with the referred genus. The multivariate analysis performed over skull and mandible measures show similar results. Didelphis has great tolerance to diverse habitats conditions, occupying in current times different environments as wooded areas, open contexts and arid to temperate climates but closely to freshwater bodies, which is congruent with environment and climate conditions proposed for the Sopas Formation. It is a success generalist feeder, occupying an important role in intermediate levels of the trophic chain.

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## The early Pleistocene fish fauna of Rhodes (eastern Mediterranean)

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The goal of this work is the study of early Pleistocene fish assemblages of Rhodes using fish otoliths and also the reconstruction of the palaeobathymetry. In the late Pliocene the eastern part of the island of Rhodes (southeastern Aegean, eastern Mediterranean) was strongly affected by tectonic movements that lead to the submergence of this area and the deposition of early-middle Pleistocene sediments. Those sediments formed the three main formations of the island: Rhodes formation (including Kritika and Damatria members), Ladico-Tsampika formation and Lindos-Acropolis formation. For the purpose of this study a plethora of fish otoliths was extracted and studied from 13 bulk samples of lower Pleistocene sediments of Kritika member in Kallithea area. The otolith findings are used here to determine the marine fish fauna and reconstruct the paleoenvironment in the study area. In the early Pleistocene, the fish assemblage included mostly subtropical taxa with most abundant the Gobius paganellus, Deltentosteus quadrimaculatus, Apogon imberbis, Dentex dentex, Atherina boyeri, Aphia minuta, Echiodon dentatus, Ophidion barbatum, Phycis blennoides and Conger conger. From palaeoenvironmental point of view, the main focus was the reconstruction of the palaeodepth and also the identification of sea-level fluctuations. From Faliraki 1 outcrop they extracted three samples with specimen from Faliraki 1/1 sample could not be identified and Faliraki 1/2 and 1/3 samples indicates depth between 10-15m with species Echiodon dentatus and Ophidion barbatum that lives deeper than 120m and 150m, respectively, also be presented in the assemblage. From Faliraki 2 outcrop they extracted four samples with Faliraki 2/1 and 2/2 samples indicates depth between 1-97m. In Faliraki 2/3 the water column was deeper than 1m and in Faliraki 2/4 the water depth was up to 333m. From Kritika (Military post) outcrop they extracted six samples. In Kritika 1 and 2 the depth was 150-1456m and 150-333m, respectively. In Kritika 6 most species of the assemblage lived between 0-97m but the species Echiodon dentatus and Ophidion barbatum that coexist in depths between 150-1456m, were also present. In Kritika 8 the depth was 150-1456m. In Kritika 9 the depth of water column was up to 333m and in Kritika 10 the depth was 150m.



Speaker

# Fossil record of early Lophiodontidae (Perissodactyla) and the intraspecific variability of *Eolophiodon laboriense*

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Lophiodontids is an emblematic family of European Eocene perissodactyl mammals. Known in all western Europe from the early Ypresian (MP7) to the late Bartonian (MP16), their high specific richness and abundance in the deposits make them a biostratigraphic marker of choice between during this period. However, after more than a century and a half of study, and the accumulation of numerous authors and data, the systematic of this group remains complex and ambiguous. Many synonymies have been established and some distinctions between taxa have been based on variable characters. The phylogenetic relationships of Lophiodontidae with other families of perissodactyls are not well known as the basal radiation of Lophiodontidae remains poorly documented.

In this regard, a review of basal lophiodontid fossil record is proposed. An updated map of early Eocene localities that have yielded lophiodontid remains is provided. Two localities of the Ypresian of Southern France, Tourouzelle and St-Eulalie (Aude, France) have yielded new early lophiodontid fauna. The geological context of these localities is presented in detail. Furthermore, the new remains are described and compared to other taxa, and their important characters are highlighted.

In addition, the locality of La Borie, located near the city of Toulouse (Aude, France), has delivered numerous remains of *E. laboriense* since the description of the holotype, the only published specimen. These remains constitute the largest collection of basal lophiodontids, allowing for the first time an exhaustive study of the intraspecific variability of a lophiodontid close to the initial radiation of the group. The intraspecific variability of *E. laboriense* is high with more than 20 discrete variable characters on the dentition, including many additional crests and cusps. High variability is also visible on the mandibles and postcranial remains, largely due to a strong sexual dimorphism. This variation is compared with other Lophiodontidae and the status of the genus Eolophiodon is validated.



Speaker

## First Fossil record of the spitting Elapidae in the Cradle of Humankind (South Africa)

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There are currently 151 snake species in Southern Africa, distributed among 7 families, but little is known about their diversity and evolution during the past 23 million years. Snakes are poorly represented, even in the richly fossiliferous Plio-Pleistocene deposits in the Cradle of Humankind. This is especially true for the venomous snakes of the family Elapidae which comprises the cobras, rinkhals, mambas and African garter snakes because their remains are quite small. The Locus X Cave from Bolt's Farm Cave System in the Sterkfontein Valley (Cradle of Humankind World Heritage Site) yielded part of a snake maxilla carrying a complete fang, and this specimen was extracted from the cemented matrix (breccia) mainly by acid preparation in the Plio-Pleistocene Palaeontology section of the DNMNH. The present study shows that this fossil belongs to a spitting snake, today only known in elapids. It is currently impossible to report at specific level as only one piece of the fragmentary maxilla was discovered and there are no vertebrae associated with it, but it could belong either to rinkhals, represented in Southern Africa today by an endemic species Hemachatus haemachatus or to the Afronaja species. A well- established methodology exists in Europe for comparing fossil and extant osteological material of snakes in palaeontology as well as in archaeology, but this has not been the case in Southern Africa. This study indicates that it is now also possible in Southern Africa; the methodology is preliminary, however, and is yet to be developed. This sets the stage for a new approach to research – not only in palaeo-herpetology but also in herpetology in general.



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# The forgotten fossils of the Cradle of Humankind: the example of the Plio-Pleistocene lizards of Bolt's Farm

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The Plio-Pleistocene sites of the Cradle of Humankind (UNESCO site), at Taung and also Makapansgat Limeworks, all in South Africa, have yielded a rich collection of macrofauna but also an abundance of microfauna. This has been validated by different publications on rodents, insectivores, elephant shrews and birds. Very few fossil remains of reptiles are also present but these animals are cited usually just in the faunal list at reptile level, except for the turtle and for the varanid lizard which has been discovered at Sterkfontein and Swartkrans. The extant small lizards (smaller than the varanid) in Southern Africa present a large diversity and are represented by 53 families and by 433 species. In Europe, there is a long tradition in the study of small reptiles for the Neogene and the Quaternary, which, until now, did not exist in South Africa. This is probably due to the access to comparative osteological collections (the comparative material is usually rarely completely prepared, making the study almost impossible). The excavation and preparation methods have probably also played a negative role in the collection of small fossil remains (small lizards included). The fossiliferous breccia blocks are prepared mechanically and not by acid as at the Ditsong National Museum of Natural History. Different loci of Bolt's Farm Cave System (BFCS), as BPB, and ACI yielded some lizard mandibles. The first comparative study suggests that these mandibles are characteristics of two different groups: the Agamas (Agamidae) and the Cordylids (Cordylidae). A more precise study permits us to suggest that the first one belongs to the sub-family of Agaminae, probably to the genus Agama or Acanthocercus, and the second to Crag lizards (pseudocordylids). The Crag lizards are rock specialists and need suitable crevices for protection from predators and climatic events. These lizards have some climatic demand. This study shows that it is possible to have the finest determination of the fossil lizards found at the Cradle of Humankind.



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## Paleogene Cetaceans from the estuary of the Westerschelde at the Belgium - Dutch coast

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During the last centuries large amounts of cetacean remains from the Miocene and Pliocene have been dredged from the North Sea floor between Belgium, The Netherlands and The United Kingdom. In 1996 an archaeocete vertebra was recognized amongst newly found bones. Since then, 9 additional archaeocete vertebrae have been discovered. In 2016, the most probable locality of these finds could be traced. This is in the tidal channel 'Het Scheur' in the Westerschelde Estuary, near the Belgian- Dutch border. Strata of the middle Eocene Maldegem Formation, Lutetian to Bartonian in age, subcrop at the seafloor on this particular site. Based upon morphology, four types of vertebrae may be recognized. Vertebral centra of type A, B, and C are large and have basilosaurid characteristics. A comparison is made with formerly described genera. The basilosaurid characteristics are indicative of an origin from the uppermost strata of the Maldegem Formation, Bartonian in age. Affinities of vertebral centrum, type D, are still uncertain. Studies have not yet been completed and the vertebra awaits description at another moment. Although all vertebrae are ex situ finds, the seafloor at 'Het Scheur' appears to be one of the richest sites of archaeocetes in Europe, both in number of finds as in number of taxa.

Speaker

# Evolution of morphological diversity of chelicerate groups through time

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Chelicerate arthropods, today well known as spiders, scorpions, mites and alike, have a long evolutionary history, also reflected by a long fossil record. Since their early beginnings numerous distinct chelicerate groups evolved but also vanished, only leaving behind their fossil footprint. Today about 100,000 extant species of chelicerates are known, with super-diverse groups such as web spiders and mites. Chelicerates are known from terrestrial habitats all over the world, but also marine (sea spiders, horseshoe crabs) and freshwater (e.g., water mites) representatives are known. The sizes range from microscopic scale, represented by small mites or micro-whip scorpions with a body length smaller than 0.1 mm, to the largest forms represented by extinct sea scorpions with body lengths of over 2 meters.

However, morphological diversity within chelicerates is not only represented by their size, but also by their body organization. As all arthropods, chelicerates show a segmented body, in which several of these segments are organized into different functional units, called tagmata. These tagmata are specialized to perform different tasks like walking, swimming or food uptake, differing in their shape and equipment (appendages), resulting in different morphologies.

Here we aim at improving our understanding of the evolution of morphological diversity of chelicerate groups through time. The question is whether the diversity of body organization was affected by the extinction of groups such as Eurypterida, Chasmataspidida, Phalangiotarbida or Trigonotarbida, or whether representatives of other groups filled the "gap" formerly occupied by the now extinct forms.

To approach such a question morphospaces are an interesting tool. Morphospaces are multidimensional spaces representing the form of organisms, or mostly different structures of an organism in detail, based on measurements of these structures. These measurements include different lengths and widths of the specimen, e.g. the maximum width of the prosomal shield or the length of the trunk. After size correction these measurements can be plotted as a morphospace which yields information about the body organization and tagmatization. Including specimens from different geological periods also provides information about changes of morphological diversity through time. We present first preliminary results and discuss in how far this approach is improving our evolutionary understanding.



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# Ostracods from the Upper Cretaceous Jiaozhou Formation of Zhucheng, Shandong, China and their biostratigraphical and palaeoenvironmental significance

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Abundant fossil ostracods have been recovered from Mesozoic non-marine sediments over a vast area of China including the Jiaolai Basin, a late Mesozoic fault basin in the Jiaodong Peninsula, East China. Cretaceous strata are well developed in the Jiaolai Basin, yielding abundant fossils such as hadrosaurids, tyrannosaurs, various types of dinosaur eggs, bivalves, gastropods, ostracods, clam shrimps, insects and plants. However, few studies have focused on the ostracods. During a geological investigation in Zhucheng City, eastern Shandong Province, East China, we found a new exposure of the Jiaozhou Formation which constitutes the uppermost part of the Cretaceous-earliest Paleogene strata (encompassing the K/Pg boundary) in the Jiaolai Basin. Samples from the exposed Jiankou section near Jiankou Village, Zhucheng City, yielded abundant ostracods assigned to thirteen genera and twenty-seven species, reported for the first time from the Jiaozhou Formation in this area. The assemblage is composed entirely of non-marine taxa, including species of Cypridea, Talicypridea and Candoniella. An ostracod biostratigraphical study indicates this section to be Campanian-early Maastrichtian in age; the upper part of the Jiaozhou Formation therefore potentially contains the K/Pg boundary, but unfortunately it is not exposed at present. A palaeoenvironmental analysis of the species composition of the assemblages obtained, combined with a study of valve ornamentation, suggests fresh to oligohaline water with an increase in water depth and salinity through the Jiaozhou Formation during the Campanian.



Speaker

## New giant paleoburrows (Paleotocas) from Santa Catarina state, South Brazil

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The South American giant paleoburrows (Paleotocas) occurrences exceeds the sum of one thousand. In Santa Catarina state, south Brazil the sum of paleoburrows and krotovinas occurrences exceeds the hundred all through the state, but mostly concentrate at the south portion of the state. A new discovery of a series of paleoburrows at Morro Grande municipality, south coast of Santa Catarina, were made at the bottom of Canyon Aparados da Serra, bringing new perspectives to paleofauna understand. The initial prospection was motivated by narratives of residents of different regions about tunnels and excavations attributed to native indigenous of the region. The prospection proceeds through Atlantic Rainforest to locate the paleoburrows locations. At Pingador locality two occurrences were registered, with entrances near to each other. The first is almost straight with 23 m long, oval outline in cross-section, 1,45 m height and 1,65 m wide. The original walls of the paleoburrow preserved richly the claw dig imprints. Any anthropic imprint was located in this site. The second have large proportions. Composed by branching excavations with points with more than 2,5 m height and 2 m wide, its total length reaches about 100 m long. The dig imprints are rare and many anthropic marks are recorded through the walls. At Três Barras locality three other structures are found, known as Furnas dos Xokleng (Xokleng Den) due the presence of Xokleng indigenous in the region. The three structures are near from each other and also reach great proportions, with more than 150 m long, when not buried by erosion. Anthropic imprints are present. The digging marks are perceptible but have suffered intense weathering, maybe increased by the presence of multiple openings to the caves, which increased the air circulation and water entrance. The Pingador and Três Barras structures are understood as bioerosive structures dug by big mammalians at least 10 thousand years ago. During its existence the strutures very likely have being inhabited by indigenous and, as perceived for its depredation, by current population. Due its characteristics (shape, dimensions and claw imprints), the smaller structure is very likely dug by a megafauna Xenarthra, like the paleoarmadillo Propraopus genus, while the larger structures are much likely dug by larger megafauna Xenarthras, like the giant sloths of Mylodon genus. Strategies are being drawn to transform the region a geopark.

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# The Cruzeiro do Oeste bonebed: transportability analysis of pterosaur bones from Caiuá Group, Cretaceous of Paraná Basin

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The Brazilian pterosaur fossil record are mainly registered at Brazil Northeast region. The rare discovery of pterosaur bones in Brazil South region, at Cruzeiro do Oeste municipality, Paraná state, brings together with the taxonomical, palaeohistological, paleobiological and paleobiogeographical studies, the taphonomic approach. This occurrence from Paraná Basin are inserted in eolian sandstones wet interdunes of Caiuá Group and preserved in large concentrations, forming bonebeds. Aiming to identify and interpret characteristics related to hydraulic transportation and the direction of water flow, the Voorhies (1969) transportability patterns were adopted. The pattern was developed based on hydrodynamic behavior of bones in aqueous currents, according to their morphology, size and density. In order to analyze the water flow direction and the transportability difference between distinct bones, four blocks were selected with presence of long bones used in the description of the Caiuajara dobruskii specie, housed at CenPaleo (Contestado University Paleontological Center) - Museu da Terra e da Vida (Life and Earth Museum) collection. The blocks, taphonomically oriented during the excavation, had the bones identified and numbered. The direction of the vectors of each bone were tabulated and arranged in rosette diagrams. The strike were taken from 8 bones from CP.V 1001a block, 8 bones from CP.V 1001b block, 8 bones from CP.V 1024 block and 129 bones from CP.V 1450 block. Based on the bones directions is possible to recognize a preferential East-West water flow for blocks CP.V 1001a, CP.V 1001b and CP.V 1450. For the CP.V 1024 block a Northeast flow were recognized, based on the position of the heaviest apical portion of blocks long bones. The origin of those water flows are interpreted as sporadic flooding in a desert paleoenvironment (Caiuá Paleodesert), where the skeletal remains were carried to a lake, suffering hydrodynamic selection during this process and preserved at the wet interdunes of this geological unity.



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# New occurrence of the continental gastropod Viviparus sp., (Late Santonian) Cretaceous, Bauru Basin, Brazil

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The fossil record present at the São Carlos Formation, Bauru Basin, is characterized by an unusual diversity and quantity of fossils. The stratigraphic unit crops out in the eastern Bauru Basin and the reference section is located at the Nossa Senhora de Fátima Farm, São Carlos city, São Paulo State. The outcrop is composed by 6 m of black shales, and has been interpreted as a result of the deposition in a lacustrine fresh-water system, with low sedimentation rates. The anoxic conditions at the sediment-water interface allowed for the preservation of the organic matter, as well as the activity of sulfate-reducing bacterias, as observed by the presence of pyritized fossils. Several invertebrates occur within the same beds: conchostracans branchiopods, bivalve gastropods and mollusks, and all of them are outnumbered by ostracods. Bivalves and gastropods of the Bauru Basin are being recently redescribed. The occurrences are restricted to Physa sp., Hydrobia sp., and Viviparus sp. among the gastropods, and to Anodontites sp., Monocondylaea sp., Itaimbea sp., Taxodontites sp., Florenceia sp., Sanctiorolis sp., Diplodon sp., Castalia sp., ?Musculium sp. among the bivalves. Most of the paleontological studies on these beds are focused on the vertebrate records from crocodilians, dinosaurs, teleosts, and testudines. 55 specimens of a gastropod were collected from the basal beds; they are preserved as molds, piritized casts and possibly as carbon films. Also, they are mostly preserved with their longest axis (height) parallel to the bedding plane, aperture down (covered). Specimens vary in having 3-4 whorls in the spire. No umbilical view was found so far. This is the first time this gastropod (Viviparus sp.) is observed at these beds. At the Bauru Basin, similar gastropods were classified as Viviparus souzai Mezzalira, 1974. Further studies will answer questions on its family group and other taxonomic characteristics, habitat, and fossilization processes.



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