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ABSTRACT BOOK



Keynote

The big three extinctions: Lessons from deep time

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Of the five big mass extinctions, three stand out: the End Ordovician, End Permian and End Cretaceous. The causes and consequences of each were different, (i) a short, intense ice age, (ii) a runaway greenhouse and (iii) an asteroid strike. Organisms survived but ecosystems were transformed or almost extinguished. In all three, habitat destruction was a key player and adaptation to changing environments whether relatively gradual or sudden, crucial for survival. The near extinction of the Pleistocene megafauna, heralded a new age of biotic extinction with almost 1000 species going extinct since 1500 AD. Relatively few scientists would now dispute that these extinctions are related to anthropogenically-induced climate change manifest by global heating, changing weather patterns associated with droughts and flooding, ocean acidification and oxygen depletion; the pace of habitat loss and extinction is now on human timescales. Past extinctions indicate that life is resilient but ecosystems, much less so.



Two hundred years of palaeontology: Henri Marie Ducrotay de Blainville and the science of ancient beings

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The word "palaeontologie" was coined in 1822 by the French anatomist and zoologist Henri Marie Ducrotay de Blainville (1777-1850), a former disciple of Georges Cuvier who had turned against his mentor and rejected catastrophism. Although he was generally considered as a difficult, ill-tempered person who had few friends, Blainville was an eminent scientist, who published abundantly on many groups of animals, including molluscs, reptiles, birds and mammals, both extinct and extant. The meaning and significance of the new word "palaeontology", as compared with older designations such as "oryctology" are discussed. Blainville was a devout Roman Catholic who defended a creationist interpretation of the fossil record and rejected both catastrophism and evolution. Paradoxically, the science of fossils, which has contributed enormously to our knowledge of the evolution of living beings, owes its name to a scientist who strongly opposed the concept of biological evolution.

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Keywords: Palaeontology, Henri Marie Ducrotay de Blainville, history of science



Keynote

Progress in the geology and palaeontology of Thailand

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Palaeontology in the 21st century: Contributions from China

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Session 1 - ORAL

Fossil hunting in the Far East: the history of palaeontological collecting in eastern Asia

A French Jesuit and his Chinese museum: the palaeontological researches of Emile Licent in northern China

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Emile Licent (1876-1952) was a French Jesuit missionary who spent more than twenty years in China, where he built a large and modern natural history museum (Hoang ho-Pai ho Museum) in the city of Tianjin. Although initially an entomologist, Licent started an extensive programme of palaeontological research in northern China. With the help of various foreign missionaries, he located a number of fossil vertebrate localities, mainly of Neogene and Pleistocene age, in the course of long collecting trips across the basin of the Hoang He. Among his major discoveries were the Late Pleistocene sites with fossil mammals and Palaeolithic tools in the Ordos region of Inner Mongolia and the Early Pleistocene vertebrate localities of the Nihewan basin NW of Beijing. His discoveries attracted the attention of French palaeontologists, notably Marcellin Boule at the Paris Natural History Museum, who sent to China another Jesuit, Pierre Teilhard de Chardin, to assist Licent in his researches. Relations eventually deteriorated between the two men, and Licent had to leave his museum and return to France in 1938. Although some specimens were removed to Beijing by Teilhard de Chardin (and are now at the IVPP), the Hoang ho Pai ho Museum in Tianjin still holds remarkable natural history collections and remains a tribute to Licent's indefatigable energy and devotion to the Chinese natural heritage.

Buffetaut, E. (2019). Un Jésuite et son musée chinois. *Espèces*, 32, 82-86.

Keywords: Emile Licent, Hoang ho Pai ho Museum, Tianjin, fossil vertebrates





Session 3 – ORAL

Hidden histories revealed in scientific revision of paleontological collections

"UMUT-CA --the first fossil curating system in Japan"

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From the Meiji Era (since 1868), the government collected local specialties including fossils, transported them to Tokyo and held exhibitions in order to promote industries. In 1877, the University of Tokyo was founded, and lectures in geology and palaeontology were given by German teachers, using a textbook of palaeontology by Karl A. von Zittel (Zittel, 1876). Teachers showed the students fossil specimens which were originally collected in Japan as well as specimens collected by Krantz imported from Germany. Krantz's specimens number more than 13,000.

The University Museum at the The University of Tokyo (UMUT) was established in 1965 with 12 departments: geography, mining geology, geology and palaeontology, mineralogy, petrology, zoology, botany, medicine, pharmacy, archaeology, anthropology and prehistory, and cultural anthropology. UMUT was the first university museum in Japan.

Since the latter part of the 19th Century, taxonomists have considered that type specimens are important in order to stabilize the name of species. In 1961, the International Code of Zoological Nomenclature (ICZN) was legislated. In accordance with the rules of the ICZN the registration system for fossils of the University of Tokyo was established and the UMUT registration number was prefixed according to time periods (R: Recent, C:Cenozoic, M:Mesozoic, P:Paleozoic) and taxa (M:Mollusca, A: Arthropoda and so on).

No 0001 of the UMUT collection is a specimen of *Vaginoceras grabau* Kobayashi, 1927, an Orthoceras of Ordovician age (Yajima, 2017). Now, the number of specimens housed in the UMUT exceeds 10,000. The specimens are well organized, and digital information are available. The UMUT-specimens have to be deposited together with the original paper.

After the establishment of UMUT, the universities in Japan, such as, Hokkaido, Tohoku, Nagoya, Kyoto, Kyushu and so on, established university museums and started a registration system for specimens.

Kobayashi, T. 1927. Ordovician fossils from Corea (Korea) and south Manchuria. Japanese Journal of Geology and Geography, 5(4), 173–212.

Yajima, M. 2017. Gifts towards 21st Century from Teiichi Kobayashi.. Fossils (The Palaeontological Society of Japan), no.101, 1-2.

Zittel, K. A. 1876. Handbuch der Palaeontologie. Mitw. v. Wilhelm Philipp Schimper.

Keywords: The University Museum, The University of Tokyo (UMUT), International Code of Zoological Nomenclature (ICZN), type specimen, "Unkon-shi", university museum,





The dietary shift toward more abrasive food among ornithopod dinosaurs revealed by dental microwear texture analysis

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Dinosaurs were the dominant mega-herbivore during the Cretaceous, when angiosperms, flowering plants, emerged and diversified (Barrett, 2014). How herbivore dinosaurs responded against increasing angiosperms was largely unknown due to the lack of the evidence of the diet of herbivore dinosaurs taken directly from their body fossils. We applied the dental microwear texture analysis (DMTA) that evaluates microscopic level three-dimensional tooth surface texture (Scott et al., 2005; Schultz et al., 2010) for the first time against ornithopod dinosaurs. We found Late Cretaceous ornithopods have rougher dental microwear texture compared to pre-Late Cretaceous ornithopods and a model fitting showed a temporal trend toward rougher dental microwear indicating the dietary shift toward more abrasive food. A model fitting also showed that a dietary variation reflected in dental microwear texture increased in hadrosaurids, the derived Late Cretaceous ornithopod clade. These changes were likely due to the ingestion of more phytoliths that are more concentrated in angiosperms than other major plant groups. Our result showed, when applied to the occlusal enamel surface, DMTA can reconstruct the diet of herbivore dinosaurs with a resolution superior to conventional methods. Its application to other herbivore dinosaur clades will reveal how different dinosaur clades reacted against the diversification of angiosperm.

Barrett, P. M. (2014). Paleobiology of herbivorous dinosaurs. *Annual Review of Earth and Planetary Sciences*, 42(1), 207-230.

Schulz, E., Calandra, I., & Kaiser, T. M. (2010). Applying tribology to teeth of hoofed mammals. *Scanning*, 32(4), 162-182.

Scott, R. S., Ungar, P. S., Bergstrom, T. S., Brown, C. A., Grine, F. E., Teaford, M. F., & Walker, A. (2005). Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature*, 436(7051), 693-695.

Keywords: ornithopod dinosaurs, angiosperm, dietary reconstruction, dental microwear texture analysis





Modelling aquatic specialisation in ancient whale hind limbs

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Significant change occurred in the aquatic locomotion of stem cetaceans (archaeocetes), evolving from early quadrupedal surface paddlers to the submerged oscillatory swimming style of modern cetacea. During this transition, the primary propulsive surface changed from the limbs to the tail, with external hindlimbs eventually lost completely. With very little fossil material definitively indicating the presence of a fluke (enlarged surfaces at the end of the tail) in archaeocetes, it is difficult to determine when this change occurred.

Using computational fluid dynamics, we sought to use the more extensively-preserved archaeocete hindlimb fossils to investigate significant changes in hydrodynamic performance across the land-water transition. We produced 3D reconstructions of the feet of a range of archaeocete species spanning the transition. These models were virtually sculpted around digitised fossils, using previously-established regression equations to inform volumetric reconstruction. Water flow was simulated around each model, in order to approximate their effectiveness in providing propulsion during swimming. We estimated the coefficients for drag and lift produced by the feet at a range of angles of attack, imitating the angles observed in potentially analogous extant swimming mammals. Our results demonstrate significant changes in drag and lift coefficients over time related to increased aquatic specialisation in archaeocetes.

Keywords: Archaeoceti, Computational Fluid Dynamics, Land-WaterTransition





The first fossil larva of Mecoptera (Insecta) reconstructed with advanced imaging techniques

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Scorpion flies (Mecoptera) are among the oldest holometabolous insects with approximately 650 extant species and many extinct lineages. Although they were once an important part of the entomofauna and are therefore often found in the fossil record, so far nothing has been known about their preimaginal stages. A well-preserved Panorpidae larva was discovered in the Eocene Baltic amber. The larva is eruciform, with the strongly sclerotised opisthognathic head capsule, three pairs thoracic legs and eight pairs of abdominal prolegs. The head capsule is without shallow furrows on the lateral surfaces. The compound eyes are protuberant with distinct ommatidia and long three-segmented antennae, similarly to larvae of extant *Cerapanorpa* Gao, Ma & Hua, *Dicerapanorpa* Zhing & Hua and *Panorpa* Linnaeus. Four-segmented thoracic legs are with triangular tibial lobe. Ventral prolegs on abdominal segments I-VIII are of similar size. The dorsal annulated processes on the abdominal segments I-VIII are short, in contrary to these processes on the three last abdominal segments, which are strong and long. The distribution and size of setae (SV1-3, L1-2, D1-2) on the abdominal segments are similar to extant species of *Panorpa*. The shape of antenna and annulated processes points on the third/four stage of fossil larva. The set of visible morphological characters points on the closest affinity of larva to larvae of genera *Cerapanorpa* and *Panorpa*, without possibility of certain assignment to any of extant genus of Panorpidae. Larvae of this lineage are known as euedaphic or hemi-epedaphic what is also possible to conclude for described fossil larva. Advanced imaging techniques, including synchrotron microtomography, have made it possible to reconstruct the body structure of this larva, which is more than 40 million years old, with great accuracy.

Keywords: Baltic amber, Eocene, scorpionflies, synchrotron, immature stage





Untangling the web of arachnid systematics: using confocal microscopy to image Devonian trigonotarbids

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Trigonotarbids are an extinct order of armoured arachnids, with fossils ranging from the late Silurian (Jeram *et al.*, 1990) to early Permian (Dunlop & Rößler, 2013). Comprising some seventy species, trigonotarbids are characterised by the partitioning of their opisthosomal tergites into discrete median and lateral plates (Garwood & Dunlop, 2010). As prominent predators, these extinct spider-like arachnids played a critical role in the earliest terrestrial food webs (e.g. Shear *et al.*, 1987; Dunlop & Garwood, 2017). However, the phylogenetic position of trigonotarbids relative to extant arachnids remains disputed (see Dunlop & Penney, 2012). In this study, we use confocal laser scanning microscopy (CLSM; e.g. Edgecombe *et al.*, 2020) to image some of the earliest known land-dwelling arachnids in 3D (see Hirst, 1923; Hirst & Maulik, 1926; Dunlop, 1994). A re-examination of the mouthpart morphology of the Lower Devonian (~408 Ma) trigonotarbid, *Palaeocharinus*, from the Rhynie Chert of Scotland, yields an unprecedented level of morphological detail crucial to untangling arachnid systematics. By comparing the Rhynie trigonotarbids to new CT scans of their closest extant relatives, we aim to adjudicate between the two competing hypotheses for the sister group of trigonotarbids, the ricinuleids (hooded tick-spiders) or tetrapulmonates (spiders, whip scorpions and whip spiders). The Rhynie Chert trigonotarbids demonstrate the power of confocal laser scanning microscopy in the elucidation of fossils and their phylogenetic placement.

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Keywords: Rhynie chert, Devonian, Trigonotarbida, Tetrapulmonata, Ricinulei, Arachnida, liquid feeding, confocal laser scanning microscopy (CLSM), computed tomography (CT), 3D model





Solving the six decade-long mystery: Phylogenetic relationships of the Cretaceous Canadian tardigrade amber fossils

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The tardigrades, or water bears, are a charismatic phylum of microscopic invertebrate ecdysozoans that are well known for their extreme survival capabilities. Molecular estimates suggest that tardigrades diverged from other panarthropods before the Cambrian, but the fossil record of these microscopic animals is extremely sparse. There are only four fossils that can be ascribed to the tardigrade crown-group known to date, but only two of them have well resolved phylogenetic affinities (i.e., *Milnesium swolenskyi* and *Paradoryphoribius chronocaribbeus*). The remaining two – *Beorn leggi* and a yet unnamed putative heterotardigrade – have the distinction of being the first ever discovered tardigrade fossils and are both embedded in the same piece of Cretaceous-aged amber. Since their initial discovery along Lake Cedar in Canada, their relationships to other extant tardigrades have remained unresolved because the only available images of these rare fossils come from the original taxonomic paper describing them (Cooper 1964). Unfortunately, the original description does not provide critical morphological information that would be essential for understanding the affinity of these fossils, such as the claws and cuticle. In this study, we visualized the two fossils using modern imaging techniques to solve their phylogenetic identities. Specifically, we employed confocal fluorescence microscopy, to obtain high-quality images of their claws and cuticular features. We used geometric morphometric analysis to compare the shape of the claws of the fossils to extant tardigrades to assess their similarities and to improve character coding. We performed morphology-based phylogenetic analyses to determine the relationship of the two fossils relative to extant tardigrades. Ultimately, we were able to resolve the phylogenetic relationships of *Beorn leggi* and the second unnamed tardigrade, which allowed us to use them as calibration points for molecular clock estimations and to reconstruct the evolution of taxonomically important characters in tardigrades.

Cooper, K.W. 1964. The first fossil tardigrade: *Beorn leggi* Cooper, from Cretaceous amber. *Psyche* 71(2), 41-48.

Keywords: invertebrate paleontology, Eutardigrada, *Beorn leggi*





Virtual taphonomy of trilobite cranidia: understanding deformation processes using 3D modelling and rigid body simulation

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The deformation of fossils during fossilization processes has caught the attention of paleontologists for decades. As paleontology primarily deals with morphology, the deformation of fossils can cause problems, if not properly handled, in diverse areas of paleontology such as functional morphology, systematics, and phylogenetics. There have been attempts to find ways to restore the original shapes of deformed fossil specimens, i.e. retrodeformation. Retrodeformation inevitably requires an adequate understanding of the deformation process itself. In this study, we investigate factors that might cause changes in the shapes of fossil specimens during fossilization processes. 3-D models of trilobite cranidia recovered from carbonate rocks are subjected to deposition and compaction simulation by utilizing rigid body simulation and scaling features of the open source 3-D software Blender. Rigid body simulation results show that trilobite cranidia can settle down on the seafloor with a certain degree of variation regarding rotation along sagittal and transverse axes. The shape of cranidium, especially that of suture line, as well as the slope and shape of the seafloor, and the composition of sediments all take part in deciding the final angle of pose. As the specimen and surrounding sediments get pressured and compacted during lithification, such variation can translate into apparent shape differences larger than they originally were. By comparing these results with the specimens recovered from shale, we would be able to better understand the taphonomic process itself and also find ways to interpret such deformation and its implication on trilobite taxonomy.

Keywords: trilobite systematics, taphonomy, retrodeformation, rigid body simulation, 3D-modelling





Troubling trilobites: Bayesian phylogenetic methods clarify evolutionary history of turbulent trilobite orders

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Despite their exceptional fossil record and long history of study, disparate classification schemes and disputes over higher-level groupings plague the study of trilobites at present. This issue deeply hampers research into evolutionary questions. The most recent comprehensive Trilobita classification (*sensu* Adrain 2011) places Aulacopleurida as an order distinct from Proetida, and includes families formerly assigned to Ptychopariida by Fortey (1997 Treatise). Subsequent parsimony analyses based on a broad sampling of trilobite taxa across multiple orders challenged this conception (*i.e.* Lamsdell and Selden 2015). Still, group support was low in this analysis and divergence times remain unknown. The apparent appearance of the Proetida in the Ordovician is troubling due to their cryptic Cambrian history and unknown sister group. Additionally, despite attempts at cladistic analyses of certain groups within trilobites, divergence times and evolutionary rates have rarely been quantitatively analysed.

Here we present phylogenetic analyses using the largest and most comprehensive character matrix to date, which comprises >340 characters, including dependencies and continuous characters. The analyses include 57 exemplar species from all families assigned to either Proetida (*sensu* Fortey 1997), Aulacopleurida (*sensu* Adrain 2011), and those previously assigned to Ptychopariida (*sensu* Fortey 1997) that were excluded from Aulacopleurida. We conducted Bayesian phylogenetic analyses using the fossilized birth-death model to produce trees that would co-estimate topology, divergence times and evolutionary rates. We also assess leaf stability, character influence and stratigraphic fit, as well as different models of morphological evolution. We found that the Aulacopleurida forms a non-monophyletic group, and suggest a new systematic paradigm incorporating some 'aulacopleurid' families back into a monophyletic Proetida with a ptychopariid sister group that has a divergence time in the early Cambrian. Rates of morphological evolution are largely constant through the Cambrian except for some specific taxa with elevated rates, and there is a distinct shift in evolutionary rates around the Cambrian-Ordovician boundary. This wholistic phylogenetic approach provides much needed insight into the evolutionary history of troubled trilobite groups.

Adrain, J. M. Class Trilobita Walch, 1771. In: Zhang, Z.-Q. (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa* **3148**, 104 (2011).

Fortey, R. Classification. in *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita, Revis* (ed. Kaesler, R. 289–302) (Geological Society of America and University of Kansas Press, 1997).

Lamsdell, J. C. & Selden, P. A. Phylogenetic support for the monophyly of proetide trilobites. *Lethaia* **48**, 375–386 (2015).

Keywords: Trilobites, Bayesian phylogenetics, fossilised birth-death, evolutionary models, morphology, Paleozoic, systematics





The modular organization of the trilobite head

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The trilobite head served multiple functions and was composed of several fused segments. Modeling the head as being composed of modules, or subunits which vary and thus have the potential to evolve semi-independently, can reveal underlying patterns of organization. Hypotheses of modular organization based on comparative developmental biology of arthropods were evaluated using geometric morphometrics. The degree and structure of modularity were assessed using the covariance ratio (CR) and the fit of different models compared using an effect size measure derived from the CR (Adams & Collyer, 2019). Previous analyses based on datasets of two-dimensional (2D) (semi)landmarks collected from two Ordovician trilobite species, *Calyptaulax annulata* and *Cloacaspis senilis*, indicated high covariation between the eyes and the anterior region of the head compared to other modules of the head. These results can be interpreted as a developmental signal corresponding to the anteriormost ocular segment (Scholtz & Edgecombe, 2006) of early arthropods that is retained throughout development.

Newly collected three-dimensionally preserved material of the trilobite *Ceraurus pleurexanthemus* was examined to assess whether these results are consistent in three-dimensions (3D). Morphologically mature silicified cranidia were picked from sieved residues of dissolved rock and then microCT scanned. To rigorously quantify shape, 3D meshes were produced from scan reconstructions and high-density geometric morphometrics was performed (Goswami et al., 2019). In the most complex modular hypothesis, landmarks were divided into eight (8) partitions and the degree and structure of modularity was assessed using CR and the associated effect size measure as before. Results of 3D analyses are consistent with prior 2D analyses. The eyes highly covary with the anterior glabella with and without inclusion of the eye ridges. The developmental coupling of the eyes with the anteriormost region of the head may have imposed a constraint on patterns of diversification that may have either impeded or enhanced the rate of evolution depending on its congruence with selective pressures. Assessment of this will require further study of modularity across trilobite groups throughout the Paleozoic.

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Goswami, A., Watanabe, A., Felice, R.N., Bardua, C., Fabre, A.C., Polly, P.D. 2019. High-density morphometric analysis of shape and integration: the good, the bad, and the not-really-a-problem. *Integrative and Comparative Biology*, 59, 669-683.

Keywords: Trilobites, modularity, integration, 3D morphometrics, micro-computed tomography





How environmental changes governed the predation scenario in Indian turrnelline-dominated assemblages through time?

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Turrnelline gastropods (Family Turrnellidae) are usually found in huge abundance in the modern oceans as well as in fossil records as densely populated concentrations, because of their high fecundity rate, since the Late Jurassic and are described as turrnelline-dominated or rich assemblage (TDA/TRA). The constituent turrnellines of TDAs show prey–predator interaction with naticid gastropods (Family Naticidae) throughout its evolutionary history. Herein, we studied the environmental constraints on prey–predation interactions between turrnelline prey and naticid predators from three different time segments ranging from the Late Jurassic to the Miocene in the Indian subcontinent. TDAs in the Indian subcontinent are mainly reported from four geographic localities, i.e., Jurassic (Oxfordian) of Kutch, western India (out of total molluscan fauna ~89% are turrnellids), Cretaceous (Maastrichtian) of Rajahmundry, southern India (~86.71% turrnellids of all molluscs), Miocene (Aquitainian and Burdigalian) of Kutch (~85.71% turrnellids of all molluscs) and Dwarka, western India (~96% turrnellids of all molluscs). Drilling Intensity (DI), an indication of predation, is measured as the ratio between the shells of complete drill holes and the total number of shells. Overall DI data for the TDAs reveals relatively low DI in both Jurassic (9.49%) and Miocene (5.77%) with a high value during the Cretaceous (26%). Prey effectiveness (PE) is the ratio between the number of incompletely drilled specimens and the number of completely drilled specimens. PE and multiple drilling intensity (MULT, is the ratio between the number of drill holes in multiply drilled specimens and the total number of drill holes) are very low (3-5%). But stereotypy of predation, indicated by the concentration of drill holes in a particular site or area on a prey shell, show strong positive correlation in all the four TDAs. During the Oxfordian, low DI and low PE clearly indicates low abundance of naticid gastropods. However, well-developed behavioral stereotypy since the Oxfordian along with high drilling intensity during the Cretaceous suggest that naticid predators already became specialized in hunting their turrnelline prey. From the Cenozoic onwards, both naticid and turrnelline gastropods maintained morphological stasis and so far, it is observed that turrnellids have not developed any anti-predatory adaptation against their predators. Many turrnellines show two distinct life modes in their ontogeny, i.e., juveniles being infaunal whereas adults live epifaunally. Thus, the adults are more vulnerable to drilling gastropods as they can be easily subjugated by the naticid predators. Still, it is observed that there is a considerable decline in DI within the Miocene TDAs which is supposedly due to paleobiogeographic constraints due to development of Gomphotherium land bridge which caused the closure of the sea way between Tethys and the Indo-Western Pacific Ocean, resulting in low abundance of the escalated predators. Moreover, during the Cenozoic, turrnelline gastropods started shifting their habitat from shallow marine environment (during the Jurassic and Cretaceous) to relatively deeper and cooler waters where they are mainly provided with high nutrients by the ocean upwelling events. On the other hand, naticids preferred living in shallow marine subtidal environment. Thus, overlap of ecological niche of both the prey and predators considerably got reduced which apparently resulted in lowering the DI in TDAs during the Miocene.

Keywords: Changing environment, naticid predation, through time, Indian scenario



Session 6 - ORAL

Palaeoenvironments in Palaeontology: methods, tools and limits. A review to go further

Element mapping by μ XRF in several morphotype of Lower Cretaceous coprolites from the French locality of Angeac

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Hundreds of coprolites were found in the Lower Cretaceous locality of Angeac-Charente in the Southwest of France, along with abundant vertebrate remains (teeth/bones) from dozens of species, encompassing dinosaurs, crocodylomorphs, turtles and actinopterygians (Rozada et al., 2021). Previous studies evidenced the potential of coprolites to preserve biological inclusions in much greater detail than adjacent sediments like for instance complete insects (Qvarnström et al., 2021), implying the existence of chemical microenvironments highly specific to fossilized faeces. The present research offers to characterize, for a first time to the microscopic scale, the chemical composition of an assemblage of coprolites, using that of Angeac-Charente, to (1) assess the original vs diagenetic contributions of the elemental composition, as well as to (2) determine the existence of some chemical variability among defined coprolite morphotypes. Using elemental μ XRF maps, we observe a global preservation of these objects dominated by Ca and P, followed by Fe and S as for major elements. For minor elements, Ce, Y and Sr are the most abundant elements. Spatially now, these minor elements turn out to be more relatively concentrated within the outer margin of the coprolites. When likewise mapped within their surrounding sediments, coprolites show higher concentration in Ca, P, Ce, Y and Sr elements, while Fe and S remain concentrated in pyrite crystals. All these observations strongly suggest a origin from the producer diet for Ca and P, but a diagenetic origin for the minor elements by precipitation from fluids inside the coprolites.

A complementary work will analyse the phosphate oxygen isotopic composition of those coprolites, to assess if the $\delta^{18}O_p$ signal they contain could be used for palaeoenvironment and paleoclimate reconstructions. Such a new proxy would be highly valuable in palaeontology, using coprolites to inform on conserved isotopic ratios, instead of teeth/bones sometimes too precious for destruction.

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Keywords: Coprolites; Lower Cretaceous; elemental mapping; μ XRF; stable isotopes



A Callovian Oceanic Anoxic Event recorded in the SW Tethys Margin

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The Jurassic and Cretaceous are characterized by intensive plate tectonic activities, high atmospheric CO₂, and high temperature. Consequently, sea level rise and increasing continental weathering and nutrient flux resulted in high marine organic productivity, organic matter burial, and low dissolved oxygen in oceanic and shelf basins, leading to the onset of numerous oceanic anoxic events (OAE). This study has integrated multiple (C, O, Sr) isotopes with sedimentological data collected in the Callovian carbonate rocks from the Tethyan shelf margin, including the Arabian intrashelf basin and its adjacent shallow marine epeiric platforms, where widespread organic rich sediments were deposited. A striking positive excursion of C-isotopes in early Callovian carbonate rocks is correlated with an outstanding negative excursion of O-isotopes plus elevated Sr-isotopes. These isotope trends turned around toward the end of Callovian, as a positive O-isotope excursion goes along with a negative C-isotope excursion plus decreasing Sr-isotopes. The negative and positive O-isotope excursions from the early to late Callovian form a complete warming-cooling climate cycle. The positive C-isotope excursion in carbonates is the result of a massive accumulation of ¹²C-enriched organic matter. The positive and negative C-isotope excursions form an isotope stratigraphy sequence (the 3rd order transgressive-regressive sequence). The elevated Sr-isotopes along with high terrigenous content suggest sea-level rising in the early Callovian, whereas the decreasing Sr-isotopes along with the cooling climate indicate a falling sea level. Moreover, the OAE-associated carbonate rocks contain black mudstone beds, gamma ray spikes, fossil species in anoxic environments, and elevated content of redox sensitive trace elements (e.g., Ni, Cr, and Co). These geochemical features and patterns, similar to the typical isotope shifts and geochemical features associated with the other Jurassic-Cretaceous oceanic anoxic events including T-OAE, OAE1a, OAE1b, and OAE2 (e.g., Jones & Jenkyns, 2001; Lu et al., 2017; Beil et al., 2020) suggest an OAE occurred during the deposition of these carbonate rocks. The interpretation is also consistent with the paleoclimate model and the Callovian OAE reported from Europe, Africa and North America (e.g., Soua, 2014). It is noteworthy that the Callovian OAE-associated isotope signals are present in the late Jurassic Oxfordian and Kimmeridgian carbonates, but much less widespread and smaller in scale, suggesting a paleoenvironmental change to restricted conditions.

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Key words: Tethys Margin, Arabian Plate, Callovian, Oceanic anoxic event, isotope excursion



Session 6 - POSTER

Palaeoenvironments in Palaeontology: methods, tools and limits. A review to go further

Reconstructing Dinosaur Ecology and Niche Utilization in the Jurassic Using C, O, and Ca Stable Isotopes in Teeth

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Stable isotopes of carbon, oxygen, and calcium can preserve information about diet and ecosystem structure in the fossil record that might not be discernable from body fossils alone. Studying these isotopes has allowed for a greater understanding of many ecosystems, and here we apply it to a Late Jurassic North American ecosystem. Sauropod dinosaurs are the largest known terrestrial herbivores, and here we studied isotopes from the teeth of two sauropods, *Camarasaurus lentus* and *Diplodocus longus*, and one theropod, *Allosaurus fragilis*, to determine niche partitioning between herbivores and if these herbivores were being eaten by this significantly smaller carnivore. The Morrison Formation preserves abundant large-bodied herbivores, including multiple types of sauropods. The large size of these animals suggests that food would be scarce in an environment with this many herbivores, and niche partitioning would be necessary to have so many large species in a single locality. Their large size also suggests that predators would not actively hunt large prey, but would preferentially seek out young, old, or injured individuals. We hypothesize that *C. lentus* and *D. longus* occupied different niches and will preserve isotope ratios indicative of feeding on upper and lower canopy, respectively. We also hypothesize that *A. fragilis* will preserve Calcium isotope ratios consistent with modern predator-prey isotope fractionation. Here we examine $\delta^{18}\text{O}$, $\delta^{13}\text{C}$, and $\delta^{44}\text{Ca}$ of carbonate preserved in the enamel of *C. lentus*, *D. longus*, and *A. fragilis*. Higher C and Ca isotope ratios indicate higher browsing in the canopy, and modern predators preserve lower $\delta^{44}\text{Ca}$ values than their prey. Using this information, we will hypothesize the diet of these Late Jurassic dinosaurs. First, the level of diagenesis of the specimens must be determined, so we will examine the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of the fossils to see if homogenization has occurred indicating diagenesis. If not, we will continue to analyze isotope values in each of our specimens, potentially targeting annual variation.

Keywords: Jurassic, Dinosaur, Morrison, Paleoecology, Isotope, Geochemistry, Sauropod, Theropod, enamel

Session 6 - POSTER

Palaeoenvironments in Palaeontology: methods, tools and limits. A review to go further

Evidence for metabolic diversity in Meso-Neoproterozoic stromatolites (Vazante Group, Brazil)

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Deciphering the evolution of ecological interactions among the metabolic types during the early diversification of life on Earth is crucial for our understanding of the ancient biosphere. The stromatolites from the genus *Conophyton cylindricus* (Meso to Neoproterozoic) have typical conical shapes, that have been considered a result of a competition between microorganisms for space, light and nutrients. Well-preserved records of this genus from the “Paleontological Site of Cabeludo”, Vazante Group (Southern Brazil) present *in situ* fossilized biofilms, containing preserved carbonaceous matter. Petrographic and geochemical analyses revealed an alternation between mineral laminae (light grey laminae) and fossilized biofilms (dark grey laminae). The dark grey laminae comprise three different biofilms recording a stratified microstructure of microbial communities. These three biofilms composing the dark grey laminae tend to be organized in a specific pattern that repeats through the stromatolite vertical section. Iron and manganese are distributed differently along the dark and light grey laminae; X-ray absorption and luminescence data showed possible different areas with authigenic iron and iron provided from diagenetic infiltration. Cryptocrystalline apatite in the lowermost biofilms in each dark grey laminae may suggest past metabolic activity of sulfide-oxidizing bacteria. These findings suggest that the microorganisms reached a complex metabolic diversification in order to maintain an equilibrium situation between the three different biofilms along the vertical section of the structures, thus benefiting the whole microbial community. This means that the stromatolites from the *Conophyton* genus may have formed as a result of a greater complexity of interactions between microorganisms, and not only from competition between photosynthesizers.

Keywords: Proterozoic, *Conophyton*, microbial metabolism, sulfide-oxidizing bacteria, biomineral, biofilm



Session 7 – KEYNOTE

Palaeontological heritage, geoparks and geotourism

From Palaeontology research, Geological heritage sites, and Geoparks to Thailand sustainable development

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Thailand has a long history of fossil discovery and palaeontology research since more than a hundred years ago. Moreover, the palaeontology research has been continuously published as the international articles until the present such as trilobite in Satun, dinosaur in Khorat, and conodonts in Phatthalung, etc.. However, applying this important academic knowledge to benefit the general public still has been a major problem in the past. In that time the palaeontology research was no directly related to people or their life or economy. Recently, the designation of the UNESCO Global Geopark required a geological heritage of international value based on the international peer-reviewed published research conducted on the geological sites within the area.

Satun UNESCO Global Geopark is the first UNESCO Global Geopark in Thailand, having been accepted and announced in April 2018. It was accepted for its international geological significance regarding abundant and highly diverse early Paleozoic fossils in Southeast Asia, along with the interbedded, datable volcanic ashes that can provide absolute age estimates. The Satun UNESCO Global Geopark is important for paleontology research among geologists for more than a half-century ago. In 1957 Teiichi Kobayashi reported the evidence of Cambrian trilobites as the oldest fossil in Thailand from the Ao Mo Lae geological heritage site at Tarutao Island. Many international researchers have visited and studied the Cambrian and Ordovician fossils and sediment successions at Tarutao Island. The UNESCO IGCP 668 is one of the geological research projects that was research on trilobite evidence and the age dating in the area. This evidence is one reason for international geological significance that led UNESCO to accept the Satun Geopark as Satun UNESCO Global Geopark. Improved geological knowledge at Satun Global Geopark is important not only for researchers but for the people, economy, and sustainable development of Satun Global Geopark. It means that the palaeontological research can support the story and history of geological heritage sites then to set up in the geopark in the area. It is not only the increasing of the people income but it is also for getting better life and society. According to their home economy is getting better, so their young family members were come from working in the big city back to their hometown instead. This situation supports the sustainable economy and development. Especially Royal Thai Government realized about this success of the geopark policy and included the geopark promotion plan in its 20 years Thailand strategy in order to sustainable development of the country.

The result of the successful development in Satun UNESCO Global Geoparks such as the increasing the number of tourists and also communities' income in the area leads many geological heritage sites in another areas in Thailand try to promote their areas to be the geoparks. Recently, Thailand has 10 geoparks in three levels; one global geopark, four National geoparks, five local geoparks. Khorat National Geopark is under UNESCO consideration as a global geopark of Thailand. It international geological significant sites exist with evidence on the Jurassic-Cretaceous stratigraphical sequence as well as on fossil fauna and flora and thus with a remarkable quality of conservation. Paleontology is an undisputable highlight of the Khorat Plateau, namely the Cenozoic mammals and Cretaceous reptiles. Recently, palaeontology research can be related to people and their life by geotourism of geoheritage sites and geoparks. It seems fossil can be eaten that means it can support the sustainable development in some areas of Thailand as their geological heritage sites and geoparks.

Keywords: Palaeontology research, Geopark, Geological Heritage site, IGCP668, Satun



Session 7 – ORAL

Palaeontological heritage, geoparks and geotourism

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Keywords: Community museums, Scientific divulgation, Museum exhibition, Paleontological tourism.



Session 7 – ORAL

Palaeontological heritage, geoparks and geotourism

Bringing fossil sites to public: the Virtual Reality PROTOtype of Pedra-que-pica fossiliferous outcrop (Santa Maria Island, Azores)

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Fossiliferous outcrops provide remarkable information that allows for a better understanding of past events and what the future outcomes might be. However, fossil sites are often inaccessible to the public due to their remote location. In addition, they are often at risk of being destroyed by erosion or human activity. This is the case of the Pedra-que-pica outcrop on Santa Maria Island (Azores). This exceptional coquina from the Pliocene epoch provides unique insights into what marine life was like in the Central North Atlantic 5 Ma ago. To overcome safety and preservation issues, a virtual reality prototype of Pedra-que-pica was developed, built through a 360° experience, in which users start by watching a 2-minute 360° video explaining why, when, and how the outcrop has formed. In the end, they can virtually explore the site freely. This is the first virtual reality prototype of this kind of a fossil outcrop, and we hope that others will begin to develop a similar approach to other key locations.

Keywords: Fossils; Virtual Reality; Pliocene; Oceanic Volcanic Island; NE Atlantic



Session 7 – ORAL

Palaeontological heritage, geoparks and geotourism

Paleontological sites in the French national inventory of geoheritage, a first review

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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". With this law, geology or the "geological sciences" are for the first time included in the Environmental Code. Based on this statement, the national inventory of geological heritage was officially launched in 2007.

Today, more than 3500 sites have been inventoried throughout France (metropolitan and overseas) and more or less 1500 additional sites are expected by the end of 2023.

With several large sedimentary basins, old or still active mountain ranges, France has a great geodiversity. As so, the country has an important geological heritage and sites of paleontological interest account for about 30% of the inventoried sites.

We will present here a preliminary analysis of these sites that gives an overview of the palaeontological wealth of France. We will discuss the usefulness of such an inventory in helping to inform local authorities of the presence of palaeontological sites so that they can take them into account more effectively in their local planning policies. Finally, we will consider the way in which such work can lead to the protection or enhancement of the most remarkable of them.

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Keywords: inventory, paleontological sites, analyse, geodiversity, France



Session 7 – ORAL

Palaeontological heritage, geoparks and geotourism

Cambrian Chengjiang Fossil Site: a unique window of Cambrian Explosion

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The Chengjiang Fossil Site (Maotianshan Hill) was the first discovery site of the Chengjiang fauna, it was first recognized for its exquisite states of preservation with the discovery of the naraoiid *Misszhouia* in 1984. Since then, more than thirty years of intensive study have made this fossil fauna one of the best known in the geological column. The site has been well protected. It became a national Geopark in 2001 and a World Natural Heritage site in 2012. It represents an unparalleled record of the fundamentally important rapid diversification of metazoan life in the early Cambrian (Cambrian explosion) and the primary establishment of the modern complex marine ecosystem.

The fossils and rocks of the Chengjiang Lagerstätte provide direct evidence for the roots of animal biodiversity, over 300 species representing more than 20 phyla have been reported from the Lagerstätte, and the great diversity of metazoan body plans, many comparable with those of living groups. These fossils bear upon the fundamental questions regarding the design of animal body plans and the genetic generation of evolutionary novelties. The diverse vertebrates, representing the “missing” history between an amphioxus-like ancestor and craniate vertebrates, provide an important understanding of the early evolution of the vertebrates (Chen et al., 1995, 1999; Shu et al., 1999; Tian et al., 2022). The Chengjiang fauna is one of the earliest records of a complex marine ecosystem, with food webs capped by sophisticated predators (Chen et al., 1994; Zhao et al., 2010). The exceptional fossils display the anatomy of hard and soft tissues of a great variety of organisms in exquisite detail, for example, appendages, eyes, and nervous system (Hou et al., 2017). The mode of preservation imparts an extraordinary and rare beauty to the fossils, extending their value from the scientific to the aesthetic. The Chengjiang Fossil Site is attracting huge attention from scientists and the public and becomes a very important area for education on the evolution of life in China.

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Keywords: Cambrian explosion, soft-bodied preservation, Yunnan, Burgess shale-type, Konservat-Lagerstätten



Session 7 – ORAL

Palaeontological heritage, geoparks and geotourism

The Contribution of Paleontology in the Development of Geotourism in Northwestern Madagascar: a Preliminary Assessment

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The contribution of paleontology in relation to the creation of a Geopark is emphasized by fossils and related geology at Anjohibe and Berivotra in northwestern Madagascar. This research note presents preliminary findings while employing a simple rating system to assess two fossil-rich areas of Madagascar and their potential geotouristic values that would be essential for the development of a Geopark. The point is made that working towards Geopark status is likely to place an increased touristic and economic value, and appreciation of the geology. Essential criteria for the development of a Geopark include the presence of important geoheritage and geosite protection specified according to a management plan. Local community benefits can be derived through the promotion of natural landscape qualities and tourism-related services. This preliminary research project is a starting point in recognizing what needs to be done to value and garner the support of local people in conserving the geoheritage of northwestern Madagascar.

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Keywords: Madagascar, paleontology, fossils, geotourism, geopark.



Myanmar's Mount Popa: geoheritage and its progress towards geopark

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Mount Popa, a conspicuous landmark in the heart of the dry belt of central Burma, forms the largest and southernmost of the group of Lower Chindwin volcanoes. Mount Popa area has a remarkably rich geodiversity that includes diversified geology, landforms, flora, and fauna from past to present, as well as cultural heritage and religions that significantly affect tourism and economic growth. Two major sedimentary units that occur in a conformable sequence of the proposed geopark are the Peguan Group (Miocene) and the Irrawaddy Formation (Pliocene to Lower Pleistocene). The former name of the Irrawaddy Formation was "Fossil Wood Group" because of the abundance of petrified trunks in that area. Due to numerous fossil trunks were sold abroad, the Mount Popa Geopark Development committee was established in December 2016 to protect the geoheritage, including the petrified forests in the sandstone of the Irrawaddy Formation. The proposed geopark covers about 1,295 square km mainly west and southwest of Mount Popa around Thanbo villages. The area includes Popa Mountain Park, important habitats for wildlife and plants, where globally threatened species of mammals (e.g., Eld's deer, primates) and trees (Indaing) are found (NWCD & BANCA, 2017). The Popa Mountain Park comprises six forest types: upper mixed deciduous, lower mixed deciduous forest, Indaing forest, dry forest, pine forest, and grassland (NWCD & BANCA, 2017). In 2007, the Forest Department formed the National Institute of Biological Resources and the International Cooperation Unit on Biodiversity and Environmental Conservation to conduct research. Despite the works on modern flora and fauna, research on past diversity in the Mount Popa area is scarce. Humans have inhabited the Popa region since 10,000 years ago, as evidenced by stone tools made of petrified wood that was recognized as the Anyathian culture (Aung-Thwin, 2002). Additionally, mammal fossils (e.g., jaws, teeth, and bones of extinct elephant relatives) and other archaeological objects (e.g., some of the old iron smelters from the Bagan Dynasty) are discovered in the proposed geopark. Currently, the region's estimated population is about 40,000, of which at least 40 villages consist of more than 10,000 households scattered around the park (Zin, et al. 2019). The cultural and religious heritage of Mount Popa Geopark includes astrology, alchemy, and the worship of Nats. To the Burmese, Astrology is not only a method of tracing the courses of the planets and their influence on mortals; it is also the ritual by which the planets were appeased and made to withdraw their baneful influence. Despite facing pandemic and political challenges, Myanmar scientists, stakeholders, and local communities have been working together toward geopark establishment for sustainable development goals. In 2019, the national geopark committee successfully formed. We have also established an international collaboration project for research, educational outreach, and conservation programs to investigate fossil flora and fauna in Mount Popa Geopark and strengthen the relationship between local people and Mount Popa's natural resources.

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Keywords: Geoconservation, geodiversity, petrified forest, Irrawaddy Formation



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Palaeontological significances of Khon Kaen Geopark: Hometown of the dinosaurs

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Phu Wiang valley is located 70 km northwest of Khon Kaen province. It has an identical chicken-like mountain from the top view. A syncline Phu Wiang mountain is a member of the Khorat Group. It is composed of the Late Triassic Nam Phong Formation, the Late Jurassic Phu Kradung Formation, and the Early Cretaceous deposits, including the Phra Wihan, Sao Khua, Phu Phan, Khok Kruat and probably Maha Sarakham Formations. Phu Wiang dinosaur valley played an important role in the dinosaur evolution of Asia during the Early Cretaceous period. It yielded abundant extraordinary dinosaurs resulting from the Thai – French dinosaur expedition team from the 1980s to 1990s. There are five new dinosaur taxa and at least four dinosaur indetermines. Interestingly the numbers of carnivorous dinosaurs are incredibly high compared to those of herbivorous dinosaurs, seven to two. This ratio suggested a high food web level during the Early Cretaceous in this habitat. Furthermore, there are several baby dinosaurs from several localities in Phu Wiang valley. This evidence represent Phu Wiang valley as the hometown of the dinosaurs, the only one in Southeast Asia

Keywords: Early Cretaceous, dinosaur valley, carnivorous dinosaur, herbivorous dinosaur, Geopark



Paleontological collections as valuable part of natural history heritage

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Paleontological collections are essential in documentation of the Earth's history, evidence of the biosphere's formation and evolution. Considering the incomplete preservation of fossil remains and their rarity in some types of rocks all paleontological collections are of considerable scientific value. Their preservation and documentation are a significant task not only for museums but also for research institutions, which study fossil record from both biological and geological perspectives. It becomes also increasingly important to make the collections accessible online what expands opportunities for researchers to study morphological changes and distribution of different taxa and exploring more precisely the evolution of life on Earth. One of the possible forms of data distribution is digitization of collections through the creation of databases and photo and 3-d documentation of specimens. Databases are necessary for management of collections, while image documentation is important for specimen appearance and preservation. It is especially important for the collections, which are located in natural hazard zones (e.g. earthquakes, tsunamis), areas endangered by military conflicts and also other possible calamities (e.g. as the fire in the National Museum of Brazil in Rio de Janeiro in 2018 when almost entire collection have been lost). There are slightly different approaches to the collection management in museums and research institutions, which depends on their scope of main activities. One may generalize that the museums aim to collect, preserve and promote science through the exhibition of attractive specimens, while the research institutes are focused on the documentation and description of the type and other scientifically important material.

Preservation of existing paleontological heritage as a part of the entire museum collection is one of the main tasks of the State Museum of Natural History of NASU in Lviv and some efforts of its digitization were already carried out. Currently a database of the entire paleontological collection has been created and photo documentation of some specimens from different collections had been done. This work is not systematic and is mainly related to the research interests of museum staff. So far, totally digitized were small collections of amber with insect inclusions and stone tools, and partially fossil flora mainly from the Neogene, Devonian fishes and Cretaceous molluscs. Images of some of these specimens are available on the museum's website, whereas database is not in the open access. Paleontological collection of the Museum is divided in chronological order. Only a small number of specimens were described and they have a special status and are stored separately. For collection identification and description it is necessary to involve external specialists.

The core of the Institute of Paleobiology PAS collections were published in scientific publications with descriptions, images and other information. The online database of the entire collection has been launched recently. Data on published specimens, including images of the most representative specimens is available to the public with links to the respective publications, while non published collections are available to the research staff only. The ongoing project carried out by the collections staff is to fully digitize the most important specimens, like holotypes. There are created both photographic, photogrammetric images and tomography scans of the most fragile specimens. Low resolution images can be browsed through the database and detailed data are available upon request. Also printing of 3-d models is possible for both scientific and educational purposes. The next phase will be combining in one database the images obtained by researchers during study and preparation for



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publication. In addition some most attractive to the public specimens are exhibited in the Museum of Evolution, which is operated by the Institute of Paleobiology PAS.

Understanding the fossil record as a foundation of knowledge about the history and evolution of the living world and as a source of intellectual inspiration is the main task of both the Institute and Museum, and it cannot be obtained without preservation of collections, spreading the knowledge and sharing resources with both scientific community and general public.

Keywords: Museum, Institute, paleontological collection, digitalization, database, specimens, 3-d images



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Geoconservation and Geoheritage of the Madygen Lagerstätte (Middle-Late Triassic) of Southwestern Kyrgyzstan

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The Madygen region of southwestern Kyrgyzstan bears an exceptional geological heritage spanning the Phanerozoic, most notably the Madygen lagerstätte. This Ladinian-Carnian aged lacustrine ecosystem provides a unique window into the Triassic origin of modern terrestrial ecosystems that is unparalleled within Asia. A reconnaissance field trip in September-October 2021 generated strong international research interest in the region, precipitating further fieldwork in August-September 2022. The chief aims of the latter expedition were to better constrain the stratigraphy of the Madygen region, identify sites of geological interest, sample the lagerstätte within a systematic research framework, and prospect for fossils above and below the lacustrine unit given their relevance to the broader stratigraphic context of the Madygen ecosystem but limited prior exploration. Preliminary works have shown a huge potential of the Late Triassic and Jurassic strata overlying the Madygen Formation for preservation of floral and faunal remains in fine-grained lacustrine and alluvial deposits. Their systematic collecting and study, along with sedimentological sampling, sheds light on the Mesozoic evolution of the biota and environment in Central Asia. These objectives are central to the longer-term goal of establishing a UNESCO Geopark within the Madygen region, preserving geological heritage of Kyrgyzstan *in situ* and through the establishment of the first research collection from the locality that will permanently reside within national borders. Here we present the preliminary findings of the 2022 expedition, and their contribution to the long-term goals of continued research into an exceptional terrestrial lagerstätte.

Keywords: Triassic, lacustrine, lagerstätte, UNESCO, Kyrgyzstan, conservation



UNESCO Geoparks in the Southern Urals (Russia)

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UNESCO Geoparks are actively developing in the Russian Federation. First of all, this process is intensively going on in the Southern Urals (Republic of Bashkortostan), where geological sites of international importance are located. Some of them have the status of tiers of the GSSP of the Permian system, while others are still in the rank of candidates. The base- Sakmarian GSSP is located on the Usolka section (the year of award is 2019), and in 2022 the Dalniy Tyulkas section became the Artinskian GSSP. Both sections were included in the Toratau Geopark (aspiring UNESCO Global Geopark) as the main sites of international importance. The rocks of these sections contain a rich complex of macro- and microfossils. The most important are the conodonts, which are biomarkers of the boundaries of the Carboniferous and Permian Systems. The base of the Sakmarian Stage is marked by the appearance of the species *Mesogondolella monstra* Chernykh (Chernykh et al., 2020), the lower boundary of the Artinskian Stage is indicated by the FAD of the conodont *Sweetognathus asymmetricus* Sun et Lai. (Chernykh et al., 2022).

Among the candidate GSSP sections, the most interesting and studied in detail is the Mechetlino section, which claims to be the base-Kungurian GSSP. It is part of the UNESCO Yangan-Tau Geopark, also located in the Southern Urals. The Upper Artinskian and Lower Kungurian deposits are rich in fossil conodonts, foraminifers, ammonoids, ostracods, brachiopods, fishes, crinoids, trilobites, calamites, and calcareous algae. The Artinskian/Kungurian boundary is determined by the appearance of the conodonts *Neostreptognathodus pnevi* Kozur et Movshovitsch. In the Mechetlino section, we see a successive change in sedimentation conditions in the Early Permian. In the Artinskian, sediments accumulated in a deep sea basin of normal salinity in an arid climate. And the Kungurian deposits were formed at the last stages of the development of the Cisuralian trough, when the shallowing of the sea basin began.

As a result of the creation of the Yagan-Tau and Toratau geoparks in the South Urals, the regions of the Republic of Bashkortstan received a new impetus for their development with the emergence of new jobs for the population. This contributed to the revival of folk crafts, crafts, customs, as well as a significant interest in the geological history of the Earth. Currently, it is planned to create a geological museum complex at the Mechetlino section, which should become a major center for geotourism.

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Keywords: Russia, Republic of Bashkortostan, UNESCO Geopark, Yangan-Tau, Toratau, Kungurian, Sakmarian, Artinskian, GSSP, conodonts



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“Thinking outside the box” - a novel solution to site access: a unique collaboration provides new educational, research and publication opportunities

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Who we are: The Lauer Foundation for Paleontology, Science and Education acquires, curates, and provides access to a collection of scientifically important paleontological specimens. The collection is available to the scientific community for research, publication, exhibition, educational outreach, and is committed to providing scientific research opportunities. (<https://www.lauerfoundationpse.org/>)

The problem: In recent years paleontologists have faced increasing legal, financial, and bureaucratic barriers to gain access to fieldwork localities for student teaching, collection of specimens, and the ability to utilize these materials for research and publication. Many deposits are located on private and public lands which are largely inaccessible.

The opportunity: Bruce and René Lauer, Directors of the Lauer Foundation, were contacted by a commercial fossil dealer with an offer to sell what he believed to be a scientifically important collection of late Triassic microvertebrate fossils. These were from his New Mexico property a small (2 hectares/5 acres) patch of semi-desert badlands. The immediate response was “No” because this was not the focus of the Foundation. Instead, we proposed an alternative option; to purchase the microfossil site and the existing collection which would solve provenance issues and could facilitate both education and research opportunities.

The solution: We undertook a feasibility and risk/benefit analysis, which involved a site evaluation visit, a legal property search and a physical examination of the collection. We concluded that, with the right academic backing, the site and the collection could be a valuable resource for teaching and research. A purchase contract was drafted, signed by the dealer and the Foundation, and the transfer legally recorded.

The international team: We contacted leading paleontologists with research interests in Triassic vertebrate fossils and assembled a team of specialists to further evaluate the scientific potential of the purchase. The site and existing collection would provide opportunities for students to gain field experience and laboratory training. As a bonus the collection was deemed likely to yield new species and fill gaps in existing museum collections. A memorandum of understanding was drafted and signed by representatives of Appalachian State University, Virginia Tech University and the NHM UK. Each member of the team provides unique expertise, resulting in a multi-institution, multidisciplinary approach to study this rich microvertebrate fossil assemblage. Access to the material is coordinated within the group, which can be expanded to allow further collaboration as needed.

Progress: Legal agreements were completed in early 2020, just as COVID-19 began, so many institutions were forced to cancel in-person learning. However, our team distributed some of the

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Devonian palaeoenvironments and mass extinctions



The Bayankhoshuu Ruins section in the southern Gobi of Mongolia revisited: new sedimentological/facies data

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The Central Asian Orogenic Belt (CAOB) is the world's largest Paleozoic accretionary orogenic belt, which has evolved over 800 million years, from Neoproterozoic time until the Cenozoic. Mongolia lies in the center of the CAOB, which is composed of a large number of different terranes. Mongolia is divided into a northern and southern domain by a Main Mongolian Lineament. Mid Paleozoic deposits cover a huge area south of this lineament as it is less deformed in comparison to northern domain. Deposits of the Devonian/Carboniferous transition of the Bayankhoshuu Ruins section in the southern Mongolia likely occurred on either the Mandalovoo-or Gurvansayhan Terrane. The section exposes mainly deep-water (hemipelagic and pelagic) deposits composed of limestones, siltstones and chert. The marine sedimentary succession is interjected by volcanic rocks, basaltic lava and volcanoclastic bentonite and tuff of remarkable thickness. Shallow-water sediments are less frequent. The overall facies suggest an island arc setting with intensive volcanic activity during Middle-Late Devonian. The talk aims to contribute to a better understanding of Paleozoic rocks within the critical period of Earth's History around the D/C boundary in deeper water facies settings. Furthermore, we present new sedimentological and biostratigraphical data within the Paleozoic Terrane scheme for Mongolia, an area little facies details are known so far.





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Devonian palaeoenvironments and mass extinctions

Lower-middle Lochkovian (Lower Devonian) conodont boundary in the Spanish Pyrenees

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Valenzuela-Ríos & Murphy (1997) proposed an informal subdivision of the Lochkovian stage into three parts (lower, middle and upper) and selected the first occurrence of *Ancyrodelloides omus* (Murphy & Matti, (= *Lanea omoalpha* of Murphy & Valenzuela-Ríos), as the reference datum for the base of the middle Lochkovian. Subsequent records of this taxon in lower strata in the Prague Synform and in the Carnic Alps suggested that the base of the middle Lochkovian has to be revised and accordingly, several potential indexes to redefine the base of the middle Lochkovian have been proposed: *A. carlsi* (Slavík, 2011; Corradini & Corrigan, 2012) and *A. transitans* (Murphy & Valenzuela-Ríos, 2017). We will analyse herein the historical conodont-based threefold subdivision of the Lochkovian Stage and discuss the Pyrenean data for the interval between the entries of *A. carlsi* and *A. transitans*. This subdivision was based on records from Nevadan and Pyrenean sections (Valenzuela-Ríos & Murphy, 1997). The Pyrenean record shows that *A. carlsi* enters below the first occurrence of *L. omoalpha* (Ge. 1.1 section) and continues upward to co-occur with *L. omoalpha* and *L. eoeleanorae* (sections Se 1, Se 5). In the investigated Pyrenean sections, *A. carlsi* enters together with *Icriodus bidentatus*, slightly above the entry of *I. transiens* and below the entry of *Lanea omoalpha*. This strata recording the entry of *A. carlsi* are considered as lower Lochkovian age. Records with simultaneous occurrences of *A. carlsi* and *L. omoalpha* correspond to strata within the range of *A. carlsi* and are dated as middle Lochkovian. Furthermore, the entry of *A. transitans* in the Pyrenees is always above the entry of *L. omoalpha*. Consequently, there the entry of *L. omoalpha* takes always place between the incomings of *A. carlsi* and *A. transitans*. This observation suggests that before making any decision regarding the base of the middle Lochkovian, a thorough taxonomic study of all occurrences of *L. omoalpha*, mainly in the key areas above mentioned, must be accomplished. Besides, and as this datum is well established in the Pyrenees a detail correlation of these strata with those of relevant sections in key areas, involving high-resolution biostratigraphy, has to be carried out.

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Keywords: lower-middle Lochkovian transition, Spanish Pyrenees, conodonts





Searching for a new basal Emsian GSSP in the Prague Synform – state of the art

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The basal Emsian GSSP was defined in the Zinzil'ban Gorge in the Kitab State Geological Reserve (South Tien-Shan, Uzbekistan) based on the FAD of the conodont species *Polygnathus kitabicus* Yolkin et al. Historically, P. Carls and J.I. Valenzuela-Ríos demonstrated (in materials submitted to the Subcommittee on Devonian Stratigraphy – SDS/ICS) that the present boundary GSSP is much older than the formerly used German Siegenian-Emsian boundary and, that it correlates with middle parts of the traditional Early Siegenian (= approximately lower part of the Praha Formation). Subsequent conodont studies and detailed correlations with Mauro-Ibero-Armorican, Rheno-Ardennan and Barrandian faunas confirmed the very low stratigraphic level of the current GSSP in the lower half of the Praha Formation (Slavík et al., 2007; Carls et al., 2008).

In 2019, the SDS decided to look for alternative section for the replacement of the basal Emsian GSSP. The most promising candidates are situated in the Spanish Central Pyrenees and in the Prague Synform. In past decades, the Lower Devonian successions in the Prague Synform were extensively studied for conodont biostratigraphy as well as palaeontological, sedimentological, geochemical and petrophysical records. Slavík & Hladil (2020) summarized the conodont data from the Lower Devonian of the Prague Synform and provided the most recent conodont zonation in this area. The team concentrated on Pragian-Emsian sections in the Prague Synform in order to obtain large biostratigraphical, geochemical and petrophysical datasets. The Bohemian Graptolite Event (BGE) is a representative correlation horizon in the upper parts of the Praha Formation with a great potential for future redefinition of the GSSP. The most promising sections in regard to presence of the BGE are Pod Barrandovem, Mramorka Quarry and Požár 3 Quarry. These sections were sampled for microfacies study and faunal content: conodont samples in dense intervals, sampling of available microfauna and macrofauna, samples for magnetic susceptibility logs, samples for isotopes $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, samples for INAA geochemical analyses and GRS measurements. Conodont material obtained enabled more precise recognition of the Pragian-Emsian conodont Zones. Bulk carbonate samples have $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in the range of -10,45 to -2,08‰ V-PDB and -1,43 to 2,43‰ V-PDB (n = 175), respectively. The $\delta^{13}\text{C}$ values show a marked increase within and/or close above the BGE interval. GRS measurements have been already evaluated and MS samples have been measured. The contents of radionuclides ^{40}K (expressed in %), ^{238}U , ^{232}Th (expressed in ppm) and total natural gamma-ray (tot eU expressed in ppm) were determined. The studied sections show similar GRS patterns around the BGE.

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Keywords: Lower Devonian, Basal Emsian GSSP, Prague Synform, biostratigraphy, correlation proxies





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High Latitude biocrises at the South Pole during the Early-Middle Devonian

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Present day, high latitude (60°-90°) regions are perhaps the most bioproduative regions on Earth acting as seasonal nutrient reservoirs for the world's oceans, forming the foundations for global trophic systems. These areas are however amongst the most environmentally sensitive areas on Earth and are responsive to changes in sea-level, temperature, and salinity that are delicately balanced by a combination of astronomic and global tectonic regimes as well as Earth's rotation, among others. Changes in any of these parameters will set up positive feedback loops the result of which may be catastrophic. Most of our current understanding of how these systems and environments operate is, however, from modern day icehouse analogues with few comparators known from past greenhouse settings as experienced during much of the Devonian. The rocks of the uppermost Table Mountain, Bokkeveld, and lower Witteberg groups provide among the best opportunities globally to understand long-term environmental change at high-latitudes given that it is both fossiliferous and relatively complete, estimated to span the Lochkovian-Famennian.

This research focuses on the Early-Middle Devonian record and explores the mutual relationships between sea-level and temperature that led to the rise and fall of the Malvinoxhosan (Malvinokaffric) biota, endemic to this region. In-depth biostratigraphic research on both macroinvertebrate and ichnological material from the succession, from literature as well as from collections housed at the Council for Geoscience and Iziko Museums suggest that this bioregion persisted as a cohesive unit during Rietvlei-Baviaanskloof to Waboomberg deposition (Pragian/Emsian-Eifelian) given that many representative taxa are found in these strata. A trend of decreasing diversity through time is observed during this interval with little origination of new taxa and is correlated with local 3rd order changes in sea-level. Above the Waboomberg Formation, few representative taxa are known to continue into the upper Bokkeveld and Witteberg groups, disappearing entirely by the deposition of the Blinkberg Formation. The few fossils that are known in these strata and those succeeding it (e.g. the Swartruggens Formation) are entirely of extra-Malvinoxhosan identity. The decline of the Malvinoxhosan biota shows that epifaunal and semi-infaunal taxa were disproportionately affected by changes in sea-level with respect to infaunal, deep infaunal and nektonic taxa. This is mirrored in ichnofossil assemblages that change from diverse to disparate in post-Waboomberg strata with few epifaunal suspension and detritus feeding strategies known. Similar observations are recorded from time equivalent strata in South America. Although a linkage between sea-level and the decline of the fauna is noted, there is no obvious change in environment. This suggests that the extinction mechanism is complex; possibly linked to that which influenced sea-level.

Keywords: South Africa, Devonian, extinction, Malvinoxhosan, palaeoenvironments





Advances in the Middle and Upper Devonian stratotype section at Col du Puech de la Suque (Montagne Noire, France)

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Since the definition of the GSSP stratotype for the base of the Frasnian at Col du Puech de la Suque E section (CPS-E) in the Montagne Noire in 1982, several researchers carried out geochemical, geophysical and sedimentological studies in this section around the Givetian/Frasnian boundary. Only biostratigraphers, mainly conodont specialists, were interested in studying in more detail the Givetian and the Lower Frasnian strata. After taking up Klapper & Feist works from the 1980's and revised conodonts from unpublished data (Rodríguez 2006), we decided to augment the biostratigraphy (mainly conodonts) and to extend down into the Givetian. Consequently, we re-opened and sampled the section, focussing on specific intervals, in several fieldwork campaigns (2015, 2018, 2021 and 2022); finally we compiled previous data and new results with the intention of revisiting this reference section. Our main results in the CPS-E section are: 1) Nine conodont zones spanning from the Middle Givetian through the lower Frasnian were identified: *rhenanus/varcus*, *ansatus*, *semialternans/latifossatus*, Lower *hermanni*, Upper *hermanni*, Lower *disparilis*, Upper *disparilis*, *norrisi* and FZ1 zones; 2) Middle Givetian beds of the CPS-E section were sampled along strike in two different positions of the same beds; consequently, conodont zones were more precisely identified; 3) the base of the Lower *hermanni* is extended downwards and is currently placed in bed 7.8; 4) the position of the bases of the *norrisi* and FZ1 zones were modified (Liao et al, 2019). Now, we can correlate results from CPS-E section with the upper part of the CPS-F section (Feist & Klapper 1985, and Klapper 1985). New information on the Middle and Upper Givetian intervals approximates the position of the Taghanic Event in the CPS-E section. Also, this newly compiled high-resolution biostratigraphical data will be useful for analysis of the Givetian Biodiversity patterns in the Montagne Noire and for comparison with the recently established biostratigraphy in the Central Pyrenees (Liao & Valenzuela-Ríos, 2022).

This work is a contribution to IGCP-652 and GIUV2017-395. MIU-Next Generation EU (ZA21-005) supports J-C Liao research.

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Keywords: Conodonts, Col du Puech de la Suque, Montagne Noire, Givetian, Frasnian, Middle-Upper Devonian





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The enigmatic end-Frasnian pelagic mass extinction (top Kellwasser Crisis) – new evidence for correlation with a peak of seismically induced sedimentary events

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In the search for palaeoceanographic explanations and models, it is often neglected that the global Kellwasser Crisis at the Frasnian-Famennian boundary consisted of a discrete set of individual events. The topmost Frasnian includes two distinctive main extinctions that happened within less than 100.000 years. The extinction of benthic fauna and of the few, last Frasnian metazoan reefs occurred during climatic overheating at the base of the hypoxic/anoxic Upper Kellwasser (UKW) level while pelagic fauna, such as ammonoids (especially *Gephuroceratids*), conodonts, homoctenids, entomozoid ostracods, placoderms, and specialized bivalves (e.g. *Buchiola*) flourished in eutrophic, organic-rich, and often very fossiliferous Kellwasser facies. Without any clear explanation, the pelagic fauna disappeared, often very suddenly, at the Upper Kellwasser top. This “end-Frasnian mass extinction” has to be explained separately from the “base UKW extinction”. Has there been a peak of euxinia or changes of the salinity gradient within the water column, while oxygen isotopes support a rapid cooling right at the F-F boundary? But this cooling was less intense than at the Lower Kellwasser level and black limestones and shales are absent from large regions (e.g. Australia).

New data from the Rhenish Massif (Germany) and Morocco, in concert with published data for the Canadian Rocky Mountains, Great Basin (USA), the Montagne Noire (southern France), Holy Cross Mountains (Poland), South China, and other regions, show a peak of seismically induced sedimentation right at the F-F boundary, which was often related to a sudden, major eustatic fall.

In the northwestern Rhenish Massif, the complete northern and eastern margin of the 10th of km scale Velbert Anticline was uplifted and tilted at the F-F boundary, resulting in angular unconformities (Hülsbeck motorway outcrop), long-term non-deposition and neptunian dyke opening right after the UKW limestone (Rohdenhaus Quarry), or in a crinoidal, large-scale rippled debris flow deposition covering a condensed UKW homoctenite (new Schlupkothien section). In the eastern Rhenish Massif, there is new evidence for reworking in the long-known basal Famennian nodular bed (e.g. at the Schmidt Quarry, Kellerwald) and even in the corresponding basinal shale facies at the Winsenberg (Adorf). New thin sections document a polyphase reworking and debris flow succession right at the top of the pelagic microbialite succession at Beringhauser Tunnel.

In the eastern Anti-Atlas, the continuous upper Frasnian black Kellwasser facies shows repeated synsedimentary seismic activity, but the peak is reached at the UKW top. At Jebel Ihrs (pelagic western Tafilalt Platform), extremely fossiliferous, semi-lithified UKW beds were reworked at the base of the Famennian, redeposited in large slump folds, and later truncated by lower (*minuta minuta* Zone), middle (*marginifera* Zone) or upper Famennian (*aculeatus aculeatus* Zone) strata. At Rich Bou Kourazia (southern Maïder), the basal Famennian consists, again, of large-scale rippled and laminated debris flow beds. At the southern Variscan Front (Tisdafine Basin) and in the Moroccan Meseta (Mrirt Nappe), the top UKW is characterized by a short unconformity, with the *subperlobata* Zone missing, indicating non-deposition due to episodically increased turbulence

It seems possible that the end-Frasnian pelagic mass extinction and globally widespread seismic events were causally linked. There is currently little knowledge of tectonic processes that can culminate coincidentally at the same on different continents and in separate oceanic systems. However,





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the Devonian was a very peculiar time concerning mantle convection resulting, for example, in an extremely weak global magnetic field.





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Revision of upper Frasnian Rhenohercynian manticoceratids (Gephuroceratidae, Ammonoidea)

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The Frasnian is globally characterized by the appearance, radiation, wide palaeogeographic distribution, and eventual sudden complete extinction of *Manticoceras* and related genera of the Gephuroceratidae (suborder Gephuroceratina). The family is crucial to understand Frasnian goniatite biostratigraphy and evolutionary patterns, especially the impact of global events, such as the end-Frasnian Kellwasser Crisis, on pelagic ecosystems and palaeobiodiversity. Although many species were described more than 100 years ago from the Rhenish Massif and Harz Mountains (Germany), there have been few attempts to revise their taxonomy based on type material. This is of special importance since German taxa were supposedly recognized on a global scale. Only modern studies of ontogenetic morphometry and species variability will enable the recognition of true distributions in time and space and of global and regional diversity trends.

It was possible to trace originals and topotypes for morphometric investigations in various museum collections, which are completed by new material collected over many years at type localities. These provide the base for preliminary results:

Gephyroceras is based on a North American species group around the type-species *G. rhynchostomum* and can be kept separate from *Manticoceras* by its peculiar juvenile shell flares that have been well-illustrated in classical (e.g. Miller 1938) and more recent studies (House & Kirchgasser 2008). It is not yet clear whether the genus occurs at all in Germany. Based on suture characteristics, *Manticoceras* can be subdivided into four subgenera. The lower Frasnian group around the medium-sized type-species, *M. simulator*, keeps a rounded L-lobe through ontogeny. Typical upper Frasnian species of the *M. cordatum* Group develop an angular L-lobe and asymmetric, very high flank saddle. It includes *M. buchii*, which type has been located at Lyon. The flank saddle is much wider than high and partly semicircular in the upper Frasnian *M. carinatum* Group. Only a few upper Frasnian species, members of the *M. drevermanni* Group, develop triangular and pointed flank saddles.

The ongoing revision will include German species of related genera, such as *Sphaeromanticoceras*, *Clauseniceras*, *Crickites*, *Delphiceras*, and *Serramanticoceras*. The type-specimens of the Wiesbaden collection are suitable to re-name the invalid *Goniatites intumescens* var. *acutus* Sandberger & Sandberger, a homonym of *Gon. acutus* Münster, as a species of *Carinoceras*. It has been widely overlooked that *Gon. lamed* var. *tripartitus* Sandberger & Sandberger is also a junior homonym, of *Gon. divisus* var. *tripartitus* Münster, a Famennian prionoceratid. Therefore, the type-species of *Playfordites* requires a new name, which is complicated by the poor knowledge of its small-sized, lost, single original that may have been a *Trimanticoceras*.

Only with the help of new cross-sections, it will be possible to clarify the question whether small-sized goethitic/limonitic goniatites, e.g. from the famous Budesheim fauna of the Eifel Mountains, are really conspecific with the larger types from cephalopod limestones, as assumed by Clausen (1969). We expect a higher Rhenohercynian biodiversity than known from the classical studies, which is complemented by some specimens that clearly represent previously unknown taxa. The revision of Rhenohercynian manticoceratids will be the starting point to revise the taxonomy, biodiversity, and palaeobiogeographic relationships of faunas from distant regions, such as Eastern North America, North Africa, South China, and Western Australia.





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The Frasnian ammonoid succession of Oued Mzerreb (Dra Valley, Morocco)

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The Frasnian (Upper Devonian) ammonoids of Morocco are generally poorly studied. Many faunas and time intervals are only known from faunal lists or have been completely overlooked in the past. From the Dra Valley area in particular, not a single Frasnian ammonoid has been pictured so far. Hence, their description is essential to close significant blind spots with respect to taxonomy, palaeodiversity, and palaeobiogeography. New forms can enhance our knowledge of the evolution of ammonoids, with a focus on the Tornoceratidae that have recently been studied in detail based on German (Söte et al. 2021; Söte & Becker in press) and Meseta (Söte & Becker 2021) collections. In this context, the middle and upper Frasnian tornoceratids of the Oued Mzerreb in the eastern Dra Valley (Tata region) are investigated in order to better understand the evolution and diversity of ammonoids before and during the global Kellwasser Crisis. The locality yielded 13 tornoceratid species, with three new genera, and five new species.

The first new genus (subfamily Tornoceratinae) resembles *Tornoceras*, but displays strong flank folds. The second new genus is defined by a smooth conch and evolute coiling, resembling Famennian protornoceratids. A third new genus (subfamily Aulatornoceratinae) contains *Aulatornoceras*-type forms, which suddenly open the umbilicus in late ontogeny, similar as in the older *Nebechoceras* (Tornoceratinae).

A similar biodiversity exists for the co-occurring Gephuroceratina. New and endemic gephuroceratoid species are pictured for the first time but are not treated systematically until the revision of German types has proceeded. The investigated Oued Mzerreb ammonoid faunas are unique in composition and composed of many endemic taxa as well as cosmopolitan ones. Locally, there is a strong assemblage differentiation between the middle and upper Frasnian despite an overall similar hypoxic shelf basin facies. While an early middle Frasnian *Naplesites* fauna is mainly composed of species of *Tornoceras* and *Lobotornoceras*, the upper Frasnian succession is notably different, with a high abundance of aulatornoceratids. The species richness of the middle Frasnian is rather low, while that of upper Frasnian strata is higher. However, the alpha diversity never reaches the level of time equivalent German localities, such as Büdesheim or Bergisch Gladbach-Sand.

Keywords: Devonian, Frasnian, Morocco, Dra Valley, Ammonoids, Tornoceratidae





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The Late Devonian Hangenberg Crisis – examples from shallow-water successions in Iran

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The Hangenberg Crisis near the Devonian–Carboniferous boundary (DCB, ~359 Ma) represents one of the largest mass extinctions in Earth's history and it is noteworthy that most DCB sections worldwide are described from hemipelagic and pelagic successions while neritic facies settings are underrepresented worldwide. As a step towards addressing this problem of paleogeographic sample bias, here we present sections of the Hangenberg Crisis in shallow-water sections. The DCB represents a time of marine trans-gression/regression cycles and widespread ocean anoxia, called the Hangenberg Crisis, marked by the deposition of transgressive organic-rich shale (the Hangenberg Black Shale Event) and then regressive sandstone and limestone around the world (Kaiser et al. 2016). To get a more comprehensive picture of one of the most interesting time slices in Earth's history it is necessary to study DCB sections in different depositional settings such as in shallow-water environments. Depending on facies setting, equivalents of the regressive Hangenberg Sandstone Event can also be recognized as an unconformity and/or reworked sediments as shown by Cole et al. (2015), Bábek et al. (2016) and Kaiser et al. (2016). This eustatic sea level fall (HSS Event) is obviously associated with a glaciation on Gondwana. Evidence for this hypothesis is based on sedimentological as well as palaeontological criteria, and data are published from South America, North Africa and the Appalachians (e.g. Streel et al. 2001; Isaacson et al. 2008; Lakin et al. 2016). A specific challenge studying neritic facies settings is a detailed biostratigraphic record. The disadvantage of conodont biostratigraphy in shallow-water sections around the DCB is often linked with the lack of significant conodonts such as *Protognathodus kockeli* and *Protognathodus kuehni*. The former one was used for the new conodont biozonation (Spalletta et al. 2017) as marker species, and *P. kuehni* can be considered as a reliable index fossil for the *sulcata* Zone (see Kaiser et al. 2019, cum lit.).

However, it is interesting to note that in some shallow-water sections in Iran *Siphonodella praesulcata* and *Siphonodella sulcata* have been found instead. In contrast to most DCB sections described from Iran (Königshof et al. 2021 cum lit.) one section exhibits a characteristic lithology around the DCB known from many other places around the world. The black shales and the superimposed thick-bedded quartzitic sandstones represent equivalents of the Hangenberg Black Shale (HBS) and the Hangenberg Sandstone (HSS), respectively. The presentation provides an overview on some restudied DCB sections from central Iran with a focus on conodont biostratigraphy and sedimentology/facies.

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Facies analysis from a Late Devonian island arc setting of the Barunhuurai Terrane, Mongolia

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The mid-Palaeozoic is known for a number of events, which have been preferably recorded in hemipelagic to pelagic setting, whereas in shallow-water realms the record is still underrepresented. In order to get a better understanding of those palaeoenvironmental settings of the Late Devonian, we studied a section from an isolated ecosystem in shallow-water/neritic facies. The Hushoot Shiveetiin Gol site is located in Barunhuurai Terrane of the Central Asian Orogenic Belt (CAOB), which ranges from the Famennian to the Lower Mississippian and is composed of primarily of siliciclastic rocks including thin layers of calcareous rocks and volcanoclastics. Limestones occur in a limited number of thin-bedded layers containing various fossils, such as corals, bryozoans, brachiopods, and conodonts. Conodont biostratigraphy of the section ranges from the *Palmatolepis minuta minuta* conodont Zone to at least the *Palmatolepis rugosa trachytera* Zone. Due to the facies setting, hiatuses of several conodont zones occur. Nevertheless, due to lithological comparisons with other sections in the vicinity it seems likely that thick sandstones in the uppermost part of the section represent the Lower Mississippian rocks. Eight facies types were recognized in the Hushoot Shiveetiin Gol site which ranges from shallow intertidal to open marine palaeoenvironment and confirmed by ostracod assemblage. The recorded ostracods are ecologically equivalent to the Eifelian Mega-Assemblage (I–III) which represents an overall nearshore palaeoenvironment. The facies setting was characterized by coeval subaerial volcanism resulting in numerous pyroclastic deposits. The depositional environments and intense volcanic activity at the section limited the stratigraphic distribution, abundance and diversity of many faunal elements, such as brachiopods and microvertebrates. The latter ones show low diversity, yet abundant in distinct layers of the section, whereas ostracods are very abundant and diverse through many parts of the section. The diverse ostracod assemblage of this section is remarkable. Furthermore, the crinoid fauna is the most diverse Palaeozoic fauna collected from Mongolia. Similarly, representatives of trilobites from Late Devonian deposits of western Mongolia contain endemic nature species as well as cosmopolitan species.

Keywords: Barunhuurai Terrane, CAOB, Late Devonian, facies, volcanism



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Morphological trends in *Polygnathus* conodonts in the early Carboniferous

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The Upper Devonian is characterized by a succession of environmental variations and ends with a major biotic crisis, the Hangenberg, at the Devonian/Carboniferous boundary (D/C). A previous work on conodonts of the genus *Polygnathus* during the Upper Devonian suggested a relationship between their morphological variation and bathymetric changes, estimated by a multivariate analysis of conodont biofacies. This proxy of bathymetry relies on the relative abundances of the conodont genera, each being characterized by different preferences in terms of water depth.

Here, the aim was to investigate if the relationship between the morphology of *Polygnathus* and bathymetry hold true for the response to the Hangenberg crisis, and the subsequent Carboniferous period. Several hundred specimens of *Polygnathus* platform elements were measured in twenty levels from the Puech de la Suque section (Montagne Noire, France), documenting a sequence of two million years starting just before the Hangenberg crisis. The shape of the elements was quantified using a geometric morphometry procedure based on 2D landmarks and semi-landmarks describing the platform of the element.

A morphological trend is observed over time, corresponding to a thinning of the platform. This trend seems to be correlated with biofacies variation, supporting the relationship between *Polygnathus* shape and bathymetry. Whereas during the Upper Devonian, a widening of *Polygnathus* platform was associated to a regressive trend, the thinning trend occurs in a transgressive context during the Carboniferous. This suggests that *Polygnathus* platform shape could track bathymetric changes in a consistent but reversible manner over more than six million years.

Keywords: Conodont, *Polygnathus*, Morphometry, Carboniferous, environment, crisis





Carbon and oxygen isotope fractionation in the Late Devonian heterocoral *Oligophylloides*: implications for the skeletogenesis and evolution of the Heterocorallia

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Stable carbon and oxygen isotope research on fossil low-Mg calcite skeletons of marine organisms is mostly focused on palaeoenvironmental and palaeoecological reconstructions. Here, we present results of microstructure and stable isotope studies on exceptionally well-preserved skeletons of two species of an extinct heterocoral, *Oligophylloides*. The order Heterocorallia is characterized by extremely thick corallum wall (heterotheca), built of low-Mg calcite. The studied specimens come from the Famennian (Upper Devonian) of the Anti-Atlas, Morocco and the Holy Cross Mountains, Poland. Rigorous preservation tests (transmitted-light, scanning-electron, fluorescence and cathodoluminescence microscopy, Raman spectroscopy and accessory trace element analyses) allowed for assessment of the skeleton preservation state. The results of stable isotope analysis show that the least-altered parts of the specimens reveal carbon and oxygen isotope ratios close to those of contemporaneous marine-equilibrated calcites. The moderately-pronounced, positive correlations between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values observed for these coralla may reflect relatively minor vital fractionation effects, obscured to some degree by diagenetic overprint. Additionally, our results suggest that the isotope fractionation mechanism of heterocorals differed markedly from the significant kinetic fractionation characteristic of the modern scleractinian corals. The moderate extent of non-equilibrium fractionation during skeletogenesis in the Heterocorallia resembled the typical, environmental and metabolic CO_2 -dominated fractionation effects. Similar fractionation effects typify the extinct rugose corals, modern hydrocorals, and, in particular, modern octocorals, with which the heterocorals show notable architectural and structural similarities.

Keywords: Cnidaria, Heterocorallia, carbon and oxygen isotopes, microstructure, Poland, Morocco





Session 9 – POSTER

Devonian palaeoenvironments and mass extinctions

Highlighting pre Hangenberg faunal perturbations using vertebrates remains from the late Famennian in the Montagne Noire (France)

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The Hangenberg Crisis represents a major Paleozoic event marked by a mass extinction and associated with a major faunal turnover at the Devonian-Carboniferous boundary. However, despite the large number of studies on this crisis, little is known about the last millions of years preceding this major event. Here we present new analyses of the size and abundance of marine vertebrate dental remains within the Terminal Famennian levels of the Col des Tribes (Montagne Noire, France) in association with carbon isotope data along this section. Within the levels preceding the event, a drastic decrease in the abundance of bony fish teeth and an overall reduction in the size of vertebrate remains are observed despite the environmental stability suggested by the carbon isotope data in this region. These major changes in vertebrate communities that precede the Hangenberg are not associated with any taxonomic turnover at this time, suggesting an early phase of reorganization of marine ecosystems that precedes this Hangenberg mass extinction. The developing of new isotopic and topographic tools brings new insights on diet and feeding strategies in these groups, allowing a better understanding of trophic competition between marine vertebrates during the late Famennian.

Keywords: Hangenberg, Vertebrate diversity, carbon isotopes, vertebrate teeth, Montagne Noire





Session 9 – POSTER

Devonian palaeoenvironments and mass extinctions

Eifelian and Givetian (Middle Devonian) conodonts in the Iberian Chains

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Middle Devonian rocks are exposed in scattered, fragmentary and isolated outcrops in the Iberian Chains. They crop out in two areas (Carls & Valenzuela-Ríos, 2002): 1) the Axial Depression of the Cámaras River (DARC); the largest and more important one, where the main stratigraphic column (with gaps, chiefly for Givetian rocks) has been established and 2) the Montalbán Anticline. The detailed biostratigraphic analysis of the numerous small and incomplete outcrops allows the recognition of six stratigraphic units, which from bottom up are Monforte Fm, Moyuela Fm, Recutanda Fm, Barreras Section (positioned between the Recutanda and the Salobral Fm, but still of difficult biostratigraphic characterization), Salobral Fm and Cabeza Agudo Fm. In this report we focus in the conodont sequence around the Eifelian/Givetian boundary, which is compiled from three sections sited in the DARC, southeast of Loscos. The oldest conodonts comprise the Eifelian *costatus* Zone in the Molino Medio section; these strata show the highest occurrence of *Icriodus corniger* together with the lowest record of *Polygnathus costatus* in sample MM4. Higher strata record *P. pseudofoliatius* β (sample MM5), which after Walliser & Bultynck, 2011 indicates the base of the *australis* Zone. In the nearby Molino Alto section, the successive lowest occurrences of *P. klapperi* (sample MA 5) and *I. hollardi* (sample MA 6) identifies the next *kockelianus* Zone. Finally in the youngest section, Camino Molino, the lowest conodont record includes lower Givetian conodonts, comprising the index of the base of the Givetian, *P. hemiansatus*. Higher in this section the middle Givetian *rhenanus/varcus* Zone is identified. The compiled data and their stratigraphic arrangement from these three disconnected sections reinforces the potential of this area for analysing the Eifelian/Givetian boundary in the Iberian Chains and suggests the need for further and more detailed studies of this area. It could be of global relevance for improving the knowledge on the Eifelian-Givetian transition.

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Keywords: Conodonts, Iberian Chains, Eifelian, Givetian, Middle Devonian





Diagenetic Uptake of the Rare Earth Elements by Triassic Marine Vertebrate Fossils from South China

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The concentration and signatures of rare earth elements are critical to evaluate geochemical progressions in environmental and geological studies. In the vertebrate fossils, the rare earth element uptake is generally presumed to occur during the early diagenesis within 100 ka of their burial. However, this incorporation ceases in fossils with the loss of total organic constituents or their replacement with mineral elements. This research utilized nine fish fossils of the Triassic age from Chaohu and Louping areas, and the jaw elements of a mixosaurian ichthyosaur from the Panxian area of south China for elemental analysis (LA-ICPMS). The main purpose of this research is to know the concentration and differences of various elements in Triassic south China faunas and their rare earth elements (REEs) intake during early or late diagenetic alteration. These fossil specimens comprise a higher concentration of CaO (> 45%) and P₂O₅ (>30%) relative to other major oxides, and most trace elements in the studied faunas are significantly enriched (enrichment factor: EF>10) relative to the upper continental crust (UPCC). A significantly higher concentration of ΣREEs (>13000 ppm) has been noticed in Chaohu fauna, which is about four orders higher than the mixosaur specimen from the Panxian area. The upper and lower jaw of the mixosaur comprises relatively higher values of ΣREEs with respect to the tooth sample due to the less porous and stable nature of the tooth. However, the Louping specimens comprise a lower amount of ΣREEs (<1000 ppm). The concentrations of total rare earth elements in these vertebrate fossils are far higher than the black shales, global coals deposits, Chinese coals, North American Shale Composite, Post Australian Archean Shale, the global crust, and the modern bones. The normalization of REEs concentration using Post-Archean Australian Shale (PAAS) in the studied fossil specimens (bones, teeth, and scales) reveals the similarity to a "bell/hat shape" enrichment of normalized mid-rare earth elements, indicating their diagenetic alteration to a certain limit. Moreover, these fossil specimens have shown terrigenous sources of REEs rather than hydrogenous sources. Conversely, the tooth of the mixosaur shows less or no contribution from lithogenous or terrigenous sources but seawater REEs signals. Various redox proxies such as V/(V+Ni), Ni/Co, δU, U/Th, and Ce anomaly indicate the Early Triassic Chaohu fauna was deposited in suboxic to anoxic settings, while Louping and Panxian faunae were buried and deposited during dysoxic settings. Vertebrate fossils from the Luoping fauna are less or slightly influenced by diagenetic alteration in their rare earth elements concentration, fossils from the Panxian fauna are moderately affected by the later stage of diagenetic alteration in the rare earth elements, and fossils from the Chaohu fauna are strongly diagenetically altered in the rare earth elements.

Keywords: Rare earth elements; Fossils; Ichthyosaur; Diagenetic uptake; Redox Proxy; Seawater; South China



Session 10 - ORAL

Biotic and environmental evolution over the Paleozoic- Mesozoic transition

Carbonate laminites from the Nanzhang-Yuanan fauna in the Lower Triassic Jialingjiang Formation, South China: Origins and Significances

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The famous Early Triassic Nanzhang-Yuanan fauna (marine reptile Lagerstätten) has well documented the recovery of marine ecosystems after the Permian-Triassic mass extinction. These marine reptiles were preserved within laminated limestones (laminites) of Lower Triassic Jialingjiang Formation in Nanzhang and Yuanan, Hubei Province, South China. However, the formation mechanisms of these laminites, their indicative depositional environments as well as their significance on the excellent preservation of marine reptile Lagerstätten are still unknown. In this study, field observation in combination with petrographic and diagenetic analysis under normal light, cathodoluminescence, fluorescence and scanning electronic microscopes, as well as geochemical analysis were conducted to solve these problems. Microbially Induced Sedimentary Structures (MISS) and Reticulated Ridge Structures (RRSs) were developed on the surfaces of laminites. These laminites could be divided into two layers, respectively the light particle-rich layer and the dark organic-rich layer. Laminites packages could be classified as straight-dense laminae, wavy laminae and discontinuous laminae. There are abundant organic matters, extracellular polymeric substance (EPS) and framboid pyrites as well as clay minerals preserved within the dark layers, while light layers are rich in calcite crystals with a few celestite and dolomite crystals but rare clay minerals. *In situ* LA-ICP-MS analysis indicates different REE patterns and Ce abnormalities within different laminae. These all indicate a microbial origin of laminites (microbial laminites or biolaminites) deposited in a stagnant, reduced, hypersaline supratidal flat pond environment. Microbial-induced and/or -influenced biomineralization and organomineralization plays a very important role on the excellent preservation of Nanzhang-Yuanan marine reptile Lagerstätten.

Keywords: Early Triassic, biomineralization, organomineralization, automicrite, taphonomy



Session 10 - ORAL

Biotic and environmental evolution over the Paleozoic- Mesozoic transition

A New species of Mixosauridae (Diapsid: Ichthyosauria) from the Middle Triassic of Luxi County, Yunnan Province, China

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Multiple Middle Triassic fossil Lagerstätten had been uncovered in eastern Yunnan and western Guizhou provinces, southwestern China in the recent decades. Mixosaurids were the most commonly encountered marine reptiles in these Lagerstätten. The discoveries of mixosaurids in China can date back to 1965, and numerous exquisite specimens were collected from Panxian and Luoping biotas. But now the only undoubted valid species is *Mixosaurus panxianensis*, while other erected species are either controversial or require detailed reviews. Here a new mixosaurid species from Luxi, eastern Yunnan Province is reported. The absence of a dorsal extension of the postorbital and a posteroventral process of the jugal separates the new species from *M. panxianensis*, and the wider post-orbital portion differs it from *Mixosaurus* spp. from Monte San Giorgio/Besano Formation. The non-durophagous dentition, composed of tiny piercing mesial and swollen but pointed distal teeth, resembles *Mixosaurus cornalianus*. The foreflipper has a special morphology, including a narrow radius, the presence of a peripheral notch of ulnar, and a large metacarpal V. A preliminary phylogenetic analysis suggests a close affinity of the new taxon to *M. cornalianus* from the Western Tethys.

Keywords: Mixosauridae, fossil Lagerstätten, marine reptile





Session 10 - ORAL

Biotic and environmental evolution over the Paleozoic- Mesozoic transition

A new morphotype of nothosaurs (Sauropterygia: Nothosauridae) from the Middle Triassic of South China

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After the devastating Permo-Triassic Mass Extinction, several new groups of large predators invaded the sea in the early part of the Triassic, including sauropterygians, ichthyosauromorphs and thalattosaurs. Among these predators, sauropterygians are the most abundant group in terms of the generic/species diversity. Here we report a new morphotype of sauropterygians collected from the Upper Member of Anisian Guanling Formation in the Muta village, Luxi County, Yunnan Province, China, belonging to the very speciose family Nothosauridae. The new morphotype is represented by a single specimen that can be distinguished from other nothosaurs in the combination of the following features: premaxilla partly fused, frontal separated narrowly from the upper temporal fossa, pineal foramen in a deep trough and close to the middle of the skull table, jugal positioned forward in the check, quadratojugal present, distinctly long internal naris, mandibular articulations displaced distinctly behind occipital condyle, and anterior process of cervical ribs well-developed. The right lower jaw of the new specimen is completely exposed in medial view, providing hereto unknown information about the medial morphology of the lower jaw for nothosaurid sauropterygians, including the large splenial forming half of the inner wall of the lower jaw, the slender and elongate coronoid located in the middle of the mandible, and the meckelian foramen located within the adductor fossa bounded by surangular and prearticular. Morphological comparison with other Triassic eosauropterygians reveals previously unrecognized characters that may be used for reconstructing the phylogeny of sauropterygians in the future.

Keywords: *Nothosaurus*; *Lariosaurus*; Permo-Triassic Mass Extinction; Marine reptile





Gastropod diversity dynamics in the Triassic: extinction in the Carnian and at the end-Triassic

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The early Mesozoic experienced some of the biggest biotic crises of the Phanerozoic coupled with major climate perturbations. Following the Middle Triassic recovery from the end-Permian mass extinction, two mass extinction events occurred, one during the Carnian (Late Triassic) and one at the end-Triassic. Previous analysis by Dal Corso et al. (2020) estimated that 33% of the marine animal genera became extinct during the CPE, with gastropods (87% of genera) being the most affected group followed by bivalves (25%). They noted that the gastropod extinction rate might be exaggerated due to sampling bias. Gastropoda is one of the most diverse and abundant benthic groups in Recent marine environments, but their dominance was established in the Early Mesozoic. Gastropoda proliferated remarkably in the Triassic and exceeded their Permian diversity (Karapunar & Nützel 2021). During the Permian-Triassic transition the relative diversity of major gastropod groups changed as a result of differential success in recovery and selective extinction (Erwin 1990; Karapunar & Nützel 2021). The change in the proportional diversity of individual gastropod groups is most evident in the dwindling of the Order Pleurotomariida (Vetigastropoda). Although Pleurotomariida was one of the most diverse and abundant Late Paleozoic gastropod groups (Erwin 1990; Karapunar et al. 2022), they diversified poorly during the recovery in the Triassic with respect to other groups and their diversity declined more significantly during the Carnian (Karapunar & Nützel 2021). Analyses of the most comprehensive global Triassic gastropod list (2177 species, 429 genera) with generic range through data suggest a significant elevation of per genus extinction rate during the Carnian (45%) compared with the rates of previous Triassic ages (5%). The Carnian extinction rate was higher compared to the extinction rate at the Rhaetian (35%). If singletons are excluded from the analysis, the Carnian still shows a significant per genus extinction rate (16%) compared to the rates in Early and Middle Triassic stages (1–3%), but not as significant as the extinction rate in the Rhaetian (33%). In contrast to the extinction rates, the origination rates show a continuously decreasing trend throughout the Triassic. Shareholder quorum subsampling analysis of the PBDB data indicates that generic extinction rates elevated at the Carnian, peaked at the Norian and remained high at the Rhaetian. The analyses suggest that persistent high extinction rates were present throughout the Late Triassic. The Late Triassic biotic crises seem to impact gastropod diversity as much as the end-Permian mass extinction event.

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Keywords: Carnian Pluvial Episode, Rhaetian, mass extinction, recovery, Mollusca





Session 10 - ORAL

Biotic and environmental evolution over the Paleozoic- Mesozoic transition

A new species of *Macrocnemus* (Protorosauria: Tanystropheidae) from the Middle Triassic of southern China

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The Middle Triassic of southern China is well known for the diversified marine vertebrates, particularly reptiles. Recovered from the eastern Tethys margin, these species often show remarkable similarities to taxa that were previously known and described from the western Tethys. Here a new specimen of *Macrocnemus* is described on the basis of an incomplete specimen from the Member II of Guanling Formation (Pelsonian substage, Anisian, Middle Triassic) of Luxi County in Yunnan, China. The new form can be distinguished from other species of *Macrocnemus* by its limb elements, having a unique fifth metatarsal and slightly longer unguals. The morphology of the new specimen is consistent with a terrestrial lifestyle and phylogenetically recovered as the sister taxon of *Macrocnemus obristi*. The discovery of the new species in China provides insights on the early diversification of *Macrocnemus* and further evidence that this clade was geographically widely distributed in the Tethys region.

Keywords: protorosaurs, *Macrocnemus*, Luoping County, reptile





Session 10 - ORAL

Biotic and environmental evolution over the Paleozoic- Mesozoic transition

Bayesian occurrence-based approaches recover “early bursts” of diversification and no effect of body size in the post-extinction radiation of Triassic archosauromorphs

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Understanding the dynamics of evolutionary radiations, especially those following major extinctions, is of great theoretical interest and can also cast light on possible recovery from the current, anthropogenically-based probable mass extinction. The Triassic archosauromorph radiation was a spectacular explosion of life that ultimately begat the dinosaurs and pterosaurs, which would dominate the Mesozoic land and skies, and ultimately even the stunning diversity of modern birds. This explosion occurred in the wake of the end Permian extinction events, with archosaurs and their kin generally thought to have radiated into “vacated niches” after extinctions of other vertebrate taxa. Our understanding of this radiation has been greatly informed by phylogenetic estimates for these taxa, allowing rates of diversification and the times of origination of different groups to be understood. However, these estimates rest on uncertain foundations, and corroboration from other methods is thus warranted. Occurrence-based Bayesian approaches facilitate exactly such corroboration, being based purely on occurrence data and thus obviating the need for phylogenies. We apply the PyRate framework and a similar occurrence-based framework in RevBayes using a fossil birth-death model to a comprehensive dataset of species-level quasi-occurrences – with chronostratigraphic uncertainty generally taking the place of a true range – for Permian-Early Jurassic archosauromorphs, with associated body size proxy data (femoral length). We find broadly similar results using both methods, with a peak in diversification in the latest Permian and earliest Triassic, which is earlier than phylogenetically-based estimates and may indicate morphologically cryptic lineage splitting. Thereafter, net diversification rate broadly declines, reaching zero by at latest the Norian. These results are broadly consistent with phylogeny-based estimates, and indicate a diversity-dependent diversification rate with vacant niches indeed being gradually filled during the radiation. Analyses in RevBayes show slight peaks in the Middle and latest Triassic, and a major drop in the Jurassic, corresponding to the radiation of major groups and extinctions of pseudosuchians, respectively. Using a trait dependent diversification model in PyRate we find no significant evidence for an influence of body size on diversification, although larger taxa actually show higher diversification rates, *contra* null hypotheses that smaller-bodied taxa may reproduce and thus diverge more quickly, and possibly reflecting the radiation of large-sized groups during the interval. Overall, our results solidify our understanding of this major evolutionary transition and demonstrate the utility and reliability of Bayesian occurrence-based approaches in understanding diversification dynamics.

Keywords: radiation, Archosauromorpha, body size, PyRate, diversification dynamics



Session 10 - ORAL

Biotic and environmental evolution over the Paleozoic- Mesozoic transition

Conodonts suggest a late Spathian (late Early Triassic) for the age of *Thaisaurus chonglakmanii* (Diapsid: Ichthyosauromorpha)

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The largest biological extinction during the Phanerozoic took place during the Permian-Triassic transition. Marine reptiles start to appear in the Early Triassic. The age of these marine reptiles has important implications in studying ecosystem recovery. The primitive ichthyosaur *Thaisaurus chonglakmanii* was found in the Khao Thong hill, the Phatthalung area of the Southern Peninsula of Thailand, and the age of *Thaisaurus chonglakmanii* is controversial. To clarify the age of *Thaisaurus chonglakmanii*, we sampled Khao Thong section for conodont analysis. Seven well-preserved *Triassospathodus anhuinensis* specimens and a single well-preserved *Tr. symmetricus* specimen have been obtained. This is the first time that the conodont species *Tr. anhuinensis* has been found in Thailand. By collecting a large amount of morphological data of *Tr. anhuinensis* and its similar species, we concluded that *Tr. anhuinensis* can be distinguished from other similar species by its narrow basal cavity and numerous small fused denticles, and the definition of *Tr. anhuinensis* was revised. The *Tr. anhuinensis* zone was identified as the latest conodont zone in the Spathian of Early Triassic in Chaohu, South China and the strata yielding *Tr. anhuinensis* were referred to the late Spathian. In the Khao Thong section studied in this paper, elements of *Tr. anhuinensis* were discovered in the bed about one meter above the *Thaisaurus chonglakmanii* holotype and also in the bed producing the *Th. chonglakmanii* holotype, suggesting that the *Th. chonglakmanii* horizon may lie on the *Tr. anhuinensis* zone. Thus, the age of *Thaisaurus chonglakmanii* belongs to the late Spathian according to our conodont research.

Keywords: conodont, *Triassospathodus anhuinensis*, Thailand, *Thaisaurus*, Lower Triassic



Session 10 - POSTER

Biotic and environmental evolution over the Paleozoic- Mesozoic transition

Extinction of ophiacodontids, edaphosaurids and sphenacodontids near the Cisuralian/Guadalupian boundary

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Up to four mass extinction events have been recognized in the Permian fossil record of synapsids. From oldest to most recent, these occurred: 1, in an interval ranging from late Sakmarian to early Kungurian; 2, near the Kungurian/Roadian (Cisuralian/Guadalupian) boundary; 3, near the end of the Capitanian; and 4, near the Permo-Triassic boundary. We collected detailed stratigraphic and phylogenetic data to study the two oldest putative crises. For this, we needed to resolve a long-standing controversy about the age of the youngest Permian amniote-bearing North American strata, the San Angelo Formation (Pease River Group, Texas) and the Chickasha Formation (El Reno Group, Oklahoma), that have yielded synapsids. Our age determinations of these two formations are based on an extensive review of the available evidence from lithostratigraphy, magnetostratigraphy, palynomorphs, embryophyte body fossils, marine fossils (fusulinids and ammonoids from nearby formations that can be reliably correlated with the San Angelo and Chickasha formations), and, of course, the vertebrate fossils. These data suggest that the San Angelo is likely of early Roadian age, although the possibility that it straddles the Kungurian/Roadian boundary cannot be excluded. The Chickasha is more recent and entirely within the Roadian. We developed a new method to better date the extinction of lineages. This new method, based on the Fossilized-Birth-Death model, is shown to outperform other methods in terms of precision of the estimate, while retaining an acceptable type I error rate. Our analyses show that the extinctions of individual species of ophiacodontids, edaphosaurids, and sphenacodontids are staggered over several millions of years. We find no evidence for the first of the four Permian extinction events, and the second only appears to be a protracted period of decline. The taxa Ophiacodontidae and Edaphosauridae probably became extinct in the Kungurian, but Sphenacodontidae became extinct later, probably in the Roadian, although all three taxa may have persisted somewhat later.

Didier, G., Laurin, M. 2021. Distributions of extinction times from fossil ages and tree topologies: the example of some mid-Permian synapsid extinctions. *PeerJ* 9:e12577. doi : 10.7717/peerj.12577

Laurin, M., Hook, R. W. 2022. The age of North America's youngest Paleozoic continental vertebrates: a review of data from the Middle Permian Pease River (Texas) and El Reno (Oklahoma) Groups. *BSGF - Earth Sciences Bulletin*. doi: <https://doi.org/10.1051/bsgf/2022007> (in press)

Keywords: Permian, Cisuralian, Guadalupian, mass extinctions, synapsids, amniotes, fossilized birth-death process





Session 12 - KEYNOTE

Ichnology

Integrating ichnology, palaeoecology, and sedimentology for reconstructing dynamic palaeoenvironments

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Use of trace fossils for palaeoenvironmental reconstructions is one of the main streams of applied ichnology. Although the methods for their application have evolved and refined soundly to date, most of them remain to delineate relatively “static” environmental conditions, such as water depth, salinity, and oxygenation. Environments are however characterized by dynamic interplay of physical, chemical, and biological processes. As trace fossils can record the animals’ activities responding to changing environmental factors, integration of ichnology with precise knowledges on tracemakers’ palaeoecology and well reconstructed physicochemical environments recorded in sedimentary rocks will expand the horizons of palaeoenvironmental reconstructions based on trace fossils. In this presentation, I would like to demonstrate two examples of such integrative studies.

1) *Rosselia socialis* is a vertically oriented, funnel-shaped tube characterized by concentrically laminated, thick, muddy lining and occurs in most of the Phanerozoic shallow marine deposits worldwide. Nara (1995) found out that the trace fossil was a fossil dwelling tube of a terebellid polychaete that collected organic detritus for food. Later, he described a stacked morphotype of *R. socialis* and interpreted it to be the result of the burrower’s response to catch up with the intermittently aggrading seafloor by frequent sedimentation (Nara, 1997). Then, the terebellids were proven to have been highly tolerant to such repeated burials. The stacked *R. socialis* locally occur exclusively and quite densely in shallow marine sediments. Nara (2002) found that this characteristic ichnofabric occurs exclusively in transgressive shelf deposits, where abundant influx of sediment and land-derived organic matter occurred due to ravinement processes. The combination of frequent burial stress and abundant nutrient supply probably induced the establishment of the ichnofabric. Thereafter, it has been proven to indicate similar settings, such as transgressive shelves (Nara, 2011; Netto et al., 2014) or delta fronts (cf., Campbell et al., 2016).

2) During 18–16 Ma, the SW Japan arc rapidly rotated clockwise due to the spreading of its back-arc. To the south of the arc, another back-arc concomitantly opened and started forced subduction underneath the arc. The Misaki and Tanabe groups, where abundant soft-sediment deformation features, seismites, and tsunamiites occur (Nara and Aikou, 2016; Imai and Nara, 2022), are siliciclastic shallow marine successions deposited in the fore-arc basins at that time. Offshore to offshore-transition sediments of the groups are significantly less bioturbated compared to those of the nearest coeval continental margin deposits. The least bioturbated sediments are those of the Misaki Group, whose hinterland was particularly uplifted due to magmatic intrusions. The facies characteristics and regional tectonic background suggest that the tectonically induced over-sedimentation strongly affected the shallow marine benthic communities and deposited the ichnofabric-deficient sediments (Nara and Aikou, 2016).

Nara, M. 1995. *Lethaia*, 28, 171–178. Nara, M. 1997. *Palaios*, 12, 489–494. Nara, M. 2002. *Palaios*, 17, 268–276. Nara, M. 2011. *28th IAS Meeting of Sedimentology Abstracts*, 375. Netto, R.G., Tognoli, F.M.W., Assine, M.L., Nara, M. 2014. *Palaeo-3*, 395, 107–113.

Campbell, S.G., Botterill, S.E., Gingras, M.K., MacEachern, J.A. 2016. *JSR*, 86, 380–393. Nara, M., Aikou, K. 2016. *Palaeo-3*, 453, 80–92. Imai, S., Nara, M. 2022. *Jour. Geol. Soc. Jpn.* 128, 129–130.

Keywords: trace fossils, ichnofabric, depositional environments, reconstruction, tectono-sedimentation





Assessing the potential of different ichnologic metrics

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The need for quantifying secular changes in animal-substrate interactions has prompted the proposal of several metrics, such as degree of bioturbation, ichnodiversity, ichnodisparity, ecospace and ecosystem engineering cubes, ecosystem engineering index, and spindle diagrams. However, not all these approaches have been applied from a macroevolutionary perspective to the same extent and accuracy. Measuring the degree of bioturbation as a proxy to make inferences on the degree of infaunalization has been a popular approach in evolutionary paleoecology (e.g. ichnofabric index, bioturbation index, bedding-plane bioturbation index). If integrated within the framework of a time-environment matrix, measuring the degree of bioturbation results in useful ways of tracking changes in intensity of bioturbation along the depositional profile through time. However, there are many pitfalls that are apparent when this approach is used without proper evaluation of the sedimentologic and stratigraphic context. To undertake a more in-depth reading of the trace-fossil record, it is important to take the actual composition of ichnofaunas into consideration. Changes in ichnodiversity through time have long been used to unravel the macroevolutionary dynamics of evolutionary radiations and colonization trends in different environments. Construction of ichnodiversity curves requires critical ichnotaxonomic re-evaluation to avoid using inconsistent schemes. Ichnodiversity is the number of ichnotaxa present at a certain ichnotaxonomic rank and, accordingly, is more a measurement of taxon richness rather than of morphological diversity. More recently, there have been attempts to quantify abundance as well, allowing evaluating both the number of ichnotaxa and the degree of dominance. A related concept, ichnodisparity, has been introduced to capture variability of morphologic plans in trace fossils, yielding insights into large-scale innovations in body plan, locomotory system and/or behavioral strategy. Hence, ichnodisparity aims to reflect large-scale innovations that are more substantial than those captured by ichnodiversity. To assess ichnodisparity, categories of architectural design have been defined. Emphasis on assessing ichnodiversity and ichnodisparity trajectories should not be done at the expense of overlooking what each of the ichnotaxa means in terms of behavior and styles of interactions with the substrate. Appreciation of the latter can be done by analyzing patterns of ecospace colonization and ecosystem engineering using cubes summarizing information on tiering, motility, feeding mode, and ways in which organisms interact with and modify the sediment. Finally, spindle diagrams have been recently used to plot changes in ichnodiversity at ichnospecific rank. Whenever possible, all these tools should be used in an integrated fashion to offer a more accurate and holistic reading of the trace-fossil record.

Keywords: Ichnology, trace fossils, ichnodiversity, ichnodisparity, ecosystem engineering, bioturbation, bioerosion, evolutionary paleoecology





Temporal constraints on the ichnofacies paradigm

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The great strength of ichnofacies as environmental indicators relies on the stability of individual ichnofacies through time. For the most part, this stability has been proven through a series of studies building on the original work of Seilacher from the 1950s and 60s, and refining the concept into our present understanding of the ichnofacies paradigm. However, something that is rarely taken into consideration is the uncertainty that surrounds ichnofacies at their point of inception – an ichnofacies cannot exist before tracemaking organisms have colonized the relevant sedimentary environment. As such, ichnofacies “originate” when a community of animals first colonizes a new habitat, and then gradually stabilize (or “evolve”) as niches are created and occupied in different ways, until they reach their archetypal form. This means that in the early Palaeozoic, when many new ecological niches were colonized for the first time, there was far less stability. This is highly significant for the use of ichnofacies to distinguish early Palaeozoic sedimentary environments, as the ichnological signature of those environments may not have yet stabilized to match the signal of the archetypal ichnofacies. This issue is further compounded by secular changes in animal-substrate interactions through geologic time, such as increases in ichnodiversity, ichnodisparity, degree and extent of bioturbation, and complexity of tiering structure. Knowing when this occurred allows the ichnofacies paradigm to be employed more accurately by ichnologists, palaeontologists, and sedimentologists alike.

An obvious example of the early-stage evolution of an ichnofacies is the *Scoyenia* Ichnofacies. Before the Silurian, there is no conclusive evidence for permanent non-marine animal communities, and hence before this point there is no *Scoyenia* Ichnofacies. In the Silurian and Early Devonian, when alluvial ecosystems were initially colonized, *Diplocraterion* and *Arenicolites* were characteristic ichnotaxa from these systems, yet for most of the Phanerozoic they were occasional minor constituent trace fossils, and hence not typical of the *Scoyenia* Ichnofacies. Similar scenarios can be reconstructed for any continental ichnofacies. In turn, marine examples are represented by the rapid build-up of the *Cruziana* Ichnofacies in the earliest Cambrian, followed by the *Skolithos* Ichnofacies later in the early Cambrian, and the more gradual establishment of the *Nereites* Ichnofacies through the Ordovician. In this presentation we will discuss the varying points of establishment of different ichnofacies, and how they “evolved” to reach their established form following their inception.

Keywords: Ichnofacies, evolution, sediment, Palaeozoic, trace fossil, ichnology





***Zoophycos* colonization in tempestites deposits of carbonate ramp: Example from late Bathonian of Kachchh Basin.**

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The Ichnogenus *Zoophycos* is one of the famous trace fossils with diverse morphology and strong bathymetric preference. *Zoophycos* evolved from shallow marine deposits in the Paleozoic and shifted their environmental preference to the shelf during Mesozoic and deep marine in Cenozoic. In Kachchh Basin, *Zoophycos* occurs in three stratigraphic horizons, primarily as low diversity ichnoassemblage. These stratigraphic horizons are Bathonian *Zoophycos* composite ichnofabric at Jumara Dome, monospecific middle Callovian *Zoophycos* ichnofabric at Jara Dome and early Oxfordian *Zoophycos* composite Ichnofabric occurring in the entire basin. The present study deals with Bathonian carbonate storm deposits, i.e., tempestites of Jumara dome. This work documents a detailed ichnofabric analysis of a 30-meter thick succession comprising 27 individual beds. An individual limestone beds are tempestites with with erosional lower boundary and fining upward graded bedding of shell accumulation, overlying these shell accumulations are thick bioturbated micritic lime mud. These shell accumulations are interpreted as storm deposits while the micritic mud are interpreted as post-storm event. The bioturbation in the micritic mud consist of *Zoophycos* seen as several lobed or spiral spreiten. Bioturbation of the bed is intense to moderate, and diversity of trace fossils is scarce. Other trace fossils present include *Chondrites intricatus*, *Chondrites targionii*, *Paleophycus* isp, *Thalassinoides* isp. and *Zoophycos* isp. The Ichnofabric analysis results demonstrate that the relatively diverse organism did the initial colonization in the post-storm phase. *Zoophycos* were emplaced in deep tiers, while *Paleophycus* and *Thalassinoides* were emplaced in the middle tier. Both tiered trace fossil denote that, the trace makers behaved opportunistically and colonized the initial post-storm sediments. Trace makers of *Chondrites intricatus* accomplished the second and youngest event of colonization with *C. targionii*, showing cross-cutting relation with the all earlier emplaced trace fossils (*Zoophycos*, *Thalassinodes* and *Paleophycus*). Based on the Ichnofabric analysis, a clear distinction between the storm and post-storm evens can be envisaged. Additionally, the bioturbation events are restricted to individual beds. They do not cross the bed-boundary, suggesting that the deposits were affected by frequent storm events, of which nearly 20 episodes of storms/high energy conditions can be identified in the late Bathonian studied succession. Such high frequency of storms are typical documented within the storm wave zone on the carbonate ramp environment. Thus, the *Zoophycos* occurrence on the late Bathonian carbonate succession suggests trace makers' adaptability in the tempestites deposits.

Keywords: Ichnology, *Zoophycos*, Paleoenvironment, Tempestite, Storm deposits.





Deep-sea neoichnology: applications in paleoenvironmental reconstructions

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The number of detailed deep-sea neoichnological studies has increased during the last decades, mainly through advances in the visual instrumentation used to observe this underexplored environment. The appearance of new technology (e.g., cameras on autonomous and remotely operated underwater vehicles) has enabled the acquisition of highly detailed images over large-scale areas of the deep-sea floor, and the subsequent characterization of biogenic traces (lebensspuren) and trace makers. Here, we provide some examples of new deep-sea neoichnological studies which have helped us to assess environmental conditions (e.g., bottom currents, food supply, substrate consistency) that are known to be important in paleoichnological (trace fossil) studies:

1) At an abyssal site in the NE Pacific ('Station M'), high-energy periods associated with benthic storms have been related to the impoverishment of lebensspuren abundance and ichnoassemblage diversity (Miguez-Salas et al., 2020). The local-scale erosion and re-suspension of unconsolidated surface sediment inhibits the formation of previous softground traces and led to the redistribution of organic matter resources. Also, these brief energetic events (<3 days) involved the appearance of exhumed surface patches; however, no hardground traces developed. These findings may offer a new perspective on the temporal gap needed for the development of hardground traces in deep-sea settings. 2) Studies of deep-sea echinoid trails ('Station M') revealed that the small-scale, patchy distribution of food may be the major factor influencing echinoid feeding movement patterns rather than the bulk quantity of detrital food stuff reaching the seafloor (Miguez-Salas et al., 2022). Meandering trail patterns were related to food patch consumption. This might suggest that echinoid trace fossils (i.e., *Bichordites*, *Scolicia*) with guided meanders could be related to the spatial distribution of detrital food stuff on the seafloor during the past. 3) Rosette-shaped lebensspuren related to echiuran feeding activities have a radial morphology. In a study of the Porcupine Abyssal Plain (NE Atlantic), seafloor consistency, together with the locally dominant megabenthos feeding group (e.g., suspension vs. deposit feeders), seemed to control factors that determined rosette areal coverage. We believe that the rapidly increasing capture of seafloor images in deep-sea environments offer great scope for significant advances in neoichnological research. However, there are still many steps to be taken to establish a standard procedure for the description, identification, and classification of these deep-sea lebensspuren. Similarly, characterization of endobenthic lebensspuren, remains a significant challenge in deep-sea environments.

Miguez-Salas, O., Huffard, C.L., Smith Jr, K.L., McGill, P.R., Rodríguez-Tovar, F.J., 2020. Faunal assemblage changes, bioturbation and benthic storms at an abyssal station in the northeastern Pacific. *Deep Sea Research Part I: Oceanographic Research Papers*. doi.org/10.1016/j.dsr.2020.103277.

Miguez-Salas, O., Vardaro, M. F., Rodríguez-Tovar, F. J., Pérez-Claros, J. A., Huffard, C. 2022 Deep-sea echinoid trails and seafloor nutrient distribution: present and past implications. *Frontiers in Marine Science*. doi.org/10.3389/fmars.2022.903864.

Keywords: Deep-sea, neoichnology, lebensspuren, environmental features, trace fossils



Session 12 - ORAL

Ichnology



Experimental investigation into the doomed pioneer hypothesis: transport and bioturbation in allochthonous environments

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Trace fossils provide *in situ* evidence for organisms and their activities and are widely applied as palaeoenvironmental indicators. But what if the organisms are allochthonous to the depositional environment? This is the concept behind the “doomed pioneers” hypothesis (Föllmi and Grimm, 1990); that organisms living in a well-oxygenated environment could be subjected to a turbulent flow and transported to a oxygen deficient environment. These organisms can survive transport and create trace fossils in anoxic sediment, at least for a short time, before eventually succumbing. The feasibility of this occurring has important implications for interpreting trace-fossil material in deep-marine settings (Grimm and Föllmi, 1994). Through a series of systematic experiments using the polychaete *Alitta virens*, we establish i) the mortality/survivorship potential of *Alitta virens* after undergoing transport; ii) the difference in burrowing rates of *Alitta virens*, from those that had been transported and those that had not; and iii) the adaptation of *Alitta virens* to environmental changes in temperature and oxygen conditions after significant transport. Results show significant differences in burrow rate between transported and non-transported individuals. There were also marked changes in burrow styles depending on environmental conditions. Careful consideration must be employed when using trace fossils associated with event deposits to reconstruct benthic marine communities, oxygen availability, and their trophic structures.

Föllmi, Karl B., and Kurt A. Grimm. "Doomed pioneers: Gravity-flow deposition and bioturbation in marine oxygen-deficient environments." *Geology* 18, no. 11 (1990): 1069-1072.

Grimm, Kurt A., and Karl B. Föllmi. "Doomed pioneers: allochthonous crustacean tracemakers in anaerobic basinal strata, Oligo-Miocene San Gregorio Formation, Baja California Sur, Mexico." *Palaios* (1994): 313-334.

Keywords: Doomed pioneer hypothesis, bioturbation, experimental taphonomy, *Alitta virens*





Session 12 - ORAL

Ichnology

Integral revision of the ichnogenus *Daedalus* Rouault and the first record in South America

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The ichnogenus *Daedalus* is one of the most enigmatic ichnogenus in the literature. It is documented in Ordovician to Silurian successions in both Laurasia and Gondwana. Seilacher (2000) amended the ichnogenus diagnosis; proposed new ichnospecies (*D. verticalis*), and pointed out the arthropycid fingerprints. He also modified the diagnosis of *D. archimedes* (Ringueberg), that was assigned for him to another author and later moved into *Daedalus*. Then, problems with the first mention, type locality and material exist, while the new ichnospecies is not in agreement with ichnotaxonomical rules and demands a future reexamination before it is validated. The complexity of the ichnogenus ichnotaxonomy has multiple reasons as *Daedalus* is not the result of the simple activity of a vertical J-shaped tube with lateral displacement as traditionally was interpreted, but a result of a more complex tube morphology and vertical to arcuate, with lateral, spiral or vertical displacement. Sometimes, one specimen exhibits morphological changes that represent a combination of more than one type. *Daedalus* is characterized by ichnospecies that reflects a simple constructional pattern and others more complex that forms spirocones. These two groups coexisted since the oldest records of the ichnogenus in the Lower Ordovician and until the end in the Silurian. The analysis of the material documented in the Silurian of Argentina, in the Ventana System, constitutes the first record of the ichnogenus in South America. It shows partial resemblance with the *D. verticalis* from the USA. Nevertheless, these specimens are the result of an animal that displaced vertically, in some cases 0.8 metres and sometimes exhibiting a progressive change in the angle of causative tube. In this sense, specimens with a vertical spreiten with constant width and a pseudo U-shaped morphology, occur with other levels with specimens that increase the width upward. The last two of them, show a progressive reduction of the inclination in the angle of the tube resulting in spreiten that vary the curvature and also the symmetry with respect to both sides of the structure, suggesting a new ichnospecies. The epichnial expressions in some ichnospecies are surfaces crowded of specimens that are extended by kilometers. The ichnogenus has been interpreted as a deposit feeder, a specialized one that had the ability to feeding in the meiofauna. The interpretation of a producer with the head pointing down and searching for food, is acceptable for the simplest morphologies of some ichnospecies but clearly do not explain up to three levels of calices or spindles documented in the type ichnospecies *D. desglandi* (Rouault). The opportunistic behavior suggested for the ichnogenus is questionable for several reasons. Firstly, large structures demands bioirrigation and walls stabilizations for keeping the oxygenation into the structure. Secondly, ichnospecies with several levels or long vertical penetration suggest a permanent domicile structure, rather than ephemeral occupancy. Finally, in the material of Argentina, was documented that *Daedalus* obliterate a pioneering bioturbation with *Skolithos*. The lateral extent by kilometers of beds with *Daedalus* observed in several parts of the world, suggests time condensation in such levels and the potential use in stratigraphy or paleoenvironmental schemes. The revision of the ichnogenus allows to conclude that not gap exist form the oldest to the last one record of *Daedalus*, and its apparent absence in the Upper Ordovician is the result of some incorrect assignments to other ichnogenus, as is the case of the records in southern Africa.



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Ichnology

Seilacher, A., 2000. Ordovician and Silurian arthropycid ichnostratigraphy. In *Geological Exploration in Murzuq Basin*, pp. 237-258. Elsevier Science BV.

Keywords: *Daedalus*, Ordovician, Silurian, shallow-marine, Gondwana, Laurasia, ichnotaxonomy





Evolutionary history of horseshoe crabs from the perspective of trace fossils

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For a better understanding of the evolution of animals, not only the studies of the evolution of morphology, but also those of the evolution of behavior are crucial. The behavior of extinct animals can only be studied by the observation of trace fossils. Horseshoe crabs (limulids) are one of the most suitable research targets for the reconstruction of the evolutionary history of the animals that includes the evolution of behavior, because trace fossils of horseshoe crabs sometimes co-occur with body fossils, and thus the animals leaving the traces are remarkable. Recently the evolution of morphology of horseshoe crab is reviewed by comprehensive studies of body fossils (Bicknell & Pates, 2020). On the other hand, the studies of the trace fossils are usually focused on their taxonomy, or body size changes through geological time or at the mass extinction event (e.g., the P-T boundary event) (e.g., Moreau et al., 2014; Shu et al., 2018), and the discussions on the behavior of fossil limuloids based on trace fossils are scarce. *Kouphichnium*, a trace fossil genus of horseshoe crabs, consists of several morphological component parts, which correspond to a variety of morphological features of animals, such as appendages and a telson (Caster, 1938). However, the gait patterns of extant limulids have not been clarified, because the neoichnological approach at that time targeted only the movement out of the water, and thus the buoyancy effect to the animal body could not be considered. In addition, animal behaviors, which left traces, have not been fully studied, and even recently, only general comparisons of morphology of traces with supposed behaviors have been conducted (Gaillard, 2011).

In this paper, first, the movements of the appendages and other body parts of younger individuals of extant American horseshoe crab (*Limulus polyphemus*) during their walking behavior are taken from the video from the ventral side in the laboratory. The movements of each body part, especially the walking rhythms of appendages, are analyzed. Furthermore, the traces of their movements can be recorded by the newly-developed casting method under the water. Combining these results, the relationship between the movements of the appendages and other body parts of the recent limulids and their corresponding traces can be clarified. Second, the fossil records of *Kouphichnium* are thoroughly reviewed from the references in the world. It is revealed that the detailed morphologies of *Kouphichnium* in the Carboniferous or earlier age significantly differ from those of extant limulid traces, whereas those in the Permian and later age are similar to recent ones. *Kouphichnium* in the Carboniferous or earlier age cannot be interpreted based on the gait pattern of the present limulid species, and the walking behavior and also the morphologies of the appendages of the horseshoe crabs at that time are probably different from those of the later age. The ichnological data suggests significant change of their walking behavior probably occurred in the Permian, almost same time when significant morphological evolution in the horseshoe crabs was recognized from body fossil record. Thus the “true” evolution of the horseshoe crabs can be revealed by the combination of the body fossil record and trace fossil record in future.

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Ichnology

Moreau, J. D., Fara, E., Gand, G., Lafaurie, G., Baret, L. 2014. Gigantism among Late Jurassic limulids: new ichnological evidence from the Causses Basin (Lozère, France) and comments on body-size evolution among horseshoe crabs. *Geobios* 47(4), 237-253.

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Keywords: horseshoe crab, trace fossil, ichnology, evolutionary history





Neoichnology of black backed sea gulls trails in the intertidal flat at the Mont Saint Michael hypertidal system, France

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Neoichnology is a powerful tool in linking the geological record of bioturbation with modern examples produced by invertebrates and vertebrates. Nevertheless, not always the use of actualism is possible. It is clear the absence of modern analogues of certain extinct groups or behavioral convergence difficult the connection of producer in the past with neoichnological examples. The value and limitations of the neoichnology were analyzed in detail by Zonneveld (2016). Notably, other reasons preclude the study of the ichnofossils from present day records of bioturbation. For instance, some of them have extremely low preservation potential, with an ephemeral existence, mainly as a consequence of controls related to the environment where they are produced. In general, sedimentary environments with high frequency changes of physical parameters tend to preserve low ichnological record. However, it is important to distinguish if the bioturbation is produced on surfaces (epichnia) exposed to high environmental changes or into the bed (endichnia). In the first case, the preservation potential is scarce, while in the second one it is high. In this sense, tidal flats are an example where both situations occur, particularly in the case of hypertidal ones with ranges higher than 4m (Archer, 2013). Interestingly, sediment grain-size, climatic-zone location and fluvial discharges are also influential factors. The UNESCO heritage site of bay of Mount Saint Michael situated in Normandy, France, is one of the places studied by Archer (2013). The walk-out of a part of the bay in the summer of 2018 during the ebb tide, close to the spring part of the tidal cycle, allowed to observe the famous and incorrect named “quick sands”. In this site, abundant sedimentary structures and bioturbation in areas between tidal channels, have also been documented. The attention is here particularly focused in trails with a W-shape ending part and with a series of transversal arcuate ridges that present alternation in the grain-size noted by differences in the sediment color. Similar trails were reported from the Wadden Sea, one of the largest tidal-flats in the world, and others from China and New Zealand. The latter, was investigated by Gregory (1999) that assigned the trails to black backed sea gulls foot-paddling for feeding, as a peculiar case of “aviturbation”. This type of gulls is abundant in the Mount Saint Michael and is the most suitable producer of the trails. Nevertheless, some features observed in the trails differ from the studied previous case. For instance, they are recorded mostly in a rippled bed rather than a flat one, and evidence some records with almost not ridges, suggesting a dominant resting behavior. Regarding the orientation, they are parallel to the flood-ebb currents and not necessarily are related with the wind direction as was suggested. Moreover, the bioturbation was not observed at the moment of the generation but occurred just before exposure. The zigzagging or curved courses observed in a previous study are in favor of other control than wind and looks like related to the feeding activity.

Archer, A.W., 2013. World's highest tides: Hypertidal coastal systems in North America, South America and Europe. *Sedimentary Geology*, 284, pp.1-25.

Gregory, M.R., 1999. Unusual “paddling” trails left by gulls and “aviturbation” in Rarawa and Mangawhai Estuaries, Northland, New Zealand. *New Zealand Natural Sciences*, 24, pp. 27-34.

Zonneveld, J.P., 2016. Applications of experimental neoichnology to paleobiological and evolutionary problems. *Palaios*, 31(6), pp. 275-279.

Keywords: Neoichnology, tidal-flats, foot-paddling, sea gulls, hypertidal, France





A new coastal sauropod-theropod tracksite in the Upper Cretaceous El Molino Formation, Torotoro National Park, Bolivia

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The El Molino Formation (Maastrichtian) in south-central Bolivia has one of the best records of dinosaur tracks known today in the world. Recently a new site has been fortuitously found during construction of a new road near the town of Torotoro, Torotoro National Park (GPS 20K 208245E, 7996212S). The tracks occur as concave epireliefs in three different layers (lower layer L1 25-cm thick, middle layer L2 37-cm thick and a directly overlying upper layer L3 6-cm thick) of oolitic packstone. L1 and L2 are separated by 1.65 m of massive mudstones and siltstones. A 15-cm green siltstone with desiccation cracks directly underlies L2. Layer L2 was not sufficiently exposed to carry out ichnological study. The upper layer L3 shows only theropod tracks in 80 trackways with 2-20 tracks each, and 21 isolated tracks. Thirty-two trackways have at least one missing track in the succession. Both shallow (<0.5 cm deep) and deep (1-3 cm) tracks occur and degree of preservation varies from poorly preserved to excellent, albeit both depth and degree of preservation are uniform in each trackway. Five trackways consist of straight, deep, 10-45 cm-long grooves, in alternating successive left and right position, often showing a well-developed proximal displacement rim and a linear or semi-curved distal, narrow groove. We interpret these grooves as swim scratch traces made by digit III of the feet of paddling theropods in shallow water. Lower layer L1 shows five sauropod trackways, one isolated sauropod track, five theropod trackways and five isolated theropod tracks. In this level the longest sauropod trackway consists of 19 tracks with 4 manus tracks; the others sauropod trackways lack the impression of the manus and have 11, 6, 3, 2 pes tracks. The theropod trackways have 3, 3, 3, 4, and 8 tracks, plus two isolated tracks. An additional theropod trackway consists of six sets of separate impressions of digits III and IV, long, subparallel to each other with a slight lateral convex curvature, lacking the impression of digit II and thus having the appearance of didactyl tracks. Other didactyl dinosaur tracks have been reported in the Lower Jurassic and Lower Cretaceous of North America, China and South Korea, Lower Jurassic of Morocco, and the ?Middle Jurassic of Agadez (Niger), but they are shorter than those reported here. Didactyl morphology might be genetic or taphonomically conditioned by the physical properties of the substrate; however, the fact that the other theropod trackways in this site are tridactyl suggests that the didactyl tracks are primary and not the result of post-impression substrate deformation. Recent studies of didactyl tracks attribute them to deinonychosaurian (dromaeosaurid and troodontid) theropods. To this date, didactyl tracks in the Upper Cretaceous (Maastrichtian) have only been reported in Poland and probably in Alberta, Canada. Thus, despite the excellent record of dinosaur tracks in South America (mainly Argentina, Bolivia and Brazil), didactyl tracks are lacking in this continent, except for probable dromaeosaurid tracks from the Campanian Torotoro Formation, in the TTNP (Apesteguía et al. 2011). The finding reported here could confirm that dromaeosaurid tracks occur in the South American continent up to near the K-Pg boundary. Layer L1 has yielded several abelisaurid and crocodylian teeth, and *Pucapristris* teeth of sclerorhynchid rays, which to this date are only known from Maastrichtian strata. The two layers of oolitic packstones with abundant dinosaur tracks underlain and overlain by green mudstones and red siltstones suggest that water level oscillated in the region, with emerged areas where dinosaurs walked





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leaving their tracks printed on soft substrates, followed by rapid water level rises during which dinosaurs swam and left scratches on the still soft substrate.

Apesteguía, S., De Valais, S., Cordero, G. R., and Ramirez, O. M. 2011. New ichnological record from the late Campanian Toro Toro Formation at Toro Toro, Potosí (Bolivia): First probable dromaeosaurid tracks from South America. *Ameghiniana* 48(4): 662-668.

Mudroch, A., Richter, U., Joger, U., Kosma, R., Ide O., et al. 2011. Didactyl tracks of paravian theropods (Maniraptora) from the ?Middle Jurassic of Africa. *PLoS ONE* 6(2): e14642.

Keywords: Torotoro National Park, El Molino Formation, theropod tracks, didactyl traces, Upper Cretaceous





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Analysis of theropod trackways with associated tail traces from Carreras Pampa, Torotoro National Park, Bolivia

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To date, reports of dinosaur tail traces have been limited to a small number at a single tracksite and have not included an in-depth analysis of the trackways associated with the tail traces (Kim and Lockley, 2013). Carreras Pampa is a Late Maastrichtian theropod-dominated tracksite in Torotoro National Park, Bolivia. Here we report ten trackways with associated tail traces in five sites of the Carreras Pampa mega-tracksite in the Torotoro National Park, Bolivia. The track-bearing surface is a bioclastic to oolitic grainstone overlain by a very thin layer of green mudstones directly covering the tracks and thin layers of very fine sandstones above. These trackways represent the first theropod trackways with associated tail traces from the southern hemisphere and the youngest theropod tail traces known at this time. Carreras Pampa preserves the largest number of theropod trackways associated with tail traces in the world, allowing us to compare similarities among these trackways in order to better understand how the animals were moving when the tail traces were formed. The tracks and trackways were measured with precision, orientation taken, and GPS coordinates collected for each track using a high precision GPS device. The results of the analysis of this data indicate that the dinosaurs leaving tail traces were all of a similar size, with an estimated height at hip of 145-178 cm. All of the trackways indicate that the dinosaurs were moving at a walking gait, with estimates of speed of 3.4-5.8 km/h. The tracks of these trackways range from very shallow (0-0.5 cm) to very deep (10-15 cm), often having large ranges in track depth within the same trackway. Many of the trackways preserve deep, elongate tracks caused by the metapodium leaving an impression in very soft sediment. The tail traces are not straight but show sinuosity. Most of them are not continuous between consecutive tracks. The co-occurrence of deep tracks and tail-drag traces may indicate that the tail was brought closer to the ground due to the animal sinking into the sediment thereby increasing the likelihood of it making contact with the ground or a specific pattern of motion in which the dinosaur lowered its tail to obtain stability while walking on an unstable substrate.

Kim, J. Y., and Lockley, M. G. (2013). Review of dinosaur tail traces. *Ichnos*, 20 (3), 129-141.

Keywords: Theropod tracks, Tail traces, Upper Cretaceous





Ichnofacies distribution in ancient gateways: the importance of hydrodynamic conditions

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Oceanic gateways have modulated ocean circulation and have influenced climatic variations throughout the Earth's history. During the Miocene, the Mediterranean Sea was connected to the Atlantic Ocean through the Rifian Corridor gateway (Morocco) in the west and to the Indian Ocean through the Indian gateway (Cyprus) in the east. Both gateways show a near-continuous sedimentary record that can be observed onshore through dominant calcareous (Cyprus) and clastic (Morocco) outcrops. A variability of deposits is recognized comprising shallow marine sandstones, channelized sandstone contourite facies, deep-sea turbidites, sandy calcareous contourites, hemipelagites, and pelagites. However, the facies puzzle is clearly different between these two gateways, revealing the variable influence of paleoenvironmental (i.e., ecological and depositional) conditions. This variation in facies is also observed in the ichnological record.

In the Indian Gateway (Cyprus), muddy chalky contourites, hemipelagites, and pelagites, at the base of the succession, characterized by the presence of *Chondrites*, *Planolites*, *Thalassinoides*, *Taenidium*, and *Zoophycos* allow assignment to *Zoophycos* ichnofacies (Miguez Salas and Rodríguez-Tovar, 2019). The transition to the first sandy calcareous contouritic interval with dominant *Thalassinoides* and disappearance of *Zoophycos* reveals a gradual sea-level fall determining an increase in proximity and energy conditions, favouring development of distal *Cruziana* ichnofacies. Continuous sea level fall trend determined more proximal and higher energy settings and then transition to the proximal *Cruziana* ichnofacies inside the contourite deposits as revealed by the presence of *Teichichnus*, *Gyrolithes* and *Ophiomorpha*. In short, development of ichnofacies in the calcareous contourite drifts of Cyprus, emplaced at the exit of the Indian Gateway, is mainly controlled by complex interactions between various paleoenvironmental factors with sea-level dynamics playing a major role.

In the Rifian Corridor (Morocco), turbidite deposits are typified by trace fossil assemblages with dominant *Ophiomorpha*, assigned to the *Ophiomorpha rudis* ichnosubfacies into the *Nereites* ichnofacies. Channelized clastic contouritic sandstone exhibits high density and low diversity trace-fossil assemblage, with predominant *Macaronichnus* and *Scolicia*, assigned to the proximal expression of the *Cruziana* ichnofacies. Shallow marine environments are dominated by vertical trace fossils (e.g., *Conichnus*, *Ophiomorpha*, *Skolithos*), allowing an assignment to the *Skolithos* ichnofacies. Highly energetic conditions typical of shallower settings are present in deeper-water environments (i.e., slope), contributing to ichnodiversity impoverishment into the ichnofacies (Miguez-Salas et al., 2021).

In both gateways, but especially in the Rifian Corridor, hydrodynamic energy reveals as the major factor controlling trace maker communities and ultimately the type of ichnofacies development.

Miguez-Salas, O. and Rodríguez-Tovar, F.J., 2019. Ichnofacies distribution in the Eocene-Early Miocene Petra Tou Romiou outcrop, Cyprus: sea level dynamics and palaeoenvironmental implications in a contourite environment. *International Journal of Earth Sciences*, 108(8), pp.2531-2544. <https://doi.org/10.1007/s00531-019-01775-x>.

Miguez-Salas, O., Rodríguez-Tovar, F.J. and de Weger, W., 2021. The Late Miocene Rifian corridor as a natural laboratory to explore a case of ichnofacies distribution in ancient gateways. *Scientific Reports*, 11(1), pp.1-10. <https://doi.org/10.1038/s41598-021-83820-x>

Keywords: Deep-sea, ichnology, ichnofacies, gateways, bottom currents, trace fossils





Spatio-temporal diversity in the paleoecology of early and middle Miocene rhinocerotids: impact of climate changes

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The Miocene is a time of major climatic and ecological changes, documented in terrestrial ecosystems. The Rhinocerotidae are abundant and diverse in the fossil record of this epoch, making it a very interesting clade to investigate the paleoecological impact of these changes. Through dental microwear texture analyses (DMTA; short-term diet proxy) and enamel hypoplasia (stress indicator), we studied the paleoecology of 19 rhinocerotid species belonging to four sub-tribes and an unnamed clade of Rhinocerotidae, and coming from nine localities in Europe and Pakistan covering the early and middle Miocene (MN2 to MN7/8). Our DMTA results suggest that all rhinocerotids studied were browsers or mixed-feeders (no grazers nor frugivores), but highlighted a clear niche partitioning based on feeding resources at Kumbi 4 (MN2, Pakistan), Sansan (MN6, France), and Villefranche d'Astarac (MN7/8, France). On the contrary, dietary overlap is observed for Béon 1 (MN4, France) and Gračanica (MN5/6, Bosnia-Herzegovina) rhinocerotids, although subtle differences are noted. The prevalence of hypoplasia was moderate (~ 10%) to high (> 20 %) at all localities but Kumbi 4 (~ 6 %), and varied greatly depending on the species, the tooth locus, the locality, and the time period. One rhinocerotid species was particularly affected by hypoplasia regardless of the context (at all localities but Sansan): the very large hippo-like *Brachypotherium brachypus*. On the contrary, the early-diverging elasmotheriines, probably having had a great dietary flexibility (Xafis et al., 2020; Hullot et al., 2021), were very little affected. The variations in hypoplasia prevalence documented quite well the local (e.g., seasonal droughts at Béon 1; Hullot et al., 2021) and global (middle Miocene Climatic Transition; Sansan and Devínska Nová Ves) conditions.

Hullot M., Laurent Y., Merceron G. & Antoine P.-O., 2021. Palaeoecology of the Rhinocerotidae (Mammalia, Perissodactyla) from

Béon 1, Montréal-du-Gers (late early Miocene, SW France): insights from dental microwear texture analysis, mesowear, and enamel

hypoplasia. *Palaeontologia Electronica* 24 (2), 1-26, <https://doi.org/10.26879/1163>

Xafis, A., Saarinen J., Bastl K., Nagel D., and Grímsson F.. 2020. Palaeodietary traits of large mammals from the middle Miocene of

Gračanica (Bugojno Basin, Bosnia-Herzegovina). *Palaeobiodiversity and Palaeoenvironments*, 100:457–477, <https://doi.org/10.1007/s12549-020-00435-2>

Keywords: Rhinocerotidae, Miocene Climatic Optimum (MCO), microwear (DMTA), enamel hypoplasia



Session 15 - ORAL
Evolution and extinction of giants

New skeletal material and footpad impressions reveal locomotory adaptations of the large Pliocene diprotodontid *Zygomaturus keanei* (Marsupialia)

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Diprotodontids were the largest marsupial herbivores and an integral part of Australian ecosystems until their extinction approximately 40,000 years ago. Despite the frequency with which their remains are encountered, key aspects of their morphology, systematics, ecology and evolutionary history remain poorly understood. During the late Cenozoic, Australia became increasingly arid, which drove the diversification of taxa better adapted to open habitats. By the Pleistocene, many diprotodontid taxa had evolved graviportal limb adaptations, but little is known about when and how this occurred. Here we describe the first known partial skeleton of *Zygomaturus keanei* from the Pliocene of northern South Australia. This is only the third partial skeleton of a late Cenozoic diprotodontid described in the last century, and the first with associated soft-tissue structures. The disparity in postcranial morphology between *Z. keanei* and the Pleistocene *Z. trilobus*, despite similar dental morphology, suggests that more complete specimens are needed to obtain a comprehensive ecological and systematic understanding of the family. Features of the forearm, manus and pes reveal that *Z. keanei* was more graviportal than Miocene diprotodontids, which likely correlates with the late Pliocene expansion of grasslands in inland Australia.

Keywords: Diprotodontidae, locomotion, taxonomy, Australia, megafauna





Session 16 - KEYNOTE

The appearance and loss of flight in paravians

Fly you fools: our growing understanding of the origin (s) of flight in paravians

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Since the turn of the millennium a series of discoveries coming mostly out of Asia have redefined our notion of how dinosaurs look, lived and behaved. The plethora of feathered fossils, both avian and non-avian alike, preserved in great detail has allowed for a range of new methods and approaches to investigate a series of fundamental questions about theropod biology that were only speculative a few years back. One of the most critical of these is when, where and in what context did flight evolve in theropods. Here I will both review some of the recent major works on this topic, focusing on the contributions of myself and my colleagues, but also present some of the newest lines of investigation to address the biomechanical, physiological and biophysics challenges that need to be overcome to turn a terrestrial creature into a volant one. I will also discuss the growing realization that flight in theropods is not a singular occurrence, several lineages attempted it in their own way, and that even within early avians there is much experimentation in the ecomorphospace of aerial travels. Gaining a greater understanding for how, when and why certain paths succeeded while others didn't requires looking beyond the fossils themselves to include paleoecological interactions as well how ontogeny influenced evolutionary possibilities. How do you make a wing may seem like a simple question, but as recent work has shown there is much hidden complexity, nuance and room for discovery in that question.

Keywords: Origin of birds, flight, gliding, wings, Mesozoic, take off, evolution, theropods





Session 16 - ORAL

The appearance and loss of flight in paravians

Testing hypotheses regarding super-precocial flight in Enantiornithes

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Since their origin, birds have been enormously successful quickly diversifying into numerous lineages and encompassing significant ecological diversity. While their non-avian dinosaurian relatives appear to be predominantly precocial, developmental patterns in extant bird taxa vary along a spectrum from altricial to precocial, accompanied by marked differences in their early physiology, anatomy, and behavior (Starck and Ricklefs, 1998). At one end of the spectrum, altricial hatchlings enter the world highly vulnerable: naked, blind, and entirely reliant on their parents. At the other end, precocial birds hatch covered in natal down with well-developed hindlimbs that allow them to forage independently, relying on their parents primarily for protection. An exception are the super-precocial Megapodidae, the so-called mound-builders, which can fly after emerging from the mound and receive no post-hatching parental care (Jones and Göth, 2008). The most abundant and successful clade of Mesozoic birds is the Enantiornithes, a group of predominantly arboreal birds that dominated terrestrial avifaunas throughout the Cretaceous (Chiappe and Walker, 2002). All available information suggests these birds were developmentally highly precocial, hatching fully independent and flight capable (Xing et al., 2017; Zhou and Zhang, 2004). This evidence includes highly ossified and or fledged embryos and hatchlings with fully developed remiges. To test the hypothesis that enantiornithine hatchlings were flight capable, we quantify growth trajectories in enantiornithines and compare them to ontogenetic changes in extant birds across the altricial-precocial developmental spectrum. This data supports previous interpretations that enantiornithines were precocial.

Chiappe, L. M., and C. A. Walker. 2002. Skeletal morphology and systematics of the Cretaceous Euenantiornithes (Ornithothoraces: Enantiornithes); pp. 240-267 in L. M. Chiappe, and L. M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*. University of California Press, Berkeley.

Jones, D., and A. Göth. 2008. *Mound-builders*. CSIRO Publishing, Collingwood, Australia.

Starck, J. M., and R. E. Ricklefs. 1998. Patterns of development: the altricial-precocial spectrum; pp. 3-30 in J.M. Starck, and R. E. Ricklefs (eds.), *Avian Growth and Development*. Oxford University Press, New York City.

Xing, L.-D., J. K. O'Connor, R. C. McKellar, L. M. Chiappe, K.-W. Tseng, G. Li, and M. Bai. 2017. A mid-Cretaceous enantiornithine (Aves) hatchling preserved in Burmese amber with unusual plumage.

Gondwana Research 49:264-277.

Zhou, Z., and F. Zhang. 2004. A precocial avian embryo from the Lower Cretaceous of China. *Science* 306:653.





Session 16 - ORAL

The appearance and loss of flight in paravians

The Early Cretaceous aviary from the Las Hoyas wetland: a new specimen and insights into enantiornithine life-history and flight

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The Early Cretaceous (129-125 Mya) Las Hoyas wetland in Cuenca (Spain), contains the richest Cretaceous avifauna in the European continent. More than 30 years of paleontological excavations at this site have resulted in the discovery of many relevant enantiornithine fossils. Among these, *Iberomesornis romerali*, *Concornis lacustris*, *Eoalulavis hoyasi*, stand as the most iconic holotypes of the site. The former, *Iberomesornis*, was later recognized as a juvenile, and the intriguing aggregation of four juvenile birds at distinct ontogenetic stages in an alleged pellet, is now being reviewed in the light of new knowledge about the taxonomy and life-history of these birds. *Eoalulavis* afforded direct evidence of diet (crustacean remains in its stomach) well before abundant discoveries in the Jehol Biota of China, and it documented for the first time the evolution of the alula among early birds. Such critical discovery provided initial evidence of enhanced flight performance during take-off and landing in enantiornithines. Consistent with this, an exquisitely preserved enantiornithine wing (revealing a set of flight feathers and patagia, including calami insertions) demonstrated the presence of a modern-like subcutaneous network of feather muscles and ligaments, which in modern birds assists flight biomechanics by stiffening feather response to the requirements of the airfoil. A tiny hatchling from the site showed evidence of thin down-like covering and a wing feather much longer than the body. The presence of these integumentary structures was interpreted as a sign of precociality, a notion that may need to be reassessed given the fact that the most extreme types of precociality in crown-group birds entail reduced parenthood and locomotor independence, and it is hardly possible that this hatchling was able to leave the nest and walk, let alone fly, given its notable skeletal immaturity. A new enantiornithine specimen is presented here, and together with the new paleobiological insights derived from the Las Hoyas avifauna, we argue that this site provides important evidence for understanding the connection between the abundance of enantiornithine remains in this ancient wetland and the life-history, locomotion (flight), and diet of these Cretaceous birds.

Keywords: Las Hoyas, Enantiornithes, Early Cretaceous, Life History, Flight, Avian Evolution





Session 17 - KEYNOTE

Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Fossils research in Cambodia

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Before 2019, the information related to Cambodian fossils was scarce. Since 2019, the Department of Heritage Parks, General Departments of Local Community, Ministry of Environment, has gradually started a fossil survey and dissemination of the results. Currently, information and photos of fossils found in Cambodia can be easily accessed through media and information systems. During the last four years of the preliminary survey, the Ministry of Environment has discovered marine fossil sites, petrified wood fossil sites, and a dinosaur bone fossil site. Up to 2022, forty-two fossil sites have been identified in eight provinces, with estimated ages ranging from Permian to Cretaceous. In Banteay Meanchey province, eleven marine fossil sites were identified and referred to the Permian period. In Banteay Meanchey province town, there is a cluster of six different fossil sites, named the Sereysoapon marine fossil site. The sites with the greatest abundance of fossils in Cambodia, found in the course of the preliminary research of the last four years, will be the subject for future research. Currently, the research team still faces a lack of human resources, budget and technical supports, storage space, room for fossil preparation and cleaning, and young experience in paleontology. We strongly hope that fossil research in Cambodia will be improved and a greater variety of fossils will be discovered in the rest of the provinces. We are seeking and calling for the support and good collaboration from national and international institutions, non-government organizations, and expert teams, who pay attention and are interested in providing contributions for future development of Cambodia's fossil research in cooperation with nearby countries.





Palaeontological highlights of Brunei Darussalam (North Borneo)

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We have been conducting intensive palaeontological research on Brunei's Neogene deposits since 2014. During our field surveys we discovered some exceptional fossil assemblages. Most of the remains come from the middle to Upper Miocene shallow marine deposits of the Miri and Seria formations. The fossil-rich outcrops have been recently dated with Sr-isotope stratigraphy (Kocsis et al., 2022). Here, the most remarkable finds are shown to give a taste of ancient biodiversity of the region. Some of the results are already published by our wider group, but preliminary new finds will also be briefly presented. Among the invertebrates, molluscs are plentiful in certain outcrops, and so far, gastropods were studied in detail and yielded 23 new species (Harzhauser et al., 2018). Other taxa such as bivalves, crustaceans, and corals can be also very common, and their descriptions are in progress. Regarding vertebrates, fish fossils occur frequently, and in fact, until now the most diverse Southeast Asian fossil chondrichthyan record comes from Brunei with many selachian and batoid taxa including the famed *Otodus megalodon* (Kocsis et al., 2019). Teleost otoliths are even more common, and the fauna is dominated by Sciaenidae and Ariidae. Turtle bones, and rarely crocodile teeth and scutes were also recovered. Microfossils such as pollen and foraminifera have been also studied and described from both fossil and modern settings (e.g., Goeting et al., 2021; Roslim et al., 2021). Besides, many sedimentary successions yield macroplant remains as well, and dipterocarp fossil-leaf floras and dipterocarp originated fossil tree resins (amber) were recently reported (Kocsis et al., 2020, Wilf et al., 2022). Amber can be abundant in certain layers, and it often shows the sign of bioerosion, while some contains trapped insects that wait for further investigations.

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Harzhauser, M., Raven, H., Landau, B., Kocsis, L., Adnan, A., Zuschin, M., Mandic, O., Briguglio, A. 2018. Late Miocene gastropods from northern Borneo (Brunei Darussalam, Seria Formation). *Palaeontographica, abt. A: Palaeozoology-Stratigraphy*, 313, 1-79.

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Roslim, A., Briguglio, A., Kocsis, L., Goeting, S., Hofmann, Ch.-Ch. 2021. Palynology of Miocene sediments in Brunei Darussalam: first SEM investigations of pollen and spores, and their taxonomy and palaeoenvironmental interpretation. *Palaeontographica Abteilung B Palaeobotany–Palaeophytology*. 301, 77-139.

Wilf, P., Zou, X., Donovan, M.P., Kocsis, L., Briguglio, A., Shaw, D., Slik, J.W.F., Lambiase, J.J. 2022. First fossil-leaf floras from Brunei Darussalam show dipterocarp dominance in Borneo by the Pliocene. *PeerJ*, 10:e12949 DOI 10.7717/peerj.12949

Keywords: Neogene, Late Miocene, biodiversity, palaeoenvironment



Session 17 - ORAL

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Evolution and systematics of Spinosauridae (Dinosauria: Theropoda) in Southeast Asia

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The Spinosauridae are a family of large-bodied theropod dinosaurs with an elongated snout and crocodile-like teeth from the Jurassic and Cretaceous of Gondwana and Laurasia (Samathi et al. 2021). They were presumably, at least partially, piscivorous. The Spinosauridae are traditionally recognised as a member of the superfamily Megalosauroidae. However, some authors found that the Spinosauridae belong to the basal Carnosauria, outside Megalosauroidae. The spinosaurid monophyly is well supported, whereas the relationships within the spinosaurid lineage remain largely debated. The Spinosauridae can traditionally be divided into two subclades, the Spinosaurinae and the Baryonychinae. Another study, however, found that only the Spinosaurinae, which forms a monophyletic clade, are valid, whereas the Baryonychinae are a paraphyletic series relative to the Spinosaurinae, although some studies found a polytomy where the relationships within the Spinosauridae are unresolved and need further studies (Samathi et al. 2021).

In Southeast Asia, at least four spinosaurids have been reported (Samathi et al. 2019, 2021). Here, we summarized the Southeast Asian spinosaurids discovered decades ago, and provided an update on the new materials recovered recently. They were often found in association with other dinosaurs including sauropods and large-bodied theropods, and sometimes with other different spinosaurid taxa. The presence of more than one spinosaurid taxon in the same region or stratum is common, as observed in the Kem Kem Beds of Morocco (see Ibrahim et al. 2020 for alternative interpretation), the Araripe Basin of Brazil, the Iberian Peninsula, and the Khorat Basin in Southeast Asia (Samathi et al. 2021).

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Keywords: Dinosauria, Theropoda, Spinosauridae, evolution, systematics



Session 17 - KEYNOTE

Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Cenozoic terrestrial and freshwater biota of Vietnam – a reappraisal

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The continental ecosystems of Southeast Asia form a global biodiversity hotspot today, whose evolution and palaeobiogeographic relationships remain poorly studied. During the last 15 years, a variety of fossil remains of terrestrial and freshwater biota were discovered in the thick lacustrine and coal swamp sequences, accumulated in Cenozoic pull-apart basins of the Red River Fault Zone in northern Vietnam. Several of the respective localities were and are under study within the frame of the GDRI Paleobiodiversity of Southeast Asia. The fossils, Eocene to Miocene in age, help shedding light upon the above-mentioned topics. The most spectacular fossil assemblage is preserved in Late Eocene coaly mudstones of the Na Duong Basin, comprising mammals, crocodiles, turtles, tortoises, and abundant permineralised trunks of trees and royal ferns. Bivalves, gastropods, fish and plant remains were documented from overlying mudstone beds. A similar assemblage of molluscs and fish, Early Oligocene in age, was reported from lacustrine clays in the Cao Bang Basin. The youngest biota, Early Miocene in age, were recorded from mudstones in the Hang Mon Basin, including mammals and a rich fauna of terrestrial gastropods.

Close relationships of the Eocene mammal faunas of Na Duong and Europe provide excellent biostratigraphic control, document strong biogeographic links and highlight the importance of Southeast Asia as a pool for trans-continental dispersal of mammals along the northern Tethys margin. These results are supported by the affinities of the mammals from Hang Mon, which testify to an Early Miocene (Aquitania) age, and demonstrate another phase of close palaeobiogeographic and palaeoenvironmental relationships between Europe, the Indian Subcontinent and Southeast Asia. Crocodiles, turtles and fish from Na Duong, as far as studied to date, are more closely related to Southeast Asian clades, lacking the links to Europe.

Freshwater molluscs are less mobile than vertebrates, and fossil taxa are thus generally thought to preserve a more regional pattern of diversification and dispersal. This is exemplified by the bivalve assemblages from Na Duong and Cao Bang, which are closely related to modern faunas of the Yangtze, Pearl and Red River catchment areas, and include the earliest representatives of several modern genera. The documented evolutionary relationships are tied to the geological evolution of the river catchments, and mirrored in the molecular phylogenetic framework of modern freshwater bivalves. Terrestrial gastropods often show high rates of endemism at the species level, but many genera tend to be long-lived and have regional significance. This is true, also, for the fossil gastropod fauna of Hang Mon, which includes the earliest representatives of several genera common in Southeast Asia today.

Fossil plant remains differ greatly with regard to the type and quality of their preservation. While some of the macro-remains are identifiable at genus or even species level, fossil resin and palynomorphs can often only be assigned to higher taxa. Nonetheless, pollen, spores and microalgae,





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New material of turtle from the Neogene and Quaternary from Malaysia and Philippines and a review of fossil turtles in insular South-East Asia.

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The fossil record of turtles in insular South-East Asia has been for long restricted to the Quaternary of Java Island with the renown site of Trinil and they were first studied early in the 20th century (Dubois, 1908; Jaekel, 1911). Since then, tortoises and especially large Pleistocene tortoises of the genus *Megalochelys* have been described in several places including Indonesia, the Philippines, and Timor (Hooijer, 1948; Hooijer, 1971, Hans-Volker et al., 2006; Setiyabudi, 2016). Less has been published regarding freshwater turtles and the majority of them were described in Java. Among them, *Hardella isoclina* Dubois, 1908 was recently moved to the new genus *Duboisemys* and several fossil species (*Batagur siebenrocki*, *Batagur signatus*, *Chitra selenkae*, *Pelochelys cantorii*, *Amyda cartilaginea*) have been synonymized with living species (Karl et al., 2019). *Orlitia borneensis* has been recorded from the Middle Pleistocene (Setiyabudi et al., 2016) of central Java while *Cuora amboinensis* has been reported in the Late Pleistocene of Java more recently (Setiyabudi et al., 2021). *Duboisemys* systematic and phylogenetic relationships is rediscussed here. In addition to this review, we describe here material of *Cuora amboinensis* from the early Middle Pleistocene of Luzon, which better allow to understand the timing and the origin of this species in the Philippine Archipelago and its dispersion through the Sunda shelf and beyond the Wallace Line (as of Huxley). We also describe an enigmatic femur from the Neogene of Sabah in Malaysia which might represent one if not the first fossil turtle known in Borneo.

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Keywords: Turtle, South-East Asia, dispersal



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The first dated *Megalochelys* from Chaloem Phra Kiat sandpits, Nakhon Ratchasima Province, Northeastern Thailand: an early representative of Asian giant tortoises

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Extinct giant tortoises *Megalochelys sivalensis* Falconer and Cautley, 1837 were widespread from India to Insular Southeast Asia during the Early Pleistocene (Setiyabudi, 2009; 2016). Prior to this age, the early evolution of the genus is poorly known. Large *Megalochelys* tortoises have been reported from the late Pliocene in Chandigarh, India but were not described in detail (Badam, 1981). Potential occurrence in the Mio-Pliocene beds of Myanmar was mentioned. However, no descriptions were provided (Hirayama et al., 2015). *Megalochelys* sp. has been reported from the Neogene to Pleistocene sediments of Nakhon Ratchasima province, Northeastern Thailand for more than ten years. However, their age is unprecise because the specimens were never found in a stratigraphic context. This leads to some confusion in the interpretation of the shell morphology, e.g., the important shape variation of the epiplastron (Claude et al., 2011; Naksri et al., 2019). Newly prepared specimens have been found from several sand pits in Chaloem Phra Kiat District, Nakhon Ratchasima province, NE Thailand. One of the tortoise fossil collections from the Phraput sand pit is associated with a rich mammalian fossil assemblage, commonly including early Late Miocene taxa (*Stegolophodon*, *Brachypotherium*, *Chilotherium*, 'Hipparion', *Tetraconodon*, *Propotamochoerus*, *Microbunodon*, *Merycopotamus*, *Bramatherium*, and *Selenoportax*), with a few specimens of late Late Miocene or Pliocene taxa (*Stegodon* and *Hexaprotodon*). The material includes a 114 cm long, nearly complete plastron with a rectangular projection, ventral concavity, and a deep narrow xiphiplastral notch interpreted as belonging to an adult female. An epiplastral fragment showing a ventral ridge is interpreted as belonging to an adult male. These specimens present some morphological differences from the Pleistocene specimens known from elsewhere in Asia, suggesting that the specimens from the Miocene of Thailand possibly belong to a new species.

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Setiyabudi, E., 2009. An Early Pleistocene giant tortoise (Reptilia; Testudines; Testudinidae) from Bumiayu area, Central Java, Indonesia. *Journal of Fossil Research* 42 (1), 1–11.

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Keywords: Giant tortoise, *Megalocheilus*, sandpit, Nakhon Ratchasima, Northeastern Thailand



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Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Late Quaternary occurrences data of turtles and tortoises from the archaeological record of Thailand and Cambodia

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The Late Quaternary history of most vertebrate assemblages of continental Southeast Asia remains very enigmatic because of the lack of appropriate fossil records. This is damaging to our understanding of the impact of the climate changes of the last 10 000 years as well as of the temporality and magnitude of the impact of anthropization on this now endangered tropical biodiversity. One of the ways to avoid these shortcomings is to consider archaeological assemblages of hunted animals that contain many occurrences of large and medium size taxa. In this paper, we will present a case study focused on Southeast Asian archaeological turtles and tortoises. To do so we will discuss identifications of turtle and tortoise bone remains obtained from three Pleistocene and/or Holocene localities in Thailand (Doi Pha Kan, Moh Khiew, and Khao Ta Phlai), and one in Cambodia (Laang Spean). A mean of 8 taxa from three families (Trionychidae, Testudinidae and Geoemydidae) has been identified in each site. Among the 32 occurrence data acquired, 10 correspond to taxa that are not present nowadays in the vicinity of the site. This result could suggest that the biodiversity of turtles and tortoises has evolved a lot since the Late Pleistocene but the factors and the magnitude of this phenomenon remain difficult to evaluate. Indeed, our study clearly points out the identification limits related to the absence of complete carapace/plastron in archaeological sites and the fact that most of the taxonomic identifications are based on isolated bones, sometimes poorly preserved. We will thus also present some preliminary results regarding the use of paleoproteomics analysis to identify isolated bones of Southeast Asian turtles and tortoises and discuss how this could change our view of the quaternary biodiversity of these animals.

Keywords: Holocene, Human impact, Pleistocene, Southeast Asia, Tortoise, Turtle, Zooarchaeology



New atoposaurid specimens from the promising site of Phu Sung (Sakon Nakhon, Sao Khua Formation, Early Cretaceous)

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Mesozoic crocodylomorphs from Thailand are known from the Late Jurassic to Early Cretaceous of the Khorat plateau. Those forms are mainly platyrostral, apart from an atoposaurid specimen from the Sao Khua Formation (Lauprasert et al., 2011), known as *Theriosuchus grandinaris*. Here, we present three new exquisitely preserved crocodylomorphs from the newly discovered Early Cretaceous Phu Sung site in the Sao Khua Formation (Chanthasit et al., 2019; Ditbanjong et al., 2019). The specimens have an altirostral morphology and are referable to the family Atoposauridae, a group that is otherwise well diversified in Europe. The most complete and biggest specimen includes both cranial and post cranial parts, which are quite rare in atoposaurid specimens. The second one is composed of the skull without the mandible. The third one, which is also the smallest, consists of the posterior part of the skull with a few associated post cranial fragmented remains. All those specimens are very similar morphologically and might represent an ontogenetic series. Furthermore, some features of the nasal and frontal bones are reminiscent of *T. grandinaris*. We thus discuss the taxonomic implications of those findings. The quality of preservation of the two most complete specimens also allows for a preliminary phylogenetic analysis, which confirms their attribution to Atoposauridae. Finally, the most complete specimen was CT-scanned in France, as part of the long term Thai-French paleontological collaboration. This approach, through the study of the neuroanatomy and digital preparation of the post cranial elements, enables an investigation of some aspects of their paleobiology.

Those findings are especially important because of the rare occurrences of atoposaurids in South-East Asia and bring new questions about the origin and dispersal of this group, as well as its relationships with both Neosuchia and Notosuchia.

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Keywords: Phu Sung, Atoposauridae, Crocodylomorpha, Early Cretaceous, Sao Khua Fm., CT-Scan



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Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Leaf monkeys distribution during the Last Glacial Maximum on the Sunda shelf

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From the Pleistocene-Holocene transition until the Mid-Holocene, prehistoric hunter-gatherers of the Gunung Sewu Mountains in Eastern Java Island (Indonesia) mainly subsisted on monkeys which were all in one, a source of proteins, of raw material for an osseous industry and of symbolic behaviours. Among these ritualistic remains were several excellently well-preserved monkey splanchnocrania which once have been interpreted as magical markers by some prehistorians. The *Homo sapiens* who once inhabited the caves of the area preferentially targeted the extant ebony leaf monkey *Trachypithecus* (N=96%) over the long tail macaque *Macaca fascicularis* (N=4%), and all the faces belong to the former taxon. Specifically, they most certainly belonged to the extant Javanese species *Trachypithecus auratus* although some characters and especially their orbits look more like the Bornean species *Trachypithecus cristatus*.

A long debate has been taking place among primatologists as to whether the two populations should be regarded as two distinct species or be lumped into a single one. In the present geographical configuration of Southeast Asia, those two populations which are present on two separate islands should certainly be split into two species. But when one considers that Java and Borneo were recently connected together during the 120m marine regression of the Last Glacial Maximum, the specific status of these monkeys becomes more challenging.

In this paper we compare present populations of Javanese, Bornean and other extant Southeast Asian leaf monkeys with Song Terus fossils through a contour analysis of their orbit shape by the means of elliptical Fourier decomposition. Our aims are to i) clarify the status of the Gunung Sewu fossils and ii) contribute to the debate over the biological distinction of the two insular Southeast Asian leaf monkeys. Our results directly tackle the question of recent monkey – and by association human and other faunal – populational movements during the recent past when the Sunda Shelf was exposed, and, by extension, the environmental landscape of the emerged area which was, according to some authors, then traversed by a savannah corridor, an unsuitable environment for such highly arboreal primates.

Keywords: Song Terus, Langur monkeys, Orbit shape, Geometric morphometrics, Island endemism, Migrations

Session 17 - ORAL

Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Paleobiodiversity in South-East Asia, critical assessment and perspectives

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Biodiversity in Southeast Asia is remarkable for its extraordinary richness and for its extreme vulnerability to human activities. It is also well known for its high degree of endemism with well-defined geographical sub-units separated by clear and long studied biogeographical boundaries. Although much attention has been paid to modern-day biogeography and biodiversity, palaeobiodiversity is far to be as well documented as in other regions of the world, which lets a number of questions unanswered concerning the origin of taxa but also concerning the effect of crises that have shaped present diversity. For eight years, the French CNRS has supported us thanks to an International Research Network (IRN) focused on palaeobiodiversity in South-East Asia. The network increased the scientific dynamics operated by several researchers working on the deep and recent past of South China, Thailand, Laos, Cambodia, Vietnam, Malaysia and the Philippines through systematic and associated palaeoecological studies of various taxa, and it boosted new cooperations, helping to build a more transdisciplinary and systemic approach regarding several questions in palaeontology. To support scientific exchanges, it supported joint field-work where scientists and students could confront different points of view from different disciplines. In doing so, it helped to build a more rigorous basis for the study of fossil assemblages. Palaeobiogeographic history, inter-basin correlations and the origin plus recent dynamics of modern biodiversity in Southeast Asia have been common threads behind the network and significant progresses have been achieved but clear needs have also been identified. Capacity building regarding questions above systematic expertise must be fostered, links between neontological, palaeontological and palaeoenvironmental studies need to be reinforced. The network is evolving towards more sustainable ways to go forward. There is indeed an increasing need of support for the training of students and exchanges between institutions, to ensure originality and academic excellence. Increasing the number of PhDs with joint supervision and finding ways to decrease their fees, will attract prospective students and improve their skills. We will improve local anatomical and fossil collections for educational purposes by regionally exchanging material to build more referentials. Various identified limitations such as slow bureaucracy or limited budgets will be discussed. We shall better use social networks to communicate, and we will expand our mailing list. Discussion with decision makers and academic and non academic sponsors regarding the importance of the palaeontological heritage and palaeontological education will need to be strengthened in order to collectively act as a lever for supporting initiatives in research in South-East Asia, as well as for raising funds for middle and longer term cooperation.

Keywords: Palaeobiodiversity, Southeast Asia, Palaeobiology, Palaeontology, Bioarchaeology

Session 17 - POSTER

Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Miocene palynomorphs from Ban Tha Phon, Phetchabun Bassin, Thailand

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In Central Thailand, the Phetchabun basin is famous for the diverse Miocene fish and plant assemblages discovered 20 years ago. However, no precise dating or paleoenvironmental reconstructions have been proposed for the fossil beds. During recent fieldworks in two outcrops at Ban Tha Phon, Phetchabun Province, palynology was studied from six sediment samples, collected from the bottom to the top of each locality, every 25cm. Palynomorphs were extracted using hydrofluoric and hydrochloric acids, and observed under SEM. The first outcrop, located more northerly, shows ten morphotypes of palynomorphs including one morphotype of flowering plant pollen, one morphotype of testate amoebae and eight morphotypes corresponding to unidentified structures. The second outcrop shows three morphotypes of angiosperm pollen, one morphotype of aquatic plant pollen, four morphotypes of testate amoebae, one morphotype of fungal spore and five morphotypes of unidentified structures. The low number of identified paleospores and paleopollens preclude precise paleoclimatic and paleoenvironmental reconstructions. However, these results show that the morphotypes from the two outcrops are different in taxonomic composition and are also associated to different types of sediments. The northern pond consists of a layer of creamy white clay to pale brown fine sand, which represents slow-flowing to still water. The southern pond consists of clay deposits alternating between layers of yellow-grey and creamy-white to pale grey. These differences can be explained by slightly different ecological conditions. However, both ponds have thin sediment layers of 2-5 mm thick, indicating short periods of rainfall associated with a hot and arid environment.

Keywords: palynomorph, paleoclimate, Miocene, Phetchabun basin, Thailand



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A new Miocene dicotyledon leaf assemblage from Ban Tha Phon, Phetchabun Bassin, Thailand

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Cenozoic floras of Thailand are mostly known from a series of intermontane basins outcropping along the country, usually dated from the Eocene to Miocene. This fossil record includes leaves, branches, flowers and pollen. In Central Thailand, the Phetchabun basin has yielded a rich Miocene fish fauna collected more than 20 years ago. Plant remains have also been mentioned and some are housed in scientific collections, but they have never been described. Hundreds of specimens were collected during new fieldworks in Ban Tha Phon, Phetchabun Province. Thirty subcomplete dicotyledon leaves are studied herein, using leaf morphology and leaf vein architecture to identify and reconstruct the paleoflora and paleoclimate. Leaves can be classified into fifteen morphotypes, from microphyll to notophyll and entire leaf margin. Although closely related to the modern leaf assemblage commonly found in the region, the fossil leaves are smaller, which suggests, along with the predominance of entire leaf margin types, that Miocene plants were probably able to thrive in hotter and drier environments than today. However, due to the limited number of specimens included in this study and the incompleteness of some of them, the paleoflora and paleoclimate cannot be confidently reconstructed. For a better interpretation, other sources of data such as the geological history of the locality and sedimentology should be studied.

Keywords: fossil leaf, dicotyledons, Miocene, paleoflora, paleoclimate, Thailand, Phetchabun Basin





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Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Cranial and post-cranial materials of a mamenchisaurid sauropod from Phu Noi, Phu Kradung Formation, Upper Jurassic to Lower Cretaceous, Northeastern Thailand

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The Upper Jurassic - Lower Cretaceous Phu Kradung Formation in Northeastern Thailand has yielded a rich vertebrate assemblage, including amphibians, crocodiles, bony and cartilaginous fish, turtles, and dinosaurs. Sauropod dinosaurs are the most abundant fossil remains known from the formation, especially in the Phu Noi locality, Kalasin province, where numerous isolated elements and articulated specimens have been collected. Several cranial characters observed in deformed skull fragments, such as the shape of jugal, postorbital and quadratojugal the presence of thick labiolingually asymmetric enamel on teeth, the number of alveoli on the dentary, and vertebral characters such as the procoelous anterior caudal vertebrae and the presence of pneumatic camellae, are reminiscent of Mamenchisauridae, a sauropod family commonly found in the Middle Jurassic to Early Cretaceous of China and with a few occurrences in the Late Jurassic of Tanzania. Anatomical description of post-cranial and cranial elements, including lower jaws and teeth, is used in a phylogenetic framework to establish the relationships of this probable new species, which corresponds to the second report of a mamenchisaurid in Thailand.

Keyword: Late Jurassic - Early Cretaceous, Mamenchisauridae, Phu Kradung Formation, Phu Noi, Thailand





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Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Parasite eggs in a Late Triassic vertebrate coprolite from Northeastern Thailand

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A paleoparasitological investigation of a vertebrate coprolite from the Huai Hin Lat Formation (Carnian-Norian) in Northeastern Thailand was carried out. The coprolite is elongate cylindrical with a rounded end and curves in lateral view probably produced by a crocodile-like reptile based on morphology. Three morphotypes of parasite eggs were identified in the coprolite by microscopic analysis of thin sections. The rounded or oval shape and thick shell of morphotypes I and II suggest they belong to the nematode superfamily Ascaridoidea, whereas the characteristics of morphotype III were insufficiently clear for a systematic assignment. This is the first recorded discovery of parasite eggs in terrestrial vertebrate hosts from the Late Triassic in Asia and it provides new information on parasite-host interactions during the Triassic period.

Keywords: paleoparasitology, Ascaridoidea, nematode, vertebrate coprolite, Mesozoic



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Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Early Carboniferous (Viséan) brachiopod fauna from Bukit Buchu, Terengganu, Peninsular Malaysia (East Malaya Block)

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Fossiliferous Carboniferous marine deposits are known from Bukit Buchu (hill) of Terengganu, eastern Peninsular Malaysia (East Malaya Block). They are in a siliciclastic sedimentary sequence (informally called Bukit Buchu Beds) at least 1,100 m in thickness and are predominantly comprised of mudstones and sandstones. Some fossiliferous sites have been known for several decades, as the fossils are dominated by the macrofauna mainly of brachiopods, with the minor occurrence of trilobites, bryozoans, molluscs (bivalves, gastropods, and cephalopods), crinoids, and corals. Nevertheless, no detailed palaeontological study was previously carried out on this fauna. We here present the new brachiopod results. Besides, we have recently described *Malayacyclus* Tang et al., 2021, a new genus of the rare Cyclida from this deposit: it was the first record of this enigmatic crustacean order from Southeast Asia. The Terengganu brachiopod fauna consists of fourteen species all in different genera; namely, *Argentiproductus* aff. *margaritacea* (Phillips), *Antiquatonia* sp., *Brachythyrina* (*Brachythyrina*) sp., *Eomarginifera* sp., *Hustedia* sp., *Leptagonia* n. sp., *Linoproductus* sp., *Oehlertella* sp., *Pleurogypnoides* sp., *Podtsheremia* cf. *thomasi* Roberts, *Pugilis* sp., *Punctospirifer* cf. *pahangensis* Muir-Wood, *Rugosochonetes* sp., and *Vitiliproductus* aff. *gröberi* (Krenkel). These taxa are mostly of warm-water Tethyan affinities. The possible brachiopod species correlation constrains a geological age of the Bukit Buchu Beds, most likely to be Viséan (Early Carboniferous). The Terengganu brachiopods shares some similarities with the classic 'Malayan Viséan fauna' of Muir-Wood (1948), now known to be from the Charu Formation (Viséan) of eastern Pahang, Malaysia. These Viséan fossiliferous sediments of eastern Peninsular Malaysia represent the oldest marine deposits of the East Malaya Block and provide intimate regional correlations with the coeval deposits in NE Thailand and Laos (Indochina Block). Furthermore, the Malaysian brachiopod assemblage is closely comparable with those of South China, the Tarim Basin, and further to Japan. As for the palaeobiogeographic interpretation, it is most likely that the East Malaya Block (as a peripheral submarine part of the proto-Indochina block) was in the low-latitude or warm-water region of the eastern Tethys during Viséan time.

Muir-Wood, H. M. 1948. Malayan Lower Carboniferous fossils and their bearing on the Visean palaeogeography of Asia, (with contributions by W. N. Edwards, K. P. Oakley, Stanley Smith, & C. J. Stubblefield). London, England: British Museum (Natural History) 118 pp, 17 pls.

Tang HY, Mychko EV, Feldmann RM, Schweitzer CE, Shaari H, Sone M. *Malayacyclus* gen. nov., the first Southeast Asian Cyclida (Crustacea) from the Early Carboniferous of Terengganu, Malaysia. *Geological Journal* 2021. 1–9. <https://doi.org/10.1002/gj.4128>

Keywords: Carboniferous, Viséan, brachiopod, Terengganu, Malaysia, Indochina, Tethys

Session 17 - POSTER

Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Preliminary study on a paravian-like unguis from the Early Cretaceous Sao Khua Formation of Thailand

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The Sao Khua Formation is the most dinosaur rich of the Khorat Group in northeastern Thailand. The theropod fossils in this formation consist of Megaraptora, Spinosauria, Carcharodontosauria, and Coelurosauria (Samathi et al., 2019), the most advanced non-avian dinosaur from this formation is an ornithomimosaur, *Kimmareemimus khonkaenensis* (Buffetaut et al., 2009), and an avian dinosaur is a possibly ornithurine bird known as "Khok Kong bird" (Buffetaut et al., 2005). Here, we briefly report the first record of a paravian-like dinosaur in Thailand from the Sao Khua Formation in Nong Bua Lamphu Province. Paraves is a group of feathered theropod dinosaurs. Most of them were small to medium-sized. In Asia, paravians have been found in China and Mongolia. The specimen we describe shows characteristics of a paravian-like pedal unguis forming a hypertrophied sickle-shaped claw with a strong curvature; absence of a proximodorsal lip; and symmetric blood grooves on the lateral and medial sides, significant characteristic features of the non-Eudromaeosauria (Longrich et al., 2009). This finding will improve our knowledge of paravian diversity and increase information on the biogeography during the Early Cretaceous (Barremian) period in northeastern Thailand.

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Keywords: Dinosauria, Theropoda, Paravian, Thailand



Session 17 - POSTER

Workshop on the International Research Network Palaeobiodiversity in South-east Asia

Cenozoic fossil insect assemblages in Thailand

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In Southeast Asia, the insect fossil record is mostly represented by Mesozoic forms. Cenozoic fossils are much rarer and only known from a few occurrences in Thailand and Indonesia (e.g., Chauviré et al. 2020). In Thailand, Cenozoic insects have only been reported from two Miocene sites in the Mae Sot basin, Tak Province. A unique specimen from Wat Don Koea was ascribed to the flat bug genus *Neuroctenus* (Araridae) by Endo & Fujiyama (1966). More recently, a rich assemblage from Wang Kaew was reported by Srisuk et al. (2006). This assemblage is formed of more than 100 specimens, referred to at least eight forms and five orders (Coleoptera, Diptera, Hymenoptera, Orthoptera, Hemiptera). Coleoptera are represented by very nicely preserved weevils (Curculionidae). Diptera are known by three different taxa referred to Bibionidae, Sciaridae and Brachycera. Hymenoptera are known by representatives of Vespidae and Formicidae. Orthoptera are represented by a single specimen of uncertain affinities and Hemiptera by a Gerrinae. This insect assemblage is the most complete ever reported in Southeast Asia during the Cenozoic. Moreover, the ecology of living members of these taxa is consistent with the paleoclimatic and paleoenvironmental reconstructions of the Miocene basins of Western Thailand, with seasonally dry lakes under subtropical to tropical conditions (e.g., Songtham et al. 2003).

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Northern Thailand Resulting from Extrusion Tectonics of Southeast Asian Landmass. *ScienceAsia* 29 (2003):221-233.

Keywords: Insect, Miocene, Mae Sot, Thailand, Coleoptera, Orthoptera, Diptera, Hemiptera, Hymenoptera



Session 17 - POSTER

Workshop on the International Research Network Palaeobiodiversity in South-east Asia

The first discovery of hybodontid egg capsule from Thailand

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Mesozoic freshwater shark assemblages have been reported in Thailand from the Jurassic to Early Cretaceous non-marine red beds of the Khorat Group. So far, they were restricted to isolated teeth, fin spines and dermal denticles. For a while, the richest vertebrate fossil site from the Jurassic Phu Kradung Formation called Phu Noi and located in Kalasin Province, northeastern Thailand have been excavated by the Department of Mineral Resources (DMR) and Mahasarakham University. Phu Noi has yielded many diverse vertebrate fossil discoveries including dinosaurs, crocodiles, turtles, bony fishes, lungfishes, temnospondyls, pterosaurs and freshwater sharks. According to Cuny et al. (2014), the shark assemblage from Phu Noi includes *Acrodus kalasinensis*, *Hybodus* sp., *Jiaodontus* sp. and *Lonchidion* sp. In the last few years, the DMR, led by a team from Sirindhorn Museum has continued the excavation in a bone bed made of siltstone. Among the fossils recovered are two shuttle-shaped fossils a few centimeters long, found above the dinosaur bones. Preliminary examination of their characters suggests that they belong to *Paleoxyris*, a hybodont shark egg capsule. This is the first record of freshwater shark egg capsules in Thailand. Their description together with other new Phu Noi freshwater shark remains is currently in progress and will offer a better understanding of the diversity and paleoecology of this diverse freshwater shark assemblage, notably concerning their reproduction strategies and trophic structure.

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Keywords: Hybodontid, egg capsule, Jurassic, Phu Kradung Formation, northeastern Thailand





Two temperature gradients regulate abundance and diversity of mesopelagic fish community in the Pacific Warm Pool over the past 460-kyr

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Marine ecosystem degradation is predicted based on field observations and modeling under anthropogenic ocean warming. Mesopelagic fish are a fundamental component of the pelagic ecosystem that serves as a biological carbon pump by linking the surface and deep-water systems. However, their community structure in a warmer ocean is unconstrained due to data scarcity. Here, using extraordinarily well-preserved fish otoliths extracted from ODP Hole 1115B (Solomon Sea, 9°11'S, 151°34'E, water depth 1149 m), we reconstruct a continuous mesopelagic fish community record in the Pacific Warm Pool region over the past 460,000 years. We find families Myctophidae and Bregmacerotidae strongly dominate the entire fish community. Higher fish abundance/lower diversity is evident during the interglacial periods, and vice versa. The observed cyclic glacial-interglacial pattern is explained by two hump-shaped temperature gradients, with a lower tipping point for diversity (26°C) than that for abundance (28°C). During past warmer-than-present interglacial periods (MISs 5e and 11c) when temperature exceeded the higher tipping point, both abundance and diversity decline drastically subsequently after the maximum warming phases. Members of *Ceratospelus*, *Diaphus*, and *Lampanyctus* (Myctophidae) are temperature-resilient taxa throughout the record, and the small pelagic codlets (Bregmacerotidae) tolerate super warm conditions during MISs 5e and 11c. Given the importance of mesopelagic fish community, our results therefore suggest that the mesopelagic ecosystem will be severely affected if ocean warming continues unabated in the future.

Keywords: fish otolith, fish community structure, tipping point temperature, glacial-interglacial pattern, ocean warming, MIS 5e, MIS 11c



Session 18 - ORAL
Tropical palaeobiology



Fossil history of a contrarian latitudinal diversity gradient in cheilostome bryozoans

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Living cheilostome bryozoans appear to exhibit a latitudinal diversity gradient contrary to those of most other major marine clades, with species richness peaking in the temperate zones. Their comparatively low species richness in the tropics has been linked to intense biotic interactions, including competition for space with other sessile organisms like corals and sponges. The bryozoan fossil record can potentially indicate when this curious inverse gradient arose, with important implications for the escalation of competitive interactions in marine ecosystems over geologic time. However, issues of preservation and sampling make reading this record non-trivial. Here we use an augmented geographic database of specimen counts and species richnesses in bryozoan-bearing fossil localities to document and interrogate the history of cheilostome diversity. As expected, the most diverse localities are in the temperate regions for all time intervals, but these regions are also the most well-studied. Using approaches to alleviate biased sampling, we interrogate whether and when genuine regional diversity differences can be detected using our fossil database. We discuss the quality of the post-Paleozoic bryozoan record, the kinds of inferences that can be made from it, and the implications for the role of ecological interactions in structuring global-scale diversity patterns.

Keywords: Bryozoa, Cheilostomata, latitudinal diversity gradient, biotic interactions, sampling





Paleodiversity of flora from the Early Paleogene of North-East India: an organic geochemical approach

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Early Paleogene (Paleocene- Eocene) is considered as the most dynamic period in Earth's geological history as it witnessed profound changes in biosphere and geosphere. Paleogeographic model shows that the Indian continent was present as an isolated landmass over the equator during this time following its separation from the East Gondwanaland during the Late Jurassic and its subsequent northward drift (Scotese, 2001). Moreover, this period is also significant for global temperature rise evidenced by many hyperthermals such as the Paleocene –Eocene thermal maxima (PETM; Kennet and Stott, 1991) and other prominent warming events. The present study attempts to investigate any molecular level transformations in terrestrial flora possibly imposed by these hyperthermals in a coal-bearing, shallow marine succession exposed at the Jathang section, Khasi hills, Meghalaya, India (Prasad et al., 2006). To fulfil the objective, soluble organic matter extract of the sediment samples was analysed using the conventional GC-MS and GC×GC- TOFMS. In saturated fractions, *n*-alkanes ranging from C10-C35, acyclic isoprenoids (pristane, phytane), steranes, diasteranes, pentacyclic triterpenoids consisting of different hopanoids and other angiosperm markers like oleanane, bicadinane along with aliphatic sesterterpenoids or unsaturated des-A- compounds and several other oleanoid compounds were identified. Saturated diterpenoids representing gymnosperm markers and sesquiterpenoids were also identified. The presence of bicadinane compounds reveals the occurrence of dipterocarpaceae, which had a tropical African origin and a range of expansion on the Indian plate during Paleogene (Bansal et al., 2022). Tetracyclic diterpenoids indicates the organic matter contribution from the leaf resins of conifers. Among those, phyllocladanes and ent-kauranes suggest that the organic matter was possibly derived from Podocarpaceae and Araucariaceae. Aromatic fractions comprise variable abundances of the aromatic hydrocarbons, i.e., cadalene, perylene, retene, tetrahydrotene, simonellite, bisnorsimonellite, aromatic diterpenoids, aromatic triterpenoids, and different isomers of phenanthrenes, naphthalenes, and anthracenes. Higher plant parameter (Retene/Retene+Cadalene) substantiates the fluctuating abundances of gymnosperm and angiosperm throughout the section. In a nutshell, the lower part of the section is initially dominated by the angiosperm, followed by the gymnosperm abundance, and subsequent angiospermous organic matter dominance at the top. Moreover, the Perylene/Cadalene ratio indicates increased combustion (Ghosh et al., 2022) in the middle of the section.

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Keywords: Early Paleogene, organic geochemistry, GCXGC-TOFMS, angiosperm, gymnosperm, Dipterocarpaceae





Mid-ocean carbonate buildups - Insights into the MIS 5e record of the Azores Archipelago (Portugal)

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Santa Maria Island in the Azores (central North Atlantic), the oldest in the archipelago, is remarkably rich in exposed marine fossiliferous sediments and submarine volcanic sequences. This richness is due to its distinct geological history of slow uplift and erosion during the last 3.5 Ma. Especially during the last interglacial, buildups formed by crustose coralline algae (CCA) developed both along the north (inward) and south (leeward) coasts between 2 and 7.4 above the present sea-level. These developed either directly over the basalt surface, or on top of bioclastic sediments reaching a maximum thickness of ~30 cm in the north and ~50 cm in the south. Initial growth of these buildups starts off with an encrusting form that changes into warty, lumpy and branching forms, often infilled with sediment. Fragments of mollusc shells, bryozoans and echinoderms are accessory components. Abundant bioerosive structures (*Gastrochaenolites* isp.) produced by the endolithic bivalve *Myoforceps aristatus* are frequently found in life position and incorporated in both buildups. The CCA taxonomic composition of the inward framework differs from the leeward framework only on the species level, as they are represented by the same families of Spongitaceae and Lithophyllaceae. These are commonly found or even predominate in shallow-water carbonate deposits, typically formed in warm-temperate to warm-tropical seas. The algal association found at both frameworks reflect the warmer water in which they grew during the Last Interglacial. Extant CCA frameworks do not occur in the archipelago and hence the fossil exposures are a testimony of past warmer climates. This kind of environment is rare on island settings unveiling the study site as key outcrops relevant to the study of algal reefs at mid-latitudes and mid-ocean settings during the warmer climate of the Last Interglacial, providing additional information on the conditions that were prevalent during this climatic stage.

Keywords: coralline algae, bioconstruction, palaeoenvironment, palaeoecology, hydrodynamic regime, last interglacial, volcanic islands, North Atlantic



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A new diverse tropical marine fossil assemblage from the late Triassic Cassian Formation (North Italy)

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The late Triassic Cassian Formation, situated in the Dolomites (Southern Alps, North Italy), is outstanding because of its high marine invertebrate biodiversity and excellent preservation. Several fossil Cassian assemblages were studied regarding their diversity and palaeoecology. The assemblages are mostly ecologically very different to each other. Therefore, a new assemblage from the locality Pralongia is currently being studied to better understand the complex Cassian palaeoecosystem. Preliminary examinations show that the assemblage is dominated by molluscs, mostly gastropods and bivalves. The species richness, especially of gastropods, is remarkably high. Brachiopods and echinoderm ossicles are also abundant. In addition, a high number of foraminifers is present. Many fossils are heavily encrusted, possibly indicating that they derive from a shallow-water environment. The diversity of the assemblage is very high and the taxonomic composition differs considerably from all other studied Cassian assemblages. This indicates that the complex and patchy Cassian palaeoecosystem still needs further studies for a comprehensive understanding.

Keywords: Late Triassic, diversity, palaeoecology, Cassian Formation, marine, invertebrates





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Seals, whales, and the decline of Cenozoic nautiloid cephalopods

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The Cenozoic distribution patterns of pinnipeds and nautilids from the Oligocene onward show the local extinction of nautiloids in the areas where pinnipeds appeared, eventually resulting in the present-day restriction of *Nautilus* and *Allonautilus* to the central Indo-West Pacific Ocean. In addition, the development of oxygen minimum zones (OMZs) due to enhanced ocean circulation in the Oligocene prevented nautiloids to escape predation by retreating to deeper waters, resulting in their disappearance especially from the west coast of the Americas. The demise of the nautiloid *Aturia* due to predation pressure was less immediate, probably because it avoided predation by fast swimming rather than retreating to greater depths. Ultimately, however, this might have resulted in *Aturia*'s end-Miocene extinction, because its adaptations to fast swimming prevented it from retreating to depths that allowed *Nautilus* to escape the ever-increasing predation pressure. An immediate role of echolocating whales in the demise of shelled cephalopods is not apparent; their long, delicate snouts with numerous teeth likely were ill-suited for handling large shelled nautilids. A possible exception are short-snouted Simocetidae and Agorophiidae in the Oligocene of the North American Atlantic and Pacific coasts, which appeared in this area at the same time as the nautilids disappeared.

Keywords: *Nautilus*, living fossil, pinnipeds, odontocetes, predation





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Exploring the evolutionary history and taphonomic processes in parasite-host interactions – A case study of cidaroid echinoid spine galls

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Ecosystem restructuring in response to the modern biodiversity crisis is expected to change the landscape of parasite-host interactions, and understanding the ecological, taphonomic, and evolutionary processes acting on these interactions in the recent fossil record is of critical importance to inform mitigation efforts. Echinoid-targeting eulimid gastropod parasites exhibit a wide range of parasitic behaviors in modern marine environments and have likely parasitized echinoids from early in their evolutionary history (Warén, 1983). Domicile gall-forming parasitism by eulimids on cidaroid echinoid spines is relatively uncommon behavior, exhibited by some species of the eulimid genera *Sabinella* and *Trochostilifer*, targeting specific species of the cidaroid echinoid genera *Eucidaris*, *Prionocidaris*, and *Stylocidaris*. Cidaroid spines from these genera are common in Neogene and Quaternary fossil assemblages occurring near their living descendant populations, as is the case for tropical to subtropical populations of *Eucidaris tribuloides* in the western Atlantic and *E. thourasii* and *E. galapagensis* in the eastern Pacific (Queiroz et al. 2017). Anthropogenic habitat disturbance of eulimid-targeting crabs predators has likely increased the prevalence of galling parasitism in some of these impacted echinoid populations (Budria and Candolin, 2013). Herein we present a survey of Recent and fossil *Eucidaris* spines from these populations, to explore the evolutionary history of this association and the taphonomic processes effecting the preservation of spine galls. Despite observations that galling and encrustation are common in Recent populations, no galls nor extensive encrustation is observed in the fossil spines. No gall-forming eulimids have yet been reported from these fossil assemblages either, raising the possibility that this association is recently evolved or recently spread to these regions. However, microtomography of the galls reveals that, though skeletonized, the stereom of the gall material is altered and of lower density when compared to the healthy portion of the spine, and tumbling experiments suggest galled spines are more prone to breakage. Considering this, we propose that there is likely extensive fossil record bias in preserving evidence of this biotic interaction, thus necessitating other methods for estimating parasitism intensity in recent fossil populations.

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Keywords: Parasites, sea urchin, taphonomy





First bee-pollen interaction (Hymenoptera: Apoidea) in the Paleocene (Konservat- Lagerstätte Menat, France)

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Bees (or Antophila) evolved from ancient predatory wasps (Apoidea) that lived 120 million years ago. Their closest relatives are pemphredonine wasps that are first collected from 100- million-year old outcrops, including French Vendean amber (Bennett *et al.*, 2014). Before the Middle Eocene, Antophila are very rare in the fossil record. Apart from the controversial Cretaceous Melittosphecidae and Discoscapiidae (Poinar & Danforth, 2006; Poinar, 2009, 2020), the earliest fossil bee is Turonian in age, and belongs to the Apidae Meliponinae (Michener & Grimaldi, 1988). Apidae are also recorded from the Paleocene of Menat and the lowermost Eocene Oise amber (France) (Michez *et al.*, 2007, 2009). The sister taxon to Apidae is Megachilidae (Hedtke *et al.*, 2013). The oldest known megachilid *Probombus hirsutus* is also from the Paleocene of Menat (Nel and Petrulevicius, 2003). We have recently collected fossil leaves with rounded excisions probably made by a Megachilidae and of a cut rounded fragment of leaf that probably accidentally fell on the paleolake water surface of Menat. Wedmann *et al.* (2009) indirectly confirmed from an excision in a leaf the presence of megachilid leaf-cutter bees from the Middle Eocene of Messel.

Here we describe three new Megachilidae from the Paleocene *Konservat-Lagerstätte* of Menat, which witnesses a lacustrine spongo-diatomite deposit (Wedmann *et al.*, 2018). Wing venation pattern indicates that the fossils are very closely related to *Probombus hirsutus*. Importantly, pollen grains either dispersed or in a cluster were observed on the hind legs of a specimen and the abdominal brushes of another. The pollen grains were examined under the SEM, clearly showing that they belong to at least three different species of eudicotyledon angiosperms, of which one was overwhelmingly represented. Our findings add novel occurrences of Megachilidae, and indicate that these Antophila foraged for pollen grains with a marked preference for one type. Further analyses will allow identifying the precise flowers that *Probombus* megachilide bees visited. Searching fossil pollen grains closely associated to bees is of great interest to determine whether these insects already had marked preferences for some flowers, and will add data to solve the problem of co-evolution of bees with flowers.

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Is the diversity of freshwater fish increasing over deep time? The Thai case study

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Since Sepkoski's seminal works in the 1970s, it has become clear that global biodiversity has followed a general increase over the past 500 million years. Although the reading of the dynamics of diversity over time is affected by the vagaries of the fossil record, analyzes using bias correction have shown that distinct diversity patterns characterize different paleoenvironments (Benton, 1997). In particular, the biodiversity of continental organisms has increased in an asymptotic trend while marine organisms have followed a succession of logistic trends, with the possibility to reach a plateau. Ray-finned fish (Actinopterygii) make up about half of the diversity of vertebrates and have approximately half of their diversity in the marine environment and half in freshwaters. Indeed, the analysis of phylogenetic diversity has indicated that over the last 150 million years, freshwater families increase asymptotically while for marine families, a logistic curve corresponds better to the observed dynamic trend (Guinot & Cavin, 2015).

The freshwater fish fauna from Thailand is remarkable for two reasons. Firstly, the diversity of this fauna from the Oriental region is very high (Kottelat & Whitten, 1996, Brosse et al, 2013) and secondly, the fossil record of freshwater fish from this country is unique for the tropical latitude, showing one window in the Miocene period and another one in the Jurassic - Early Cretaceous period. From the modern freshwater fish database of Thailand, there are about 800 native species and about 38 primary freshwater families. Among these fish fauna, families Cyprinidae, Nannostomidae, Danionidae, Bagridae, Gobiidae and Siluridae are relatively more dominant than other families (Froese & Pauly, 2022). Rate of endemism is about 2 % (Froese & Pauly, 2022). However, there might be a higher number of endemic species because Thailand has unique aquatic habitats and peat swamps (Vidthayanon et al., 1997, Vidthayanon, 2002).

Continental Cenozoic fossils in Thailand are known from a series of intermontane basins distributed all over the country, usually formed of an alternation of fluvial and lacustrine sediments ranging in age from Eocene to Miocene. The Miocene assemblages comprises families still present in Thailand: Amblycetoidea, Danionidae, Cyprinidae (*Hypsibarbus*, *Mystacoleucus* and *Bangana*), Bagridae (*Hemibagrus* and *Pseudobagrus*) and Pangasiidae. Several other Eocene, Oligocene and Miocene localities have yielded isolated elements referred to Cypriniformes, Siluriformes and more rarely Percomorpha (e.g., Channidae).

In the Middle Jurassic-Early Cretaceous time interval, about 15 localities with reasonably identifiable freshwater fish remains are known (Cavin et al., 2009; Deesri et al., 2017). During this time interval, a few taxa of freshwater fish are known, almost all belonging to holosteans (Holostei). They are referred to extinct lineages that share general morphology and putative ecology with extant representatives from other clades: *Isanichthys* had an elongated body with posteriorly inserted dorsal and anal fins like *Scleropages*, *Khoratichthys*, *Thaichthys*, and deep-bodied *Lanxangichthys* exhibit a variety of body morphology, fin insertions, and dentition that make them comparable to the highly diverse extant Cypriniformes of Thailand; the halecomorphs, with several representatives from the Lower Cretaceous sinamiids, recall the morphology of the channids; and isolated pycnodont dentitions indicate the





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presence of durophagous fish, ecologically comparable to mollusc-eating shark catfish (Pangasiidae) in modern Thai ecosystems.

The fossil record is very incomplete and suffers from many preservation and methodological biases. However, some very general trends can be identified. The Miocene assemblages are very close to the modern assemblage at the family and even generic level. This assemblage sheds light on the establishment of the modern assemblage in connection with the evolution of the river network of this period. The Paleogene freshwater fish record is very poor, but already shows modern elements, at least at the ordinal level. The Late Jurassic-Early Cretaceous is composed of completely different taxa from the modern fauna, but the eco-morphological categories discovered correspond to the modern categories. It should be noted that the taxa diversity of this time interval at the family level seems to have a much wider biogeographical distribution since most relatives of these Mesozoic taxa are found in East Asia, but also in western Gondwana (Africa and South America) and in Europe. We suggest that the wide geographic distribution of these clades reflects a global diversity of freshwater fishes that was much lower than the existing diversity, perhaps an order of magnitude about 10 times lower, as indicated by the curve of global phylogenetic diversity.

If this hypothesis is confirmed, its consequence is that the diversity of freshwater fishes in the world, and in Thailand in particular, has never been as high as during the Holocene since the Late Jurassic at least, which means that the current human-caused fish extinction affects an assemblage of fish that took 150 million years to form.

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Keywords: freshwater fish, diversity, Thailand



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Molluscan Assemblages of Pliocene Sedimentary Units in La Union Province, Philippines (Ilocos-Central Luzon Basin)

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Several interbedded mudstone-sandstone units containing fossil-bearing layers were encountered during a recent fieldwork in La Union Province, Philippines (northern Ilocos-Central Luzon Basin). Calcareous nannofossil analysis indicates that the units belong to the Late Pliocene Cataguintingan Formation, which was deposited in an upper shelf to intertidal depositional environment (Lorentz, 1984). A total of 280 specimens were taken from five collecting sites in two outcrops which consists of several contrasting assemblages. The pelecypod and gastropod-dominated assemblage consists of articulated Venus clams (*Callista*), scallops (*Pecten/Chlamys*), and small gastropod shells mainly from the genera *Nassarius* and *Tonna*. This assemblage transitions to the stratigraphically higher gastropod-dominated assemblage consisting of larger specimens of *Conus*, *Dolomena*, *Murex*, and *Oliva*. A different assemblage was observed in a separate outcrop consisting mostly of large, fragile bivalves (*Placuna/Ostrea*) with minor amounts of small gastropod shells of *Terebra*. The mollusc assemblages, supplemented with grain size and foraminifera data, are interpreted to possibly represent two separate paleocommunities deposited in a low-energy near-shore environment. Differences in the environmental conditions resulted to the changes and differences in the mollusc assemblages.

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Keywords: Philippines, Pliocene, molluscs, paleoenvironment





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Late Neogene-Quaternary continental ecosystems in Asia-Pacific

Sumatra – its role in mammal and hominin dispersal in the Pleistocene

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The geographical location of Sumatra relative to the rest of Southeast Asia puts it at the centre of dynamic interchanges between the Indochinese and Sundaic subregions, particularly during glacial periods when it connected Peninsula Malaysia, Java, and the now submerged Sunda Shelf. On the other hand, its geological and topographic characteristics, especially the uplift and subsequent environmental impacts of the Barisan Mountain chain, have meant much of the Sumatran landmass may have been buffered from dramatic Pleistocene changes in vegetation. These vegetation changes have been recorded for much of Southeast Asia during the Pleistocene, but little similar evidence of widespread grassland or savanna environments have been recorded for Sumatra. Here, I examine these conflicting geographical and geological forces in the context of large-range mammal and hominin Pleistocene dispersals in Southeast Asia. I provide an overview of what is known about the mammalian fossil record of Sumatra, its environmental context, and implications for faunal interchange between Indochina and Sunda. The dearth of early hominin fossils in this region will also be discussed, and whether this likely reflects a true absence of remains, or perhaps rather the result of geological and taphonomic factors unique for the region.

Keywords: megafauna, *Homo erectus*, rainforest, savanna, Southeast Asia, Quaternary





Further Quaternary *Pongo*-bearing fossil sites from karstic caves in Peninsular Malaysia

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Fossils of orangutan (*Pongo* sp.), composed of isolated teeth, were first reported from Peninsular Malaysia in 2013 (Yasamin et al., 2013). These fossil sites were chronologically dated to be Middle and Late Pleistocene (Yasamin et al., 2013). Metric variation of the fossil teeth from Peninsular Malaysia is comparable to other contemporary fossil assemblages in Asia (Lim, 2016). Many more new fossil sites with *Pongo* fossils were recovered in recent years through concerted efforts between higher learning and research institutions and local citizen science organizations. Fossils recovered were exclusively isolated teeth (incisors, canines, premolars, and molars) from the maxillary and mandibular permanent dentitions. All were found either embedded in secondary cave deposits within karstic caves or from loose sediments on cave floors. No deciduous teeth have been found, and only few specimens with preserved roots or root remnants. These new discoveries have established the occurrence of fossil *Pongo* in areas hitherto unreported, including Kinta Valley (Ros et al., 2020) and Merapoh (Ros et al., 2019) in north central Peninsular Malaysia. There are now a total of 19 sites in Peninsular Malaysia with *Pongo*-bearing fossil assemblages: Swamp Cave, Villa Cave, Gatal Cave, Cistern Cave, Bukit Takun rock shelter, Layang Rusa Cave, Layang Mawas Cave, Tabal Cave, Badak C Cave, Gate Cave, Toh Sembilan Cave, Karang Besar A Cave, Karang Besar B Cave, Gunung Masoorat, Paradise Valley Cave, *Stegodon* Cave, Crab Cave, Square Tooth Cave, and Snake Cave. The associated faunas include mammal species characteristic of the Sundaic biogeographic region. Preliminary results from the geological dating of some of the new sites suggested the persistence of *Pongo* in Peninsular Malaysia in Late Pleistocene time, and possibly well into the Holocene.

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Keywords: Pleistocene, Holocene, non-human Hominoid, Orangutan, Malaysia, Sundaic limestone caves.





***Stegodon* and other proboscidean remains from Peninsular Malaysia**

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Dental remains of Proboscidea, mostly Elephantidae, had only occasionally been reported in the past from tin mining operations and general surveys of mineral resources in Peninsular Malaysia (Lim, 2013). The first discovery of a *Stegodon* fossil in Malaysia (Muhammad et al., 2020) had, however, initiated a more intensive exploration which led to the discovery of more proboscidean tooth remains in recent years. There are now on record a total of 19 specimens from both maxillary and mandibular dentitions, including one *Stegodon* fossil (a maxillary premolar) and 18 elephantid tooth remains (complete cheek teeth or section of isolated dental plates). The *Stegodon* fossil was embedded in consolidated cave breccia while other fossils were discovered either loose or embedded in semi-consolidated or unconsolidated clastic cave sediment on cave floors and walls. The unworn crown of the *Stegodon* specimen suggests it came from a very young individual. High resolution U-Th dating (Shen et al., 2012) on the carbonate in the breccia containing the *Stegodon* fossil yields an age of 31,000 years, while other proboscidean remains from other sites are estimated to range from Quaternary to sub-recent in age. These latter specimens all show the typical dental features of Elephantidae – high crown, narrow space between plates, and complex enamel plication. Using various digital imagery techniques, the current study attempts to refine the taxonomic identity and biological age of the recently discovered proboscidean specimens. The research work has helped in the documentation of scientifically important Quaternary paleontological heritage sites across Peninsular Malaysia which are worth protecting for future generations. With a focus on Peninsular Malaysia, our team aims to understand the paleo-diversity, past ecological function, and paleobiogeography of Quaternary Proboscidean fauna, in hopes of generating baseline data for future in-depth research into the potential ecological niche of prehistoric Proboscideans and their dynamic relations with paleo-environment and paleo-climate of Peninsular Malaysia.

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Keywords: *Stegodon*, Quaternary Proboscidea, Elephantidae, cave paleontology, Peninsular Malaysia, fossil teeth





Preservation of an articulated *Panthera* fossil in cave infill – Naga Mas Cave, Perak, West Malaysia

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A large almost complete vertebrate skeleton (*Panthera tigris* or *Panthera pardus*) has been discovered on an upper wall of a small 9-m high Middle Pleistocene cave chamber in Gua Naga Mas, Perak, West Malaysia. This cave is situated 30m above ground level in Silurian-Lower Permian limestone. Most Quaternary fossils and subfossils found in caves in Peninsular Malaysia have been preserved in soft sediment, semi-consolidated or hard breccia in the form of isolated teeth and fragmented bones. The representation of the whole skeleton suggests the cave acted as a natural trap that was later subjected to continuous deposition of filling followed by post-depositional processes. Red cave infill coats most of the walls of this chamber – it has been partially removed by erosion, and in places, has been removed completely exposing white limestone walls. White stalactites have developed on the red infill. Most of the infill is massive in appearance, although in places layers of clean and transparent speleothem carbonate are present inside the infill. The well-preserved skeleton is embedded in the red cave infill, with parts of it becoming exposed due to erosion. Bone marrow cavities have been filled by coarse-grained, clear sparry calcite, which has been used for U-Th age determination and gives the age of 320,300 years (Muhammad et al., 2019). Petrographic examination of the cave infill surrounding the fossil revealed micritic calcite, with veins of sparry calcite. Detrital nodules containing iron oxides/hydroxides of about 2 mm in diameter, as well as bioclasts cemented with sparry calcite, are seen in samples about 80cm away from the fossil. SEM-EDS analysis of the infill shows the presence of Ca, Al, Si, Fe, P and Mg. Preliminary examination of X-Ray diffractograms show the presence of guano-derived phosphate minerals such as ardealite and taranakite, suggesting that the cave or cave system was a site of guano deposition. Decomposing guano can release organic acids (McAdams et al., 2021), though, in a cave environment, pH will be buffered by the presence of carbonates and bicarbonate ions, and dissolved phosphate species, as well as decreasing Eh. The presence of dissolved phosphate ions and a lowering of Eh would retard the dissolution of bone, helping to preserve fossils.

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Keywords: Middle Pleistocene *Panthera*, fossil preservation, cave infill geochemistry



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Late Neogene-Quaternary continental ecosystems in Asia-Pacific

Beachcombing in Borneo: the first major fossil vertebrate fauna from Sarawak (Malaysia)

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In the coastal region of Sarawak in the proximity of the Rajang River delta, the sea often washes up numerous vertebrate fossils. The teeth and bones have altered colours from black and grey to light brown, and are mixed up with shells of modern invertebrates. We collected a diverse fossil vertebrate fauna dominated by bony fish skeletal elements, with the foremost presence of ariids (sea catfish), and by numerous shark and ray teeth (e.g., *Galeocerdo*, *Glyphis*, and myliobatids). Reptiles are less common and include turtle shell fragments, few crocodile teeth, and some snake vertebrae. Some aquatic mammal fossils, such as a dugong rib bone, and cetacean intervertebral discs and periotic (ear) bones were found, while frequent terrestrial mammals complete this mixed marine and nonmarine fauna. These consist of suids (e.g., *Sus* cf. *barbatus* and *Sus scrofa*), cervids (e.g., *Rusa unicorn*), indeterminate rodents, tapirs, and cercopithecoid primates (e.g., macaque). Our preliminary identification indicates that most of the discovered fossils belong to living taxa, which is consistent with high Sr-isotope ratios obtained from the marine remains hinting at a Late Pleistocene–Holocene age. In the hinterland area, there is no in-situ source deposit known so far that supplies such fossils. Most of the terrestrial remains might have been reworked from terrace deposits and/or transported by sediments from the delta plain through the Rajang River. However, during glacial maxima, Borneo was connected to mainland Southeast Asia (i.e., Sundaland, the last 400kyr ago; Husson et al., 2020) and other large rivers reached the South China Sea in the nearby area from the west and southwest passing through lowland areas (Voris, 2000). Vertebrate remains may have been transported by these rivers. During higher sea-level stands, these lowland areas were flooded, and the vertebrate remains could have been reworked and further mixed. Therefore, the age range of the fossils could be wide and older fossils from previous glacial-interglacial cycles may be present in our sample collection.

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Keywords: Pleistocene, Holocene, Borneo, Sarawak, Sundaland, vertebrates, palaeoenvironment



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Mortality profiles of Late Pleistocene-Holocene orangutan (*Pongo*) assemblages from Niah Cave sites (Sarawak, Malaysian Borneo) and its conservation implications

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The excavated archaeological profiles at Niah Great Cave, ranging in age from the Late Pleistocene to Metal Age (*circa* 45,000 to 500 years before present), have yielded the longest record of prehistoric human activities known in Borneo (Barker & Farr, 2016). Excavations at different entrances of the cave since the 1950s have produced remains from about 143 different kinds of non-fish vertebrates (Piper & Lim, 2021). Orangutan (*Pongo*) cranio-dental remains, which represent discards from prehistoric hunting activities, feature prominently among the rich and diverse faunal bone assemblages from Niah. Excavated sites in Niah that contain cranio-dental remains of prehistoric orangutan include Gan Kira (n=16), Lobang Angus (n=17), and West Mouth (n=91). Their remains occur throughout the excavated archaeological profiles, and were among the mammal species most often hunted and consumed by the early modern humans (*Homo sapiens*) who frequented the cave entrances (Barker et al., 2007). In the present study, site- and cultural phase-specific age- and sex-mortality profiles of the dental remains of orangutan were determined. Distribution patterns of mortality profiles show that non-adult and female individuals account for the great majority of specimens within each assemblage, irrespective of sites or cultural phases from which they were recovered. These results indicate that certain age and sex cohorts were selectively targeted by prehistoric hunters from the area. Prolonged hunting pressures targeted at young and breeding female individuals since at least the Late Pleistocene may have partially caused the demise of local populations from the Niah area. The mortality profiles of hunted orangutans from prehistoric Niah and findings from the current investigation on prehistoric hunting strategies and their potential impacts on local populations of orangutan provide strong empirical support from the zooarchaeological evidence that, firstly, active anti-poaching programs and, secondly, where possible and most needed, reintroductions of healthy young individuals into suitable remaining wild places should be the focus in any conservation planning for the remaining populations in Borneo.

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Keywords: Late Quaternary, Sundaland forests, Prehistoric hunting, Zooarchaeological records, Megafaunal extinction, Conservation policy.





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Late Neogene-Quaternary continental ecosystems in Asia-Pacific

Diversity of Quaternary vertebrates represented by fossils/subfossils in the central plain of Thailand (Chao Phraya River beds).

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At least 60 taxa of large vertebrate fossils and subfossils have been deposited in the Chao Phraya River beds in the central plain of Thailand. Most of the specimens were obtained from the muddy river bed by diving to 5-20 m depth, and some were excavated on land, and from mainly soft marine clay and fluvial deposits, the so-called Bangkok Clay Formation. At least 39 mammalian taxa were recovered as well as four birds, eleven reptiles, and nine fishes. Six recent mammalian orders included five primates including modern human *Homo sapiens*, seven carnivorans with domestic cat and dog, fifteen artiodactyls, (with three domestic and two fossil taxa), perissodactyls (Javan rhino *Rhinoceros sondaicus*), three proboscideans (with two fossil taxa) and three cetaceans (Irrawaddi dolphin *Orcaella brevirostris*, Sittang and fin whale *Balaenoptera edeni*, *B physalus*). Four birds including larger waterbirds; pelican, crane, stork? and a jungle fowl. The most common reptiles are the snail-eater terrapin *Malayemys macrocephala* and Siamese crocodile *Crocodylus siamensis*. The most common fishes are the giant perch *Lates calcarifer* and snakehead *Channa striata*. The smallest-sized aquatic vertebrate is the fish *Cephalocassis* sp. and the largest is the fin whale. The most commonly found mammals are Schomburg's deer *Rucervus schomburgki* and hog deer *Hyalaphus porcinus annamiticus*. The four fossil mammals were hippopotamus *Hippopotamus* cf. *sivalensis*, flat-horned buffalo *Bubalus* cf. *platyceros*, Narmada elephant *Elephas namadicus* and stegodont *Stegodon* cf. *insignis*. The species indicate the palaeoenvironment was a riverine floodplain with lowland forests, of Pleistocene-Holocene age, with some prehistoric-historic artifacts of wild animal utilization including shot-marks, cut marks and some bony tools of Schomburg's deer, fishes, turtles and crocodiles. Eight domestic mammals were found including, dog *Canis familiaris*, cat *Felis catus*, pig *Sus domesticus*, cattle *Bos indicus* and *Bubalus bubalis*, sheep *Ovis aries*, horse *Equus caballus*.

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Keywords: Quaternary, Bangkok Clay, Riverbed deposit, vertebrates





A new taxon of Stegodontidae in the sand pit of Chaloem Phra Kiat District, Nakhon Ratchasima Province, Thailand

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We report new specimens of a stegodontid species (Proboscidea, Mammalia) that was found in the Miocene deposits distributed in the Phra Phut sandpit in the Chaloem Phra Kiat District of Nakhon Ratchasima, Thailand. The examined material includes an almost complete mandible with molars. Compared with *Stegodon* mandibles, the mandible has a longer and more slender body, with an alveolar process that is slightly higher angled and deflected, downward to the symphyseal region, and a greater distance between anterior and posterior mental foramina. The symphysis is elongated. The tip of the symphysis is concave, and there is a trace of the lower tusk. The third lower molar is a brachyodont heptalophodon with a very small talonid. The pretrite posterior central conules are present only on the first lophid. The interlophids are clearly separated by deep gaps filling cement at the base and cement is somewhat thick in the distal lophids. There are three or four mammillae on lophids. The mesoconelets in the four mammillae are slightly smaller than the principal cones. The worn surface clearly shows sloping distal facets (facet D) at both pretrite and posttrite main cusps, as well as mesoconelets. This character is present in only the most primitive taxa such as *Stegolophodon nasaiensis*. More derived characters such as a step-like structure are present on the enamel loop. A fine scalloped-shape occurs in the outer enamel figure on the moderately-worn surface, but such folding patterns disappear in the inner enamel. Stegodontid species belonging to two genera, *Stegolophodon* and *Stegodon*, had developed dental morphologies through time. The specimen examined is positioned at an intermediate form between the primitive and derived stages in the evolutionary process of Stegodontidae. Although intraspecific/interspecific variation in all species of stegodontids are still debated, our new findings provide significant evidence for clarifying the phylogenetic position of the Miocene stegodontid species from Thailand.

Keywords: Stegodontidae, *Stegodon*, *Stegolophodon*, Phra Phut sandpit





Miocene carnivorans from Southeast Asia improve our understanding of the paleobiogeography of Asian fossil mammals

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Palaeobiogeographical evolution of Miocene carnivoran faunas from Southeast Asia is poorly known although carnivoran mammals constitute an essential component of past and modern continental ecosystems. Over the past few decades, fieldwork carried out almost annually by Franco-Thai and Franco-Burmese teams has made it possible to collect and describe hundreds of carnivoran specimens from several lacustrine and fluvial channel deposits of the middle and late Miocene in the north of Thailand (Chiang Muan, Mae Moh and Khorat Basins) and in the central basin of Myanmar (Irrawaddy Formation of Chaungtha; Chavasseau et al., 2006). Overall, we have reported a dozen species of amphicyonids (small and large extinct “bear dogs”), mustelids (mostly otters), viverrids (civets and genet), felids, herpestid (mongoose) and percrocutid (extinct hyaena-like carnivore), including the oldest mongoose in Asia, the oldest representative of Asian palm civets, and one of the largest bone-cracking hyaena-like predators (Grohé et al., 2010, 2013, 2020; Bonis et al. 2021). The middle Miocene carnivoran assemblage of Mae Moh (14.2-12.2 Ma) is particularly noteworthy as it constitutes one of the richest assemblages for this age in East Asia and by far the richest for the Neogene of Southeast Asia.

While the presence of mainly new species in the Mae Moh and Khorat basins indicates some degree of endemism in the Thai province during the middle and late Miocene, the Chiang Muan otter and the Chaungtha civet have a broader geographical distribution extending to the Siwalik Hills during the middle-late Miocene, thus supporting the hypothesis that Southeast Asia and northern Pakistan and India were part of the same biogeographical province. Furthermore, by conducting palaeobiogeographic cluster analyses of middle and late Miocene carnivoran faunas of Asia (from Pakistan to Japan and from China to Indonesia), we suggest that a southern Asian biogeographic province, analogous to the current Oriental Realm, has existed since at least the middle Miocene (Grohé et al., 2020). These results reinforce the observation that the Himalayan Mountains and Tibetan Plateau have been significant physical barriers and an important climatic barrier (through enhanced monsoon systems) preventing north-south dispersals of mammals in Asia since at least the middle Miocene.

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Keywords: middle and late Miocene, Carnivora, Thailand, Myanmar, endemism, Oriental province





Origins and distribution changes of orangutans in Southeast Asia

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Orangutans are represented by three living species, *Pongo pygmaeus*, *P. abelii*, and *P. tapanuliensis* in Borneo and Sumatra. They display a drastically reduced geographic distribution contrasting with their wide distribution over Southeast Asia and South China (extending north of 30° latitude) during the Pleistocene. About 2 million years (Ma), orangutans lived in sympatry with *Gigantopithecus*, sharing the same food resources in the northern part of their distribution range. Their size evolved in opposite directions, becoming larger for *Gigantopithecus* and smaller for *Pongo*, so as to reduce ecological niche overlap. *Gigantopithecus* is known from the early to middle Pleistocene, whereas orangutans survived longer, in relictual forest patches and today in its present southern refuges. The causes of their local extinctions remain unknown. *Gigantopithecus* is recognized as a pongid, however the precise nature of its phylogenetic relationships with orangutans also remains unknown. Large fossil apes were present during the late Miocene in South and Southeast Asia, *Lufengpithecus* in South China, *Sivapithecus* and *Indopithecus* in Indo-Pakistan and *Khoratpithecus* in Thailand and Myanmar. *Lufengpithecus* displays more affinities with stem hominids, but other taxa are allocated to pongids. Among them, *Khoratpithecus* shares most synapomorphies with orangutans and clearly represents its closest sister group. Its subnasal anatomy, jaw symphysis structure, the lack of scars of anterior digastric muscles and its dental characters support this close relationship, excluding *Sivapithecus* from that position. A gap in the fossil record, occurring all over Southeast Asia between 6 and 2 Ma, corresponds to a period during which several lineages of South Asian apes, namely *Indopithecus* (*Gigantopithecus* ancestors) and *Khoratpithecus*, developed adaptations to hard food. In conclusion, Southeast Asia play an important role as the area of origins of orangutans.

Keywords: Orangutan, *Pongo*, *Gigantopithecus*, *Khoratpithecus*, pongid, Miocene, Pleistocene, evolution, Thailand



Session 19 - ORAL

Late Neogene-Quaternary continental ecosystems in Asia-Pacific



Evolutionary ecology of Miocene hominoid primates in Southeast Asia

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Southeast Asia is a key area for hominoid radiation and diversification in the Miocene. Today, there is only one genus of extant pongines (*Pongo*), which has a very restricted geographic distribution indicative of specific ecological needs. From the Miocene to the Pleistocene however, we see many different pongine species and genera, including an area spanning from India to southern China. We applied ecological niche modelling using Bayesian statistics with the R package SiBER of carbon and oxygen stable isotopic data to investigate if the diverse fossil pongines also display a wider array of ecological niche preferences, or if there is ecological continuity within this clade from the Miocene until today. The focus of our study is *Khoratpithecus ayeyarwadyensis*, which is considered to be a sister clade to extant orang-utans, and its associated mammal fauna from the Irrawaddy Formation (~9 Ma) in Myanmar. We compared it to other fossil pongines, like the contemporaneous *Sivapithecus* from the Siwaliks of India and Pakistan and its associated mammal fauna, and extant orang-utans. We found that *Khoratpithecus*, *Sivapithecus* as well as Pleistocene and extant *Pongo* likely were frugivorous apes living in the canopies of a forested habitat. Nevertheless, our data also show differences in habitats and their use by the Miocene pongines in comparison to younger pongines, and between the contemporaneous *Sivapithecus* and *Khoratpithecus* mammal communities.

Keywords: stable isotope analysis, ecological niche modelling, niche partitioning, ecological continuity, fossil pongines



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Late Neogene-Quaternary continental ecosystems in Asia-Pacific

Vertebrate fauna, flora and stable isotope-based palaeoecology of the Late Miocene ape locality of Tapar, Kutch, (Gujarat, India)

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The Late Miocene ape (*Sivapithecus*) locality of Tapar, Kutch, (Gujarat, India) has been recently biostratigraphically dated to ~10 Ma. This locality has yielded a diverse fossil assemblage that includes both large and small mammals (primates, insectivores, rodents, rhinocerotids, proboscideans, giraffids, anthracotheres, suids, tragulids, equuids and paleomerycid). The herpetofauna includes remains of frogs, lizards, snakes, crocodiles and turtles. The aquatic community is composed mainly of teleost fishes, sharks and rays, beside algae represented by charophytes. The bulk stable $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of large mammals from the Late Miocene of Kutch indicate the presence of a predominantly C_3 browser community living in a highly seasonal environment. Among the proboscideans, *Zygodontomys* and *Deinotherium* consumed primarily C_3 plants, however, they may have had some C_4 plants in their diet. *Deinotherium* browsed both in the woodland and forest, while *Gomphotherium*, on the other hand, browsed mostly in the woodland with somewhat more grass in its diet. The tragulid *Dorcatherium* and the suids *Tetraodon* and *Listriodon* browsed in a rather denser and wetter part of the forest. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of equid *Hipparion* indicates that it mostly browsed in drier areas, as the giraffids. The rhino *Brachypotherium* and the anthracothere *Merycopotamus* were predominantly C_3 feeders and lived close to the rivers/water bodies and so did the early paleomerycid. The small mammal fauna is very interesting with a diverse rodent assemblage. The rodents such as murines (e.g., *Progonomys*) fed mostly on C_3 plants (based on $\delta^{13}\text{C}$ values) and insects and lived in the forest, while the gerbils *Myocricetodon* and *Dakkamys* and maybe the gundi (*Sayimys*), lived under drier conditions as their extant counter parts live mostly in deserts. In contrast the bamboo rats (*Kaniamys* and *Prokaniamys*) prefer humid conditions and softer terrains to dig their burrows. The chipmunk *Tamias* can thrive in both wet and dry conditions. The small primates and tree shrews (yet to be classified) would have lived in a dense forest. The terrestrial community also included frogs (*Rana* sp.), snakes (colubrids and alethinophids), and lizards (agamids and skinks) suggesting the presence of warm and humid conditions. The aquatic community comprised the freshwater fishes cyprinids, chelonians, freshwater crocodiles, and algae. The presence of sharks *Carcharinus* sp., rays *Myliobatis* sp. and *Pristis* sp. suggests the presence of brackish water conditions very close to the site. The overall picture of the site that emerges from this assemblage and the preliminary isotope data suggest existence of a subtropical seasonal forest situated close to the ocean.

Keywords: Palaeoecology, Late Miocene, Kutch, India, Mammals, Isotopes

Session 21 - KEYNOTE

The evolution of forest ecosystems: dead trees and the stories they tell

Ancient rainforests from Panama

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Panama Isthmus offers a unique opportunity to observe patterns of speciation, extinction, and diversity. One of the regions of Panama with paleobotanical richness is the Azuero Peninsula, where we can find abundant colorful silicified woods, well preserved permineralized seeds, and a few localities with leaf impressions. Most of the areas with an abundance of woods have been mapped as Oligocene to Miocene (30 -23 Ma) as part of the Santiago Formation. However, these localities still lack geological mapping updates and biostratigraphic support data. Jud and Dunham (2017) reported 10 new morphotypes identified from wood samples collected in Ocu town and related to families Anacardiaceae/Burseraceae, Arecaceae, Euphorbiaceae, Humiriaceae, Lauraceae, Leguminosae, Moraceae and Sapotaceae, and the orders Ericales and Sapindales. We have conducted two additional Cenozoic wood projects from 2017 to 2022 with three main aims: 1) Updating the geological map through the addition of new geochronological, biostratigraphical and palynological data; 2) Reconstructing the paleofloristic composition of two geological epochs from Azuero (Eocene and Oligocene-Miocene); and 3) Analyzing anatomical data of new fossil morphotypes to approach paleoclimatic inferences. From 2018 to 2021, we conducted six field trips to over 100 localities for observation and sampling, including the collection of Eocene wood samples for the first time. Based on observations in the field, the Oligocene-Miocene woods of Azuero are from the Santiago Formation. We also obtained geochronological data from five localities with an average age of 25- 23 Ma, which was supported by palynological data. We discovered two large Anacardiaceae specimens. One of them is a ~20 m long trunk identified as a new fossil genus, *Llanodelacruzoxylon*; another is a new fossil species of *Anacardium* (Rodríguez-Reyes et al., 2021). We have also reported a new Malvaceae fossil genus (*Veraguasoxylon*) and a new species of *Prioria*, a genus previously identified from the Panama Canal paleoflora. Other discoveries include Araliaceae, Burseraceae, Euphorbiaceae, Moraceae, and diverse Arecaceae and Leguminosae. Preliminary results from samples of Eocene woods show the occurrence of families such as Leguminosae, Moraceae and Arecaceae. Based on taxonomic identities and anatomical traits, we interpret the fossils woods of Azuero as evidence of a rainforest environment in Panama during the Oligocene-Miocene. With this project, we contribute to the knowledge of the early rainforests of Panama and their geological and paleobiological scenarios.

Jud, N., Dunham, J. 2017. Fossil woods from the Cenozoic of Panama (Azuero Peninsula) reveal an ancient neotropical rainforest. IAWA Journal 38(3). DOI:10.1163/22941932-20170176

Rodríguez-Reyes, O., Estrada-Ruiz, E., Monje Dussán, C., de Andrade Brito, L., Terrazas, T. A new Oligocene-Miocene tree from Panama and historical *Anacardium* migration patterns. PLoS ONE 16(6): e0250721.

<https://doi.org/10.1371/journal.pone.0250721>

Keywords: Isthmus, Azuero, Oligocene-Miocene, Eocene, fossil wood

Session 21 - ORAL

The evolution of forest ecosystems: dead trees and the stories they tell

Mesozoic fossil wood diversity variations and paleoclimate perturbations: recent advances from China

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As an important component of plant remains, fossil wood plays a significant role in understanding the floral composition and evolution of plants in the geological past. Additionally, fossil wood is also one of the significant proxies for terrestrial palaeoclimate and palaeogeographical reconstruction in earth history. Diversified fossil wood has been documented from the Mesozoic deposits in China after a long time of investigations. During the past few years, many new fossil wood materials were reported from a variety of horizons in some fossil localities, ranging from Triassic to the Cretaceous, providing significant references for reconstructing the Mesozoic palaeoclimate by using these wood fossil proxies. We summarize the recent advances in Mesozoic fossil wood in China. Particularly, the new discoveries of fossil wood from the Upper Triassic in southern China, the Jurassic Yanliao Biota and the Early Cretaceous Jehol Biota and their paleoclimatic significance are reviewed. The future research directions of Mesozoic fossil wood in China are discussed.

Keywords: Fossil wood; diversity; palaeoclimate; Mesozoic; China





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The evolution of forest ecosystems: dead trees and the stories they tell

Pinaceae in the Cenozoic of Thailand: changing environments and climates

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At present, Pinaceae in Thailand is represented by only 2 species of *Pinus*, *Pinus kesiya* and *P. latteri* (sometimes included with *P. merkusii*), both in the subgenus *Pinus*. However, the fossil record indicates that the family was more diverse during the Cenozoic. Late Oligocene or early Miocene deposits in Nong Ya Plong Basin, Phetchaburi Province, Central Thailand, have yielded a 5-needled pine, *P. nongyaplongensis*, in the Subgenus *Strobos*, and likely Subsection *Strobos*, based on twigs. Two seed cones were found in the same basin, *Pinus* sp. 1 and *P.* sp. 2, each consisting of a single seed cone with dorsal umbos, a feature present in both subgenera *Pinus* and *Strobos*, except Subsection *Strobos*, which has terminal umbos. Neither of these cones are therefore considered to be conspecific with *P. nongyaplongensis*. A shoot of *P.* cf. *krempfii*, from the late Oligocene or early Miocene Mae Lamao Basin, Tak Province, Northern Thailand, appears to have affinity with the extant *P. krempfii*, endemic to Central Vietnam. A single seed wing of *Pinus* was found in Ban Pa Kha Subbasin, Li Basin, Lamphun Province, Northern Thailand. Plant macrofossils of Pinaceae, including *P. nongyaplongensis* and *P.* cf. *krempfii*, as well as pollen with affinity to *Pinus*, *Picea*, and *Tsuga*, indicate that Pinaceae was more diverse and that the climate was cooler, possibly subtropical, than at present during the late Oligocene and early Miocene. The climate is thought to have increased in warmth by the middle Miocene, becoming tropical, with several *Pinus* species and plants related to *Picea* and *Tsuga* becoming extinct or migrating to cooler areas to the north or east.

Keywords: Pinaceae, *Pinus nongyaplongensis*, *Pinus* cf. *krempfii*, Phetchaburi, Tak, Thailand





Session 21 - ORAL

The evolution of forest ecosystems: dead trees and the stories they tell

Developing a new perspective on the Late Oligocene to Late Miocene (Chattian-Tortonian) in the British Isles: A 20-million-year record of vegetation and climate change

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During the Cenozoic, the British Isles formed a peninsula on the northwestern edge of Europe, uniquely placed to record climatic and environmental change under the influence of North Atlantic Ocean currents. By compiling results from new palynological, geochemical and palaeobotanical studies on Chattian-Tortonian-dated deposits with previously published data, we show changes in palaeoenvironment and palaeoclimate on the edge of northwest Europe. Frost-free wetland palaeoenvironments were present during the Chattian in Lough Neagh, Stanley Bank and Bovey Basin. Recent age revisions of the solution pipe complex of ?Langhian-age Trwyn y Parc, Wales, imply Middle Miocene conditions were subtropical, and likely influenced by a proto-Gulf Stream. The Brassington Formation was used to reconstruct Serravallian-Tortonian palaeoenvironments and a revision of the palynology from the Serravallian-age Kenslow Top Pit reconstructs a warm-temperature mixed mesophytic forest biome with local wetlands. This was likely caused by the Atlantic Meridional Oceanic Circulations. Tortonian palaeoenvironments were characterized by warm-temperate mixed forests, implying an evolving cooling, and drying prior to the Late Miocene Cooling event. We are the first to present the evolution of the flora of the British Isles during this interval of Cenozoic climate change, and to provide an oceanic perspective regarding Eurasian palaeoclimates and palaeoenvironments. We provide new palaeontological perspectives on the Chattian-Tortonian palaeoclimates on the northwest edge of Europe with the combined application of nearest living relative-based approaches and Bayesian probability density functions.





Session 21 - ORAL

The evolution of forest ecosystems: dead trees and the stories they tell

Middle Miocene (Serravallian) wetland development in Central England

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The Miocene was identified as an interval of interest in the recent IPCC AR6 report as a geological analogue for middle-late 21st century anthropogenic climate change. The Brassington Formation, Derbyshire, is the most extensively studied of three onshore UK sites that contains a Miocene-age fossil flora. Previous palynostratigraphy has identified that the Kenslow Member is diachronous in age. Of the outcrops that still exist, the Kenslow Top Pit outcrops are dated to the Tortonian, whilst the Bees Nest outcrop is dated to the Serravallian. The Serravallian is an interesting interval to investigate terrestrial environments of northwest Europe - against a background of global temperature declines and increased aridity, the regional climate of northwest Europe remained warm and humid, likely caused by the Atlantic Meridional Oceanic Circulations. Despite this regional significance, the Serravallian Kenslow Member has only ever been studied using plant palynology from grab samples. Here we present the first continuous sequence of palynology through the Serravallian Kenslow Member at Bees Nest Pit. Reconstruction of two identified pollen zones showed a mixed mesophytic forest with an evolving wetland palaeoenvironment. Through high-resolution sampling, it has been possible to explore the changing wetland ecology. We propose a fallen tree influenced the depositional environment and created a forest hollow, which allowed for limited lignite preservation. Co-existence approach-based palaeoclimate reconstructions produced ranges of Mean Annual Temperature (15.7-18.4 °C) and Mean Annual Precipitation (1096-1372 mm) with no variations across the stratigraphy outside of uncertainty ranges, inferring a relatively short depositional period. Overall, the sequence shows the impact of a flat latitudinal temperature gradient in the North Atlantic during this time interval.

Keywords: Lignite, climate change, Miocene, palynology, vegetation, UK





Session 21 - POSTER

The evolution of forest ecosystems: dead trees and the stories they tell

Eocene to Oligocene vegetation and climate in the Tasmanian Gateway region were controlled by changes in ocean currents and $p\text{CO}_2$

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The Eocene-Oligocene Transition (EOT; 34.44-33.65 Ma) is regarded as a key interval in the Cenozoic climate history, marked by a shift from the Earth's greenhouse to icehouse climate state. While the EOT in the southern high-latitude is mostly marked by an abrupt sea surface temperature drop ~ 3 °C, the extent and effect on terrestrial climate and vegetation remains unresolved. Here, we present a new, well-dated, high-resolution late Eocene to early Oligocene palynological record and quantitative sporomorph-based climate estimates from the Tasmanian Gateway region (ODP Site 1172 and 1168) to reconstruct climate and vegetation dynamics. Our results show: (i) transition from a warm-temperate *Nothofagus*-Podocarpaceae dominated forest with paratropical elements to a cool-temperate one rapidly expanding and taking over regions previously occupied by warmer taxa after 37.30 Ma (ii) fluctuation between warm temperate and cool temperate climate phase from 35.50-34.49 Ma, coinciding with the initial deepening of the Tasmanian Gateway and throughflow of warm water associated with the proto-Leeuwin current (PLC) (iii) a cool climate decline phase (~ 2 °C) across the EOT (34.30-33.82 Ma) linked to declining $p\text{CO}_2$ and (iv) post-EOT (earliest Oligocene) recovery characterised by a warm-temperate forest association from 33.55–33.06 Ma and which might be linked to transient recovery of atmospheric $p\text{CO}_2$ and/or sustained throughflow of the PLC. To further test/identify the main driver(s) for the post-EOT climate recovery, we compared our sporomorph assemblages and sporomorph-based climate estimates from Site 1172 to 1168. The climate transitional events across the studied interval in the Tasmanian region suggest that changes in ocean circulation due to accelerated deepening of the Tasmanian Gateway may not have been solely responsible for the changes in terrestrial climate and vegetation, but series of regional and global events, including changes in stratification of water masses, and $p\text{CO}_2$ may have played vital roles.

Keywords: Cenozoic, Southern Ocean, Climate Change, Palynology





Session 21 - POSTER

The evolution of forest ecosystems: dead trees and the stories they tell

Earliest fossil record of the genus *Tetradium* (Rutaceae) in Asia: implications for its evolution and palaeoecology

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A new species, *Tetradium nanningense* sp. nov. (Rutaceae), is described on the basis of well-preserved mummified wood from the upper Oligocene Yongning Formation of Nanning Basin, Guangxi Province, South China. This species represents the most ancient fossil evidence of the genus *Tetradium* in Asia, the region of its modern distribution. Its occurrence in the late Oligocene is consistent with the diversification age of the modern Asian species within this genus as estimated by molecular dating: *T. nanningense* could be closely related to an ancestor of extant *Tetradium* species. The fossil record of *Tetradium* suggests that this genus migrated from North America to eastern Asia in the Oligocene. The presence of (semi-)ring-porous wood and helical thickenings on vessel walls in *T. nanningense* provides new evidence for the independent gains of these traits in the course of evolution among different plant groups from eastern and south-eastern Asia in the Oligocene. These wood features might have arisen in response to the increase in climate seasonality following the abrupt climate cooling across the Eocene–Oligocene boundary.

Key words: *Tetradium*, mummified fossil wood, late Oligocene, South China, evolution, palaeoecology





Session 21 - POSTER

The evolution of forest ecosystems: dead trees and the stories they tell

Climate and human influences on the flora of Cyprus – 5000 years BP to present

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The island of Cyprus has a remarkably long archaeological record that shows farming has been present since around 10,500 years before present (BP). Before this, hunter-gatherers (by at least 13,000 BP) and game stocking peoples (11,000 BP) were both exploiting the island. This has resulted in the island's flora (and fauna) being modified for almost all of the Holocene. Cyprus sits in the eastern Mediterranean within the semi-arid climate belt and, due to diverse topography, has a flora of nearly 2000 species. Within this flora 8.5% of species are endemic, whereas 13% have been introduced prehistorically and historically. Cyprus, along with much of the eastern Mediterranean, is remarkably vulnerable to climate changes. Variations in seasonal and annual rainfall can have significant implications for the island.

Here we present two multiproxy records covering the last 5000 years from the Akrotiri Marsh in southern Cyprus to explore the role of people and climate in shaping the flora of Cyprus. Pollen and diatom analysis of radiocarbon dated marsh sediments reveal expansion and contraction of the marsh in response to mid-late Holocene climate events. The record provides important contextual climate data to the debate surrounding the so called Early and Late Bronze Age Societal Collapse Events present in numerous archaeological archives throughout the Mediterranean and Near Eastern Region. We also document, for the first time in Cyprus, the introduction of *Juglans regia* (walnut) and propose it was brought to the island by the Romans. Previously, the introduction of walnut was considered to be in the last 500 years, we push this date back to nearly 2000 BP. Our findings show that, following the conventions of the Flora of Cyprus, *Juglans regia* should be reclassified from naturalised non-native (introduced in last 500 years) to indigenous.

Keywords: Cyprus, Holocene, introduced species, Climate Change, Roman, Bronze Age, arboriculture





Session 22 - KEYNOTE

The origin and rise of a land flora: from Laurentia to Gondwana and back again

On the fossil origins of plant development

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Within the paleobotanical community, the origin of land plants is approached largely through a phylogenetic lens - we see the fossil record primarily as a means to date the branch nodes on character-based or molecular phylogenetic trees. On the other hand, from the perspective of modern botany, the origin of land plants is now seen in terms of genomic assembly: prior algal genes, co-opted and re-purposed for development, were combined with *de novo* genes, unique to the embryophytes, to create the developmental genome of the land plants. If we view the origin of land plants through this evo-devo lens, the fossil record itself acts to guide the sequence of serial evolutionary acquisitions of plant development. This is effectively a role-reversal for the fossil record – instead of hanging fossils onto a prior phylogeny, we now use the fossil record to establish the timing and order in which the developmental genes of land plants evolved.

Drawing on the century-old antithetic hypothesis of Bower, it is clear that spores and the underlying processes of sporogenesis preceded the origin of vegetative development and this is the most obvious starting point in the fossil record of plant origins. We are not “missing” land plants in Cambrian and Ordovician strata because they were never there in the first place. This spore record begins stratigraphically in the Series 2, Stage 4 in China (Wang *et al.*, 2022) and is documented from the Wuliuan (Strother, 2016) to the Jiangshanian (Taylor & Strother, 2009) in Laurentia. Cambrian cryptospores are different from later forms, but they share a number of characters that separate them from the acritarchs, and we hypothesize that they are the reproductive propagules of aeroterrestrial charophyte algae that were adapting to subaerial environments. The earliest accounts of cryptospores in the Ordovician are from the Tremadocian of Australia, indicating an early dispersal of plant ancestors to Gondwana. By Darriwilian time, it appears that cryptospores have migrated to Baltica (Rubinstein & Vajda, 2019), although most of the diversity of cryptospores during the Middle Ordovician is documented from Gondwana. By the Hirnantian the record of cryptospores based on isomorphic tetrads and dyads seems to have expanded globally as diverse assemblages are known from Avalonia, Laurentia, Gondwana, and elsewhere, setting the stage for the recovery of plant-like tissues in the Llandovery of Avalonia and Laurasia. Organic-walled (banded) tubes and cuticle-like sheets were previously relegated to the fungi, but this designation is based on a phylogenetic mode of thinking. When re-examined in an evo-devo context, early Silurian “phytodebris” can be viewed as belonging to an evolving proto-embryophytic complex. The middle Silurian begins the long-standing fossil record of the earliest axial plants, which is reinforced by a shift in the palynoflorules in both Avalonia and Laurentia from cryptospore-dominated to trilete spore dominated assemblages. By the Devonian, the story of the origin of land plants is over, and evolutionary studies of fossil plants now shift to diversification and systematics of the tracheophytes and their downstream ecological effects on the terrestrial biosphere and the planetary carbon cycle.

Rubinstein CV, Vajda V. 2019. Baltica cradle of early land plants? Oldest record of trilete spores and diverse cryptospore assemblages; evidence from Ordovician successions of Sweden. *GFF* 141: 1–10.

Strother PK. 2016. Systematics and evolutionary significance of some new cryptospores from the Cambrian of eastern Tennessee, USA. *Review of Palaeobotany and Palynology* 227: 28–41.





Session 22 - KEYNOTE

The origin and rise of a land flora: from Laurentia to Gondwana and back again

Taylor WA, Strother PK. 2009. Ultrastructure, morphology, and topology of Cambrian palynomorphs from the Lone Rock Formation, Wisconsin, USA. *Review of Palaeobotany and Palynology* 153: 296–309.

Wang K, Xu H-H, Yin L-M. 2022. A palynological assemblage from the Cambrian (Series 2, Stage 4) of Shandong Province, China, and its implications to the transition from algae to land plants. *Review of Palaeobotany and Palynology* 301: 104645.

Keywords: plant evolution, palynology, paleopalynology, cryptospore evolution, terrestrialization





Session 22 - ORAL

The origin and rise of a land flora: from Laurentia to Gondwana and back again

Assembling the early record of land plant life using cryptospores and other resistant fragmentary remains

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The earliest colonizers of the land surface in the lower Paleozoic undoubtedly produced very few resistant biomolecules that could survive fossilization. The most noteworthy exception to this is the biopolymer sporopollenin. Sporopollenin and related molecules occur in a variety of extant organisms, including algae currently considered most closely related to land plants. Thus, the fossil record of reproductive bodies (e.g., cryptospores) from the lower Paleozoic in non-marine sediments represents the most complete record of aquatic organisms that were moving to a terrestrial environment. Thorough analysis of this record, including scanning and transmission electron microscopy (SEM and TEM), is part of an emerging picture of this key event in earth history. Spore walls in earliest cryptospores begin with an “algal-like” wall in the Cambrian consisting of only laminae. These earliest cryptospores occur singly, and in organized clusters and complexes. By the Middle Ordovician, the appearance of thicker, homogeneous walls reflects the evolution of a new type of sporopollenin deposition that today is only seen in plants that produce a sporangium. This sporangium may have been borne on a thallus with no axis, the supporting cells for such an axis having appeared later in geologic history. This presentation will review this scenario, consider the primitive status of the dyad in land plant spore evolution, and discuss walls of increasing complexity as they come to resemble those in extant land plants. Future integration of developmental studies in extant plants may shed more light on the actual events, viz. the plant thallus (i.e., the sporophyte), that occurred in the lower Paleozoic, and may provide insights on various “enigmatic” assemblages of fossils, including isolated tubes, and larger tubular masses (e.g., nematophytes).





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The origin and rise of a land flora: from Laurentia to Gondwana and back again

Ordovician cryptospores from Australia – a summary

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Ordovician cryptospores have only been recovered from sediments from the Canning Basin, Western Australia. The basin comprises a predominantly Paleozoic sequence; sedimentation commenced in the Early Ordovician (Tremadocian ~ 480 Ma) with a transgressive event into a vast graben, surrounded by ancient Precambrian uplifts: the topography of the pre-Ordovician landscape created a series of environments from open shallow sea, intertidal, subtidal, and lowlands, and with evidence of riverine input of reworked Precambrian sediments, and land plant spores. Lower and Middle Ordovician marine faunas of trilobites, shelly fossils, and conodonts provide good controls for age dating, with CA-IDTIMS numeric dating of interbedded ash layers. Above the Middle Ordovician, marine influences wane, with carbonates through to red-beds and evaporites. During the Tremadocian, the Canning Basin was within ~ 5 to 10° S of the paleo-equator (Cocks & Torsvik 2021).

The first record of cryptospores from the Canning was from a core sample of the Mallow Salt. Only two taxa, *Tetrahedraletes medinensis* and ?*Rugaletes* sp. cf. *R. vietus*, were identified, but provided the first age estimate for the unit, Late Ordovician-early Silurian (Foster & Williams 1991). Middle Ordovician cryptospores were recovered from a core sample of the Goldwyer Formation, the assemblage is taxonomically restricted, and includes thick-walled, enveloped-tetrads, and planar sets of spores suggesting affinities with *Tetraplanarisporites* (Spaak et al. 2017).

The most recent discovery (Strother & Foster 2021), of charophyte-derived cryptospores co-occurring with embryophytic hilate monads, dyads, and obligate spore tetrads in late Tremadocian (Early Ordovician ~ 480 Ma) core samples from the Nambheet Formation raises questions about both the timing and location of the colonisation of land plants into the terrestrial realm. Their occurrence is at least 10 Myr older than assemblages reported from Dapingian sediments of Argentina, and ~15 Myr older than geographically widespread, occurrences of cryptospores from the Middle Ordovician. The Australian record helps close a gap between molecular time trees that suggest embryophytes originated around 515 Ma and the first records of plant megafossils in the mid Silurian, around 70 Ma later. Further, the co-occurrence of irregularly-shaped packets of cryptospores, originally described from Cambrian deposits in Laurentia, is both evidence of charophyte algal adaption to semi-terrestrial settings, and their ancestral links with an evolving embryophyte lineage as ancestral algal and *de novo* genes were incorporated into the developmental program that defines the embryophytes today. Thus, the origin of land plants was probably not a singular event in geologic time. Did it occur independently in different geographic localities, or was plant migration responsible for global spread of the initial land flora? The Australian record of cryptospores with unambiguous embryophytic affinity demonstrates establishment of a land flora within Gondwana by Early Ordovician time. This paper summaries Australian discoveries, highlights the importance of the Nambheet assemblages, and speculates on possible causes and mechanisms for early plant migration.

Cocks, LRM & Torsvik, TH, 2021. Ordovician palaeogeography and climate change, *Gondwana Research*, **100**, 53-72
<https://doi.org/10.1016/j.gr.2020.09.008>.

Foster CB, & Williams GE (1991) Late Ordovician-early Silurian age for the Mallow salt of the Carribuddy Group, Canning Basin, Western Australia, based on occurrences of *Tetrahedraletes medinensis* Strother & Traverse 1979, *Australian Journal of Earth Sciences*, **38**, 223-228, DOI: 10.1080/08120099108727966





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Spaak, G, Edwards DS, Foster CB, Pagès A, Summons RE, et al. (2017). 'Environmental conditions and microbial community structure during the Great Ordovician Biodiversification Event; a multi-disciplinary study from the Canning Basin, Western Australia', *Global and Planetary Change*, **159**, 93–112, doi:10.1016/j.gloplacha.2017.10.010

Strother, PK & Foster, C, (2021). 'A fossil record of land plant origins from charophyte algae', *Science*, **373**, no. 6556, 792–796, doi:10.1126/science.abj2927

Keywords: Australia, Canning Basin, Early Ordovician, land plant spores, land plant origins



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The origin and rise of a land flora: from Laurentia to Gondwana and back again

Paleozoic Palynostratigraphy of the Arabian Plate: an example of successful collaboration between industry and academia

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The contribution of palynology has been fundamental to development of a high-resolution stratigraphic framework for the Paleozoic rocks of the Arabian Plate, particularly in Saudi Arabia. Since the '60s, early palynologists working in the oil industry had demonstrated the occurrence of exceptionally abundant and well-preserved palynomorph assemblages, which could be used for characterizing stratigraphic units in the subsurface and establishing stratigraphic correlation with surface equivalents at a regional and global scale. In the following decades, and especially during the '80s and '90s, the growing need for detailed understanding of the Paleozoic subsurface stratigraphy of Saudi Arabia provided a major impetus for further development and refinement of palynological biozonations. Under this stimulus, a long-term, joint palynostratigraphic project between Saudi Aramco and academic researchers of the Commission Internationale de Microflore du Paléozoïque (CIMP) was established. The ambitious aim of this project was to document in detail the Paleozoic palynostratigraphy of Saudi Arabia to provide an improved understating of the Paleozoic sediments and their geological and paleogeographical relationships to successions in neighboring countries and adjacent plates. This example of long-term collaboration between academic and industry partners has been highly beneficial and resulted in a palynological zonation of the Cambrian to Permian strata consisting of 43 palynozones based on the stratigraphic distribution of about 200 palynomorph taxa (spores, pollen, acritarchs and chitinozoans). These palynological analyses have included the formal description and documentation of new important palynological taxa. Some of these key taxa demonstrate a worldwide distribution and allow calibration of the zonation with type sections of Global Stages. In other instances, co-occurrence of macro- or meso-fossils (e.g., graptolites, trace fossils, plants) permit even more accurate correlation with the standard Global Chronostratigraphy. This joint project has led to important scientific discoveries such as among the world's oldest embryophytic spores, giving insights on early land plant evolution. The key results of Saudi Aramco-CIMP joint studies have been presented in numerous international meetings since 1992 to the present day, and have been published in the form of scientific papers in a series of five special publications. The success of this project, and others of similar scope, highlights the mutual benefits and advantages that result from the collaboration between industry and academic partners.

Keywords: Paleozoic, palynology, Arabian Plate, biozonation



Session 22 - ORAL

The origin and rise of a land flora: from Laurentia to Gondwana and back again

Palaeophytogeography of Early Devonian plants as evidenced by integrated analysis of plant megafossils and dispersed spores

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Early Devonian plant megafossil assemblages are relatively uncommon although palaeogeographically dispersed. Their analysis indicates broad patterns of palaeophytogeographic distribution including the identification of areas with a high degree of provincialism. On the other hand, Early Devonian dispersed spore assemblages are both more numerous and with much better palaeogeographical coverage. Combined analysis of the two fossil records enables a more nuanced approach to understanding patterns of palaeophytogeographical distribution among early land plants. It suggests that during the Lochkovian: (i) the floras of Euramerica (e.g. Gaspé, Anglo-Welsh Basin, Ardenne-Rhenish region) and Gondwana (e.g. North Africa and Arabia) are distinctly different; (ii) within Euramerica floras from the equator (e.g. Spitsbergen, South China) differ from those of higher latitude (e.g. Gaspé, Anglo-Welsh Basin, Ardenne-Rhenish region) in that they are much less diverse. Through the Pragian and Emsian these differences seem to diminish as lycopsids and ‘trimerophytes’ begin to dominate most floras. This trend is confirmed in the Middle and Upper Devonian. However, it is clear that the plant megafossil record is severely biased and under-represents the flora of these times, as numerous distinctive forms of dispersed spore are unaccounted for in the *in situ* spore record. In this presentation we will describe new information from the Lower Devonian sequences of Saudi Arabia, Northern Spain and Spitsbergen that are throwing new light on some of these issues.

Keywords: Devonian, palaeophytogeography, floras, spores





Session 22 - ORAL

The origin and rise of a land flora: from Laurentia to Gondwana and back again

The presence and importance of *Quadrisporites* in the Tawil Formation, Lochkovian, Saudi Arabia

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The Tawil Formation was penetrated by two wells drilled on the Arabian Peninsula. The depositional environments of the formation range from shallow marine to braided-stream fluvial. The sampled intervals fall within a fining-upward succession that is probably a transgressive systems tract (TST) representing backfilling of an estuarine incised valley.

Palynological samples were studied by Steemans et al. (2007) who reported a rich and diversified assemblage of miospores composed of trilete spores and cryptospores. Despite the absence of characteristic spores of the MN Biozone (Streel et al., 1987), a probable early Lochkovian age was attributed. The trilete spores display a strong affinity with coeval Gondwana assemblages, whereas the cryptospores are similar to assemblages that occur globally, such as in the Lorne locality of Scotland (Wellman & Richardson, 1996) from Laurussia. The palaeogeographic distribution of these two groups of miospores probably reflects the palaeoecology of their mother plants: trilete spores are produced by plants controlled by climatic and geographic barriers, whereas cryptospores are less affected by climate variations.

Among the palynological assemblage numerous *Quadrisporites* are observed. These palynomorphs are considered to be freshwater algae. Being non-marine palynomorphs they are also included by some authors in the cryptospore group. They are frequently reported from Gondwana, but are extremely rare beyond this continent. Therefore, they clearly show a different distribution pattern than other cryptospores. Some of them have an operculate opening. This morphological structure is not observed among the miospores, except for some unusual spores from the Carboniferous, such as *Vestispora*. Including algae and embryophyte spores in a same entity, the cryptospores, is problematic as it leads to confusion regarding their evolution through time and space.

Steemans, P., Wellman, C. H. & Filatoff, J. (2007). Palaeophytogeographical and palaeoecological implications of a miospore assemblage of earliest Devonian (Lochkovian) age from Saudi Arabia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 250(1-4), 237-254.

Streel, M., Higgs, K., Loboziak, S., Riegel, W. & Steemans, P. (1987). Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenne-Rhenish regions. *Review of Palaeobotany and Palynology*, 50(3), 211-229.

Wellman, C. H. & Richardson, J. B. (1996). Sporomorph assemblages from the Lower Old Red Sandstone of Lorne, Scotland. *Special Papers in Palaeontology*, 55, 41-102.

Keywords: Devonian, Saudi Arabia, Palaeoecology, freshwater algae





***Lithiotis*-type bivalves in the light of Phanerozoic bivalves gigantism events and their palaeoenvironmental preferences**

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Gigantism of bivalves occurred at least 5 times in the Phanerozoic: (i) Silurian-Devonian megalodonts, (ii) Permian alatoconchids, (iii) Late Triassic–Early Jurassic megalodonts/lithiotids, (iv) Late Jurassic–Cretaceous rudists/inoceramids and (v) Miocene-modern tridacnids, and lived mostly in warm periods of tropical shallow-marine environments of low-latitude (e.g., Isozaki & Aljinović, 2009). The most characteristic for the Early Jurassic (Pliensbachian–Early Toarcian) *Lithiotis*-type bivalves – *Lithiotis* and *Cochlearites* were typical infaunal mud-sticker forms (Seilacher, 1984) and presumably occupied restricted marine/lagoon-type areas (e.g., Debeljak & Buser, 1997). They usually constructed pseudo-coloniality buildups and are interpreted as photosymbiotic (Fraser et al., 2004) or chemosymbiotic bivalves (Isozaki & Aljinović, 2009). The other forms of this group: *Lithioperna*, *Mytiloperna*, and *Gervilleioperna* were semi-infaunal forms lived probably in restricted lagoonal palaeoenvironments with fluctuating salinity. In Africa (Morocco), Europe (Italy, Slovenia, Croatia, Albania, Greece) and Asia (Oman, Nepal) the *Lithiotis*-type bivalves-bearing beds are intercalated by shallow-marine oolitic and/or oncolitic limestones. For comparison, the Middle Permian giant alatoconchid bivalves also occurred in the palaeotropical realm and constructed carbonate buildups within subtidal lagoon settings of rimmed platforms (Udchachon et al., 2014). Sedimentological/ecological facts indicate that Phanerozoic giant bivalves events correlate with climatic, eustatic and oxygen content fluctuations.

Debeljak, I., Buser, S. 1997. Lithiotid bivalves in Slovenia and their mode of life. *Geologija* 40, 11-64.

Fraser, N.M., Bottjer, D.J., Fischer, A.G. 2004. Dissecting “Lithiotis” bivalves: implications for the Early Jurassic reef eclipse. *Palaios* 19, 51-67.

Isozaki, Y., Aljinović, D. 2009. End-Guadalupian extinction of the Permian gigantic bivalve Alatoconchidae: end of gigantism in tropical seas by cooling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 284, 11-21.

Seilacher, A. 1984. Constructional morphology of bivalves: evolutionary pathways in primary versus secondary soft-bottom dwellers. *Palaeontology* 27, 207-237.

Udchachon, M. Burrett, C., Thassanapak, H., Chonglakmani, C., Campbell, H., Feng, Q. 2014. Depositional setting and palaeoenvironment of an alatoconchid-bearing Middle Permian carbonate ramp sequence in the Indochina Terrane. *Journal of Asian Earth Sciences* 87, 37-55.

Keywords: giant bivalves, Phanerozoic, palaeoenvironments, Africa, Europe, Asia





Palaeobiogeography and palaeoecology of Middle and Upper Permian conodonts, Batain area, Oman

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The Middle to Upper Permian Qarari unit of the Batain area, located in eastern Oman, is part of WNW directed nappes that were emplaced around the Cretaceous-Paleogene boundary. In the Qarari Block, this unit is dominated by medium-bedded rhythmites (spiculitic and radiolarian hemipelagic dark lime mudstone) that accumulated outboard of a productive shelf, interspersed with rare echinoderm-bryozoan turbiditic grainstones and shelf edge-derived reef debris. The unit recorded deep-water sedimentation well below the photic zone, indicating that all recovered conodonts were pelagic during life. Two levels of white quartzitic sandstone in the Asselah area are associated with tectonic slices of the Qarari Limestone. Conodont biostratigraphy suggests that the lower sandstone unit may be associated with the Guadalupian-Lopingian Boundary (GLB) sea-level lowstand, but it remains uncertain whether the units are genetically related or superimposed by tectonics. Deposition occurred within a Neotethys Seaway, which was actively opening as recognized by the migrating Cimmerian terranes that separate this body of water from the Paleotethys Ocean to the north. Provincialism and restricted gene flow has long hampered biostratigraphic correlation across the Tethys. Middle Permian conodont biostratigraphy (Henderson, 2018) involves short-duration zones related to populations of *Jinogondolella* within the Equatorial Warm-Water Province (EWWP; Mei & Henderson, 2001) and longer-duration zones related to populations of *Mesogondolella* in cooler water provinces to the north and south. The succession of EWWP zones is nearly identical between South China and the Delaware Basin of West Texas, which were separated by the Panthalassic Ocean. The Neotethys was dominated by *Mesogondolella*, but sporadic occurrences of *Jinogondolella* may relate to a migration filter across the Cimmerian terranes. Upper Permian conodont biostratigraphy involves short-duration zones of *Clarkina* in the EWWP and longer duration zones of *Mesogondolella* in cooler waters. *Clarkina* has been postulated to have evolved during the GLB from either a *Mesogondolella* or *Jinogondolella* ancestor, but apparatus reconstruction would favour the latter. *Clarkina* populations vary morphologically across the region with differences noted among South China, Iran and Oman. It is possible that some degree of hybridization is occurring within these competing populations. A distinctive early Wuchiapingian conodont fauna occurs immediately above the lower sandstone at Asselah including *Clarkina* cf. *hongshuiensis*, *C.* cf. *dukouensis* and a few specimens of *Iranognathus movshovitchi*; an identical fauna was recovered from near the base of the Qarari Block section. A mid-Wuchiapingian fauna, including *C.* cf. *asymmetrica*, *C.* cf. *transcaucasica* and *C.* cf. *liangshanensis*, occurs within the limestone above the upper sandstone. The uppermost sample of this limestone includes three specimens of late Changhsingian *Clarkina* cf. *yini*. This mixture may be associated with microkarsting as a major sequence boundary separates this unit from an overlying transgressive succession. This latest Permian transgressive succession includes *C.* cf. *zhangii*, *C.* cf. *yini* and one specimen of *Mesogondolella sheni*.

Henderson, C. M. 2018. Permian Conodont Biostratigraphy. In Lucas, S. G. & Shen, S. Z. (eds) The Permian Timescale. Geological Society, London, Special Publications, 450(1), 119-142.

Mei, S., Henderson, C. M. 2001. Evolution of Permian conodont provincialism and its significance in global correlation and paleoclimate implication. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 170, 237-260.

Keywords: Upper Permian, conodonts, Neotethys Sea, Paleotethys Ocean, palaeobiogeography, biostratigraphy





Session 23 - ORAL

Palaeobiogeography of the Western and Eastern Tethys - migration routes (IGCP 710)

The Oman-Madagascar seaway source of the unsuspected Permian-Early Triassic palaeontological richness of the Batain (SE Oman)

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Located in eastern Oman, south of the town of Sur, the Batain Plain extends about 40km west-east and 130km northeast-southwest and is bounded to the south by the Indian Ocean. Due to the relatively scattered outcrops of the different lithologies and apparently chaotic structural situation, they were previously interpreted as "Batain Melange" with the same sedimentary succession as recorded in the N Oman Hawasina basin transported to the SW from the Neotethys. After a detailed geological mapping Peters et al. (2001), structural data, indicate a WNW directed nappe emplacement, in contrast to the south to south-west thrusting direction of the Hawasina nappes of the Oman Mountains. As strong lithological differences appear comparing to the Hawasina succession, these authors defined a Batain Group, and described four new formations, all coming from an Oman-Madagascar seaway, a boundary between Western and Eastern Tethys. Following the geological mapping, sedimentological and palaeontological research revealed an unsuspected palaeontological richness of some level of the Permian Qarari limestone. Some lower, marly light part cropping out in the central Bu Fashiqah area is very rich in pyritic ammonoids of Wordian age comprising at least fifteen genera. NE outcrops in the Wadi Khawr al Jaramah (S of Ras al Haad) are fossiliferous rich beds contain brachiopods, crinoids, blastoids, corals, trilobites, bryozoans, ammonoids, nautiloids and fusulinids. The foraminifera have been studied by Leven and Hewward (2013) showing older fusulinid assemblage than those found in the N Oman. Fortey and Heward (2014) studied and illustrated extremely well-preserved trilobite fauna, with five new species including one new genus and new brachiopods are studied by Viaretti et al. (work in progress). Until now, in the sedimentary succession of the Batain area, the Induan time was considered as a sedimentary gap (Hauser et al., 2001). Our finding of more than forty reworked boulders of lower Triassic to basal Anisan coquina and buildup limestone brought new views on the Paleozoic to Mesozoic evolution of this peculiar area and on Early Triassic recovery. Fossil richness of these Lower Triassic boulders with accumulation of ammonoids, bivalves and brachiopods is unexpected and all of these new occurrences display well-oxygenated depositional environments. Basal Triassic crinoidal meadows are described by Brosse et al. (2018) from an Asselah boulder, showing abundant holocrinids, gastropods, bivalves and five ammonoid taxa, two of which are only known in East Siberia and NE Greenland. One of the largest boulders issued of a dismantled Lower Triassic seamount consists of a 30 m high Olenekian reefal succession, partially made of up to 9 m thick continuous metazoan (bivalves, brachiopods) accumulation (Leu et al., submitted). Another ultra-condensed limestone boulder 1.2 m thick, contains more than 60 superposed ammonoids divided into 16 ammonoid zones without gap between Late Induan to Early Olenekian time (Brühwiler et al., work in progress). This boulder concerns also exceptional basal-body preservation of earliest Olenekian conodont (Souquet and Goudemand, 2019).

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Session 23 - ORAL

Palaeobiogeography of the Western and Eastern Tethys - migration routes (IGCP 710)

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Souquet, L., Goudemand, N. 2019. Exceptional basal-body preservation in some Early Triassic conodont elements from Oman. *Palaeogeography, Palaeoclimatology, Palaeoecology* 549, 109066.

Keywords: S Tethys seaway, Permian, Lower Triassic reef, ammonoids accumulation, bioherme, biostrome



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Palaeobiogeography of the Western and Eastern Tethys - migration routes (IGCP 710)

Palaeobiogeography of the Late Jurassic crabs (Brachyura) in the Western/European and Eastern/Asian Peri-Tethyan and Tethyan facies

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The widespread and rapid Callovian transgression in the whole European Peri-Tethyan epicratonic sea caused the origin of the Oxfordian cyanobacterial-sponge megafacies belt from Portugal to Romania and then Kimmeridgian coral-bearing facies (e.g., S Germany). On the other hand, in the northernmost part of the Western Tethyan Carpathian basins the Tithonian-Berriasian coral reefs (so-called Štramberk/Ernstbrunn-reef-type limestones) flourished. In all these Late Jurassic facies crustaceans, including crabs, are common benthic representatives (e.g., Müller et al., 2000; Krobicki & Zatoń, 2008, 2016). The explosion of the Late Jurassic crustaceans during the Brachyuran Oxfordian Explosion Event (Krobicki & Zatoń, 2016) has been continued to Tithonian-Berriasian decapod-rich assemblages within European part of the Tethys Ocean. It resulted in the expansion of selected “European” taxa to the Late Jurassic environments of the Asian Eastern Tethys realm. Recently have been discovered new crab species in Japan (Karasawa & Kato, 2007; Kato et al., 2010) as the first fossil record of the Jurassic crabs from the circum-Pacific rim. They are mainly represented by species of *Goniodromites*, *Pithonoton* and *Planoprosopon* genera, which are popular in European brachyuran assemblages as well, but their first occurrence in Europe is older (Middle Jurassic: Bajocian-Callovian) than in Asia (Late Jurassic: Oxfordian-Tithonian). These data indicate that the European Peri-Tethyan and Tethyan crab assemblages migrated into Asian Tethyan circum-Pacific realm during Late Jurassic time (Kimmeridgian-Tithonian) (comp. Kato et al., 2010) but this migration route is still enigmatic by the lack of finding of this fauna in-between. Another problem is related to detail knowledge on palaeoenvironmental nature of host rocks of Japanese findings which are mainly clastics (sandstones, shales) (Karasawa & Kato, 2007; Kato et al., 2010) but in some cases unpublished data indicate that “shales” are in fact carbonates “closely associated with massive coralliferous reef limestones” (Schweigert & Koppka, 2011:232). The European fauna is connected with “reefs” and from palaeoenvironmental point of view it is important to exactly know what kind of rocks hosted Japanese specimens.

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Krobicki, M., Zatoń, M. 2008. Middle and Late Jurassic roots of brachyuran crabs: palaeoenvironmental distribution during their early evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 263, 30-43.

Krobicki, M., Zatoń, M. 2016. A new homolodromioid crab (Brachyura: Dromiacea: Tanidromitidae) from the Bajocian of central Poland and a review of the stratigraphical distribution and paleoenvironments of the known Middle Jurassic homolodromioids. *Journal of Crustacean Biology* 36, 695-715.

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Schweigert, G., Koppka, J. 2011. Decapods (Crustacea: Brachyura) from the Jurassic of Germany and Lithuania, with descriptions of new species of *Planoprosopon* and *Tanidromites*. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 260, 221-235.

Keywords: crabs, Western Tethys, Eastern Tethys, palaeoenvironments, palaeobiogeography



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Palaeobiogeography of the Western and Eastern Tethys - migration routes (IGCP 710)

Baumgartner, P. O., Xin Li, Matsuoka, A., Vérard, C. 2022 submitted. Austral and Subtropical Gyre Radiolaria - latest Jurassic-Early Cretaceous Leg 123, Site 765, Argo Abyssal Plain revisited – Southern hemisphere paleobiogeography and global implications. *Micropaleontology*.

Keywords: S-hemisphere Austral, Subtropical Gyre, Neotethyan radiolaria, Jurassic-Cretaceous transition





Session 23 - ORAL

Palaeobiogeography of the Western and Eastern Tethys - migration routes (IGCP 710)

A pre-Grande Coupure in the near East? Dating the demise of Balkanatolia, the Eocene insular mammalian biogeographic province at the crossroads of Europe, Asia, and Africa

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The Grande Coupure corresponds to a major episode of faunal turnover in western Europe around the Eocene-Oligocene boundary associated with the influx of multiple clades of Asian mammals. However, Asian mammal clades appear in southeastern Europe 5-10 million years prior to the Grande Coupure. How and when these clades colonized southeastern Europe remains poorly understood, partly because the Eocene fossil record of mammals from nearby Anatolia is characterized by marked endemism and limited exchanges with Asia. We resolve this paradox by documenting the oldest Asian perissodactyls found so far in Anatolia, which date to the lower or middle Priabonian on the basis of geochronological, magnetostratigraphic, and biostratigraphic data. We show that the Eocene distribution of mammals across Eurasia supports a previously unrecognized biogeographic province, designated here as Balkanatolia, spanning the Neotethyan margin from the Balkans to the Caucasus. The Eocene fossil record supports Balkanatolia having been colonized by Asian ungulates and rodents by the late Bartonian, following a drop in eustatic sea level and a tectonically-driven sea retreat in eastern Anatolia and the Lesser Caucasus. These palaeogeographic changes instigated the demise of Balkanatolia as a distinct biogeographic province and paved the way for the later Grande Coupure in western Europe.

Keywords: Eocene, Neotethys, Biogeography, Grande Coupure, Anatolia





Session 23 - ORAL

Palaeobiogeography of the Western and Eastern Tethys - migration routes (IGCP 710)

Fossils of Nepal Himalaya: An overview with some issues and challenges

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The field of palaeontology is less studied in Nepal Himalaya. Recorded fossil materials of the country are fragmentary and mostly scattered within different sources. In the present study, an attempt is made to provide comprehensive information on fossils of Nepal including the systematic description of all types of recorded fossils found in Nepal Himalaya. A very rich assemblage of invertebrate fossils has been identified from the Tethys, Lesser, and Sub-Himalayan zones of Nepal. It includes the remains of brachiopods, cephalopods, gastropods, bivalves, bryozoans, corals, trilobites, echinoderms, and graptolites. Similarly, vertebrate fossils recorded so far are known only from the limited, well-accessible areas of the country. In Nepal, vertebrate fossils have been recorded only from the Sub-Himalaya and the Lesser Himalayan zones. Only the footprints of tetrapod have been reported from the Permian sediments of Dolpo areas of the Tethys zone. The Paleozoic and Mesozoic successions of the Tethys zone have the records of a very rich assemblage of vertebrate fossils in India. However, there is lacking such studies from the similar type of Tethyan succession of Nepal. Some palaeontological research is carried out on mammalian fossils from middle and upper Siwalik successions of Pakistan. There is a possibility of finding these biozones in Nepalese regions too. The plant remains are still very poorly studied in Nepal. Stromatolites, Gondwana plants, and Cenozoic plant fossils of Siwalik and Quaternary deposits of intermountain valley sediments need detailed investigations. Recorded fossils have significant stratigraphic importance, but their detailed biostratigraphy treatment is lacking. The fossils recorded by foreigners have no original fossil remains in the native country and descriptions of these fossils are scattered in different sources. Recently, the authors of this abstract have prepared a book entitled "Fossils of Nepal" where all the available palaeontological research carried out in Nepal by both the national and international researchers are gathered and research gaps are highlighted. The presentation will highlight this available information and the focus will be given on the stratigraphic controversies faced by Nepalese geologists in the absence of such records. There is a vast room left for the systematic studies of fossils for the establishment of detailed biostratigraphy, palaeogeographical reconstruction, and palaeoclimatic interpretations from Nepal Himalaya.

Keywords: biostratigraphy, invertebrate and vertebrate fossils, Nepal Himalaya





Session 23 - POSTER

Palaeobiogeography of the Western and Eastern Tethys - migration routes (IGCP 710)

Palaeoecology of late Miocene rhinocerotids from the Balkan-Iranian province

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The late Miocene is a period of great climatic and ecosystemic changes. The south-eastern Mediterranean region is particularly affected, with increasing aridity and habitat openness. The impact of these changes on rhinocerotids' ecology has not been studied, although rhinoceroses were a conspicuous and diverse component of the Miocene mammalian assemblages. Through dental microwear texture analyses (DMTA; short-term diet proxy) and enamel hypoplasia (stress indicator), we investigated the palaeoecology of rhinocerotid specimens coming from 12 late Miocene localities (MN9 to MN13) throughout the Balkan-Iranian province. The microwear textures of the studied specimens revealed different dietary preferences for the two main rhinocerotid species – *Ceratotherium neumayri* (mixed-feeder including grasses) and *Dihoplus pikermiensis* (browser) – consistent with the hypothesized niche partitioning mentioned in the literature (Geraads and Spassov, 2009). However, the DMTA revealed a clear overlapping between *C. neumayri* and the co-occurring chilotere species at Maragheh (north-western Iran), Samos (Aegean region; Greece), and Pentalophos-1 (continental Greece) suggesting a potential competition for food resources. Contrary to what we expected – notably for *C. neumayri* that displays morphological changes (size increase, grazing adaptations) between the Vallesian and the Turolian (Antoine & Saraç, 2005) – the DMTA did not reveal clear spatiotemporal differences, that would have been associated with dietary changes due to the climatic and ecosystemic changes. On the other hand, the hypoplasia prevalence varied greatly depending on the species, the tooth locus, the locality, and the time period. Notably, Vallesian rhinocerotid, experiencing an early aridification in the region (Koufos, 2006), displayed more hypoplasia defects (Xirochori + Pentalophos-1: 20/123 of teeth affected, 16.26 %) than Turolian specimens (all other localities: 74/761; 9.72 %). Similarly, rhinocerotid teeth from eastern localities (Samos and Maragheh) supposedly more arid (west-east gradient; Fortelius et al., 2006), had a higher hypoplasia prevalence (66/488; 13.52 %) than their western counterparts (28/406; 6.90 %). Palaeoecological insights from our rhinocerotid specimens thus challenged space and time homogeneity within Balkan-Iranian province and the associated savanna habitat, often discussed in previous studies.

Antoine, P.-O., Saraç, G. 2005. Rhinocerotidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdağı, Turkey. *Geodiversitas*, 27(4), 601-632.

Fortelius, M., Eronen, J., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I., Zhang, Z. 2006. Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238, 219-227. doi: 10.1016/j.palaeo.2006.03.042.

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Geraads, D., Spassov, N. 2009. Rhinocerotidae (Mammalia) from the Late Miocene of Bulgaria. *Palaeontographica*, A: 99-122.

Keywords: Vallesian, Turolian, Balkans, Rhinocerotidae, dietary preferences, Pikermian Biome





Session 24 - KEYNOTE
From Pangaea to the break-up of Gondwana

Keynote





Session 24 - ORAL

From Pangaea to the break-up of Gondwana

Oceanic dispersal of Cretaceous dinosaurs and paleogene Mammals

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Darwin and Wallace tried to explain the distribution of living species by invoking dispersal processes, including land bridges and oceanic dispersal via rafting, swimming and drifting. Wegener's hypothesis of continental drift and the subsequent discovery of plate tectonics seemed to eliminate the need for improbable oceanic dispersal scenarios to explain species distributions. Instead, lineages could passively drift on continental plates. However, an improved understanding of palaeogeography, biogeography, fossil diversity and molecular clocks all show that continental fragmentation occurred too long ago to explain the distribution of many clades, both modern and fossil. Pangaea fragmented in the Jurassic, followed by fragmentation of Gondwana in the Cretaceous, with continental breakup largely complete by 100 Ma. High sea levels driven by seafloor spreading created additional marine barriers in the form of seaways. Dinosaur clades becoming widespread after the formation of these geographic barriers, such as hadrosaurs and lithostrotian titanosaurs, appear to have done so via oceanic dispersal, crossing marine barriers. Following the end-Cretaceous mass extinction, the Gondwanan landmasses of Africa, South America, India and Australia were populated by placentals and marsupials of Laurasian origin, implying mammals rafted and swam between the continents. Oceanic dispersal is not just a phenomenon of obscure island clades such as Galápagos tortoises and iguanas, but populated continents. It drove major radiations like Afrotheria, Australoselphia, Hystrycognathi and Simiiformes. Many novel designs can trace their origin to lineages undergoing oceanic dispersal, including kangaroos, horses, elephants, whales and humans. Oceanic dispersal shows the extraordinary impact of low probability, high impact events in driving evolution. Everyday processes are not necessarily sufficient to explain macroevolutionary patterns, because over long periods of time, rare, once-in-a-million year events become not just possible but highly probable.



Session 24 - ORAL

From Pangaea to the break-up of Gondwana



A new definition of the old Gondwana

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The name Gondwana is derived from the “Gond” tribes residing dominantly in the central part of India. The upper limit of the Indian Gondwana is traditionally fixed at Cretaceous which is enigmatic. Plots of the major Gondwana basins of peninsular India mostly show lithological columns of the Cretaceous occurring independently. The *Ptilophyllum* flora, noted as the “Upper Gondwana” flora of India is really a cosmopolitan flora. Terrestrial vertebrates profusely occur in the Triassic red beds of India. Incidentally, the Triassic red beds are common throughout the world. The Indian Triassic vertebrates are also really Pangaeian in nature. All the Triassic terrestrial vertebrates of India, particularly the temnospondyls are found to be cosmopolitan in nature as well. Among the temnospondyls, the Early Triassic lonchorhynchine trematosaur from the Panchet Formation of Damodar valley basin in India show close affinity with Madagascar, Brazil and even some parts of Laurasia, the Middle Triassic capitosaur present in the Denwa Formation of the Satpura valley basin in India are comparable to those of Africa, Poland, North America while a sole brachyopid from the Denwa Formation is perhaps comparable to North American and Algerian forms. The Late Triassic Maleri and Tiki Formations of the Pranhita- Godavari valley basin and the Rewa basin respectively, have metoposaurs of both Laurasian and Gondwanan affinities and Gondwanan chigutisaur together with the phytosaurs. The continental Triassic formations of different parts of India are very difficult to correlate as they are not continuous above the Permian deposits. Hence, only the Permian terrestrial deposits of India, starting with a glacial deposit viz. the glacial deposits of the Talchir Formation and gradually passing over to the coal bearing sediments of the Ranigunj and equivalent Formations and having occasional vertebrates like *Endothiodon* from the Kundaram Formation, *Gondwanosaurus* from Almod beds of the Satpura valley, *Archegosaurus* and occasional fish fossils from Kashmir together with *Glossopteris-Gangamopteris* floral remains can be fixed as the true Gondwana deposits of India and thereby globally. The “Upper Gondwana” starting with disappearance of coal and the emergence of red beds from the Early Triassic period in association with their cosmopolitan floral and faunal (vertebrate fossils) remains are the initiation of a geological and palaeontological milieu which is global and not restricted to the Gondwanan continental boundaries. This is also highly correlatable from the tectonic point of view. From being the largest craton in the Palaeozoic Era, Gondwana merged with Laurasia to form the supercontinent Pangea. This justifies the cosmopolitan nature of the “Upper Gondwana” flora and fauna. “Gondwana” started breaking up in the Jurassic and the Jurassic-Cretaceous fauna is also cosmopolitan in nature as there were many land connections or straits. Thus, it is high time the definition of Gondwana deposits be limited to Permian deposits which is easily correlatable worldwide. While the cosmopolitan “Upper Gondwana” deposits be based on the names of their formations and ages respectively without grouping them into the “Gondwana” bundle of deposits.

Keywords: Gondwana, Triassic, India, temnospondyl





Session 24 - ORAL

From Pangaea to the break-up of Gondwana

New insights from varied archosaurian osteoderms from the Late Triassic of India

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Osteoderms or the dermal armours are thick plates of bone that are often ornamented, found embedded within the dermis, and are one of the best-preserved fossil elements in tetrapod integumentary skeleton. These are known in many extant and fossil vertebrates, have a high fossilization potential, and are often diagnostic thereby helping in taxonomic identification of the fossil taxa. Although their importance for phylogenetic interrelationships and functional morphology is well established, there is near absence of detailed work on the tetrapod osteoderms known from India. Rich and diverse tetrapod fossil assemblages are known from the Upper Triassic Gondwanan horizons such as the Maleri and lower Dharmaram formations of the Pranhita-Godavari Basin, and the Tiki Formation of the Rewa Gondwana Basin.

Along with well-preserved and articulated body fossil of various tetrapods, these horizons have yielded different types of articulated and / or isolated osteoderms that are the focus of the present study. Although osteoderms show positional variations, based on their distinctive external morphology, three broad and distinct morphotypes can be determined. Morphotype I, mostly known from the lower Maleri and Tiki formations, comprises subcircular to polygonal osteoderms bearing ornamentation in the form of pits and ridges on the dorsal surface, often with dorsal flexure, and a median boss /keel. Morphotype II, on the other hand is known only from the Tiki Formation, contains multiple isolated osteoderms, and is characterized by an elliptical or sometimes polygonal shape with sharp elongated and recurved spike like dorsal eminences, ornamented with rugose ornamentations in the form of sharp ridges and grooves. The third morphotype (III) is recovered from the lower Dharmaram Formation, and contains several complete, articulated and isolated paramedian and lateral osteoderms. These paramedian osteoderms are rectangular, extremely wide and ornamented with deep circular pits, radial ridges and grooves, whereas the associated lateral osteoderms are horn-shaped, dorsoventrally compressed and faintly striated. Comparison with known osteoderms of the Late Triassic archosaurs shows that morphotype I and III belonged to the phytosaurs and aetosaurs, respectively. Morphotype II, however, remains enigmatic and its taxonomic identity is still under study. The current work highlights the importance of examining osteoderms and reveals the existence of various armoured archosaurs during the Late Triassic of India.





Session 24 - ORAL

From Pangaea to the break-up of Gondwana

First report of herrerasaurian (Dinosauria, Saurischia) remains from the Upper Triassic Tiki Formation of India

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Three Upper Triassic Gondwanan horizons in India are known for diverse vertebrate fossil assemblages. These are the Maleri and lower Dharmaram formations of the Pranhita-Godavari Basin and the Tiki Formation of the Rewa Gondwana Basin. Although different types of dinosaurs have been described from Maleri and lower Dharmaram formations (Chatterjee, 1987; Novas et al., 2010), this is the first report of herrerasaurian remains from the Tiki Formation. The current study focuses on multiple, small, isolated and partially articulated post cranial elements including limb bones recovered from a rhynchosaur-dominated multitaxic bonebed, the taphonomic analysis of which revealed biological aggregation and mass mortality because of flooding (Mukherjee and Ray, 2012). Preliminary examination reveals diagnostic features such as epicondylar rugosity, antero-medially projected femoral head, sigmoidal femoral flexure with a prominent fourth trochanter, crista tibiofibularis separating fibular condyle by a small sulcus, quadrangular distal tibial articular surface with a posteroventral notch. Comparison with other similar forms suggests a basal saurischian belonging to the family Herrerasauridae. The study also discusses the taxonomic identity of *Alwalkeria maleriensis*, and other related material known from the Maleri Formation. Herrerasaurs were cosmopolitan and are known from the middle-late Carnian to Rhaetian sediments of South America (Novas et al., 2021), North America (Sarigül, 2018), Poland (Niedźwiedzki et al., 2015) and India (current study). Although Novas et al. (2021) has suggested the possibility of a herrerasaur from India, the material is identified as non-sauropodomorph dinosauriform (Novas et al., 2010) and yet to be studied in details. The current work highlights the possibility of a rich Late Triassic (late Carnian to early-middle Norian) dinosaurian record from India.

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Keywords: Dinosauria, Gondwana, herrerasaurs, India, Upper Triassic



Session 24 - ORAL

From Pangaea to the break-up of Gondwana

The Hidden Extinction in the Triassic - Carnian Pluvial Episode and its effects on the Tetrapods of India

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The Triassic period of the Earth's history is bracketed between two famous mass extinctions in time, viz. the Permo-Triassic mass extinction and the End Triassic mass extinction also known as the Triassic-Jurassic mass extinction. However, the stories of vertebrate diversity and gigantism that initiated in the Triassic were also punctuated by mass extinctions within the Triassic period. Of these the Carnian Pluvial Episode (CPE) at the Carnian deserves special attention as the immense dinosaur diversification and radiation that heralded in the Jurassic and Cretaceous period has its root in the CPE. The mid-Carnian witnessed a global climate change in the Pangea, initiated by coeval volcanism especially the Wrangellia Large Igneous Province (LIP). Heavy rainfall descended in the Pangea in four episodic cycles approx. 234 – 232 million years ago. Though, CPE has been attributed as a global event, it has never been worked upon or even reported from India. Also, the effect of CPE on the “lower vertebrates” like the fishes and the amphibians have remained unknown globally. Recent geological field work in Late Triassic Maleri and Tiki Formations of India bring forth potential geological evidence to suggest that like many other places CPE affected the Indian Gondwana deposits as well. Increase in siliciclastic material in the later part of Carnian in Maleri signifies increase in drainage which has not been studied so far. The vast Late Triassic red-beds of the Tiki Formation has been interrupted by grey laminae of silstones to mudstones suggests that an incredible dry climate turning wet and that also too intermittently. The present work not only reports the first sedimentological evidence of the Carnian Pluvial Event from India, but also studies its effect on the amphibious life that existed during that period viz. the temnospondyls. The amphibians are considered to be one of the most important indicators of climate changes as their transdermal uptake system is very sensitive to even small changes in their habitats in both land and water. Along with the extinction of the rhynchosaurs and *Parasuchus* (primitive phytosaur), chiniquodontids (cynodonts), the (CPE) also caused the extinction of the metoposaurids in India. Chigutisaurids appeared in Middle Carnian / Norian and India is the only place which accommodates definite metoposaurids and chigutisaurids fossils within the same formations the former being replaced by the latter. Among the phytosaurs, the *Parasuchus* of Lower Maleri fauna is replaced by more derived *Leptosuchus* like forms of Upper Maleri and *Volcanosuchus statisticae* in the upper part of Tiki Formation along with emergence of *Gauibasaurid*-like sauropodomorphs and *Herrerasaurus*. The post-CPE empty niche left by the amphibious metoposaurids in the Late Triassic Gondwana deposits of India was occupied by chigutisaurids. Thus, the presence of both metoposaurids and chigutisaurids within Late Triassic of India along with their faunal turnover from the Carnian to the Norian, the extinction of the rhynchosaurs (*Hyperodapedon*) and the phytosaur *Parasuchus* in the Carnian, the presence of prosauropods in the Upper Maleri Formation and undescribed dinosauriforms including theropod-like forms shed light and document for the first time the existence and effect of the Carnian Pluvial Episode in India. The percentage of extinction during CPE is lesser than the Permo-Triassic mass extinction, however, its significance lies in the fact that it marks massive “turnover” of diversity and gigantism of all life forms and the dawn of dinosaur dominion.





Session 24 - POSTER
 From Pangaea to the break-up of Gondwana

The dinosaurs of Morocco: state of art with reference to unpublished remains of a new Titanosauriformes (Dinosauria, Sauropoda)

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Since the first discovery of dinosaur remains in 1925, in the Middle Jurassic of the El Mers area near the city of Fez (Middle Atlas mountains), Paleontological discoveries have succeeded, making Morocco a privileged destination for the study of the diversification and the evolution of the dinosaurs. Mesozoic outcrops indeed delivered a rich and diversified dinosaur fauna, especially saurischian sauropods and theropods covering a stratigraphic extension ranging from the Upper Triassic (Carnian) (track sites) to the Upper Cretaceous (Maastrichtian) (Triassic and Jurassic of High and the Middle Atlas, the Cretaceous (Cenomanian) of the Kem Kem region and the Maastrichtian of the phosphate basin. Among the most emblematic taxa we can mention the sauropod *Atlasaurus imelakei* Monbaron *et al.*, 1999 (Middle Jurassic, Bathonian-Callovian, Wawmda), represented by one of the most complete skeletons; one of the biggest dinosaur sauropod (Charroud and Fedan, 1992) (Bathonian, Boulahfa); the oldest sauropod *Tazoudasauru snaimi* Allain *et al.*, 2004, and the oldest Abelisauroida, *Berberosaurus liassicus* Allain *et al.*, 2007, (Lower Jurassic, Toarcian to Early Aalenian, Tazouda); the first eurypodan from North Africa and the oldest known stegosaur *Adratiklit boulahfa* Maidment *et al.*, 2019 (Middle Jurassic, Bathonian, Boulahfa); theropods among the largest known carnivorous dinosaurs *Carcharodontosaurus saharicus* (Russell, 1996; Sereno *et al.*, 1996) and *Spinosaurus aegyptiacus* (Zitouni et Jalil 2010; Ibrahim *et al.*, 2014); and finally *Chenanisaurus* and *Ajnabia odyseus* (Maastrichtian, Oulad Abdoun). *Ajnabia* is the only duck-billed dinosaur on the African continent (Longrich *et al.* 2017, 2021). More than giving a synthesis of the dinosaurs fauna of Morocco, this presentation aims also to present unpublished remains of sauropod dinosaurs from the Aït Hanî region, among which remains of the oldest Titanosauriformes from the Middle Jurassic, (Zitouni *et al.*, 2008; Zitouni *et al.*, 2009; Zitouni et Jalil 2014).

Comparisons between field campaigns (relatively few), and the number and diversity of the described dinosaur taxa in Morocco, indicates that their fossil record is biased and suggests that dinosaur diversity in Morocco and consequently in Gondwana may have been richer. The prospects for future discoveries of new genera across Morocco are therefore very good.

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Session 24 - POSTER

From Pangaea to the break-up of Gondwana

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Keywords: Dinosauria; Jurassic; Cretaceous; Morocco.





Session 24 - POSTER

From Pangaea to the break-up of Gondwana

Learning more about pterosaur tracks from Gondwana: a case study from the lower–middle Campanian (Upper Cretaceous) Anacleto Formation, northern Patagonia, Argentina

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Although pterosaur remains are abundant in the Cretaceous of Gondwana, pterosaur tracks are relatively scarce. This pterosaur track record is only known in Morocco from the Cenomanian Kem Kem beds, the Coniacian–Santonian Anza tracksite and the Maastrichtian Tagragra Formation, and in Argentina from the Cenomanian Candeleros Formation (see Calvo and Lockley, 2001; Lockley et al., 2008; Masrour et al., 2018; Heredia et al., 2022). In this contribution, we report four pterosaur manus tracks found in a new tracksite of the lower–middle Campanian Anacleto Formation of the Neuquén Basin, within the Área Natural Protegida Municipal Paso Córdoba in the Río Negro Province, northern Patagonia, Argentina. The manus tracks are preserved in four small slabs as convex hyporeliefs from fluvio-alluvial deposits. They are longer than wide (average 6.3 cm long, 3.0 cm wide), rhomboidal in shape, tridactyl with digit impressions of different lengths (I<II<III), anteriorly directed and laterally asymmetrical. Although the four pterosaur manus tracks are similar in shape, they show some preservational differences related to variations in substrate properties. Considering that they are poorly preserved and in the absence of pes tracks, they are classified as indeterminate pterosaur tracks. This find represents the first occurrence of pterosaurs not only from Anacleto Formation but also from the lower–middle Campanian of Argentina. Moreover, it provides a more complete knowledge of the paleofauna of the Anacleto Formation and emphasizes the importance of the ichnological record to complete the diversity of a unit rich in osteological, oological and ichnological remains of other tetrapods, including sauropod, ornithopod and theropod dinosaurs (Díaz-Martínez et al., 2018 and reference therein). Finally, this new pterosaur tracksite allows us to discuss the paleoenvironmental inland preferences and the palaeoecology implications of pterodactyloid pterosaurs at the end of the Cretaceous (Campanian) in southwestern Gondwana.

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Session 25 - KEYNOTE

Fish evolution through the Mesozoic and Cenozoic

Diverse late Miocene cartilaginous and teleost fish fauna from Brunei Darussalam (northern Borneo)

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The intensive field surveys of the last eight years on late Miocene marine sediment in Brunei Darussalam yielded many fish remains including teeth and otoliths. The cartilaginous remains of Ambug Hill (Kocsis et al., 2019) and the nearby reworked site on the Penanjong beach (Kocsis et al., 2021) have been already described. As of now, the reported 24 selachian and batoid taxa represent the most diverse southeast Asian fossil chondrichthyan record from the Neogene. Here we introduce a wider spatial and timewise distribution of some of these taxa. Our knowledge on the famous *Otodus megalodon* in the region is also broadened. Previously only three teeth were known (Razak and Kocsis, 2018), however more than 20 new teeth/tooth fragments have been collected that prove further the presence of small-sized megalodon in northern Borneo during the late Miocene. Most of the studied localities also yielded plenty of otoliths. In 1962, Fred C. Stinton (1962) studied Neogene otoliths in the region and reported 62 specimens of 18 species covering 10 families. Among these taxa five were also mentioned from Brunei Darussalam. 66 percent of Stinton's fauna comprise Sciaenidae (drums and croakers) and Ariidae (sea catfish), with two and four newly described fossil species, respectively of these families. Our team recovered over 1100 otoliths from the late Miocene shallow marine deposits in Brunei. The preliminary observation concurs with Stinton's report with the dominance of Sciaenidae and Ariidae, but also with common presence of Haemulidae and Engraulidae. These faunas are currently under investigation and thoroughly being compared with that of Stinton's collection housed in the British Natural History Museum in London. The teleost fauna contains many new elements among them 2-3 possible new genera that further increase the palaeobiodiversity record of the Indo-Australian Archipelago. The fossil fish remains from Brunei also extend our knowledge on palaeobiogeographic distribution of fishes in the region.

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Keywords: shark teeth, ray teeth, otolith, *Otodus megalodon*, palaeodiversity



Session 25 - ORAL

Fish evolution through the Mesozoic and Cenozoic

Using nannofossil dating to better understand patterns of late Cretaceous evolutionary change in fish: unlocking dark data in historical museum collections

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The Natural History Museum, London (NHMUK), houses one of the most important collections of Late Cretaceous fish worldwide, and is a substantial archive of potential data. A key focus is the British Chalk Group, which has been collected from for over 200 years. The UK Chalk records an important interval in the evolutionary history of fish, including how clades responded to past global events and biotic crises such as the Cenomanian-Turonian boundary event (OAE2). Museum specimens provide a key record of how fish responded to environmental change at this time. Unlocking the scientific importance of collections is currently severely limited because most of the specimens were collected in the nineteenth and early twentieth centuries, from sites that no longer exist, and their precise stratigraphic horizons, and hence ages, are unknown.

Fortunately, chalk is composed of the fossil skeletons of tiny nannoplankton, such as coccolithophores, which can be extracted, identified, and used to determine the age of each specimen. Nannofossil biostratigraphy enables maximum age-resolution for minimal sampling; less than 0.05g of chalk matrix is removed. Each specimen was individually assessed, a condition report produced, and imaged before and after sampling. The stratigraphic details for each specimen were updated.

Working with specialist stratigraphers, a total of 276 Chalk fish fossils, including 66 holotypes, were analysed using the latest biostratigraphic framework and assigned to a nannofossil zone or subzone. The precision and accuracy of the ages of most specimens was substantially improved, and in some cases the provenance of the specimen could also be refined. Revised age data are presented here and some apparent discrepancies between the historic label data and new nannofossil derived data are discussed.

Given the results of the nannofossil dating we can now analyse patterns of evolutionary change at a higher stratigraphical resolution than previously possible. As an example, we analysed size change in Late Cretaceous lamniform sharks and the durophagous shark *Ptychodus* from the English Chalk to test whether they became smaller in response to global environmental change during the Cenomanian-Turonian anoxic event (OAE 2) and Cretaceous Thermal Maximum.

By incorporating nannofossil dating of the matrix associated with the specimens into the projects we take a major step in unlocking the Museum's fossil archive of 'dark data' to address key scientific questions, such as how fish responded to past warming and extinction. Holotypes were selected, because having the best possible age-control of type specimens will help to better constrain evolutionary rates, the dates of tips and nodes in phylogenies, and the origins of modern groups. The general approach can also be extended to other chalk taxa, and potentially to other historic collections.

Keywords: Chalk, lamniform, United Kingdom, Cretaceous, fossil fish, *Ptychodus*, nannofossils, dark data, coccolithophores, biostratigraphy, historical collections, OAE.





Session 25 - ORAL

Fish evolution through the Mesozoic and Cenozoic

Paleoecology, and diversification pattern of fishes and cephalopods in Mesozoic epicontinental seas based on otoliths and statoliths

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Majority of research on fishes and cephalopods is based on body macrofossils. The “ear stones” (otoliths in fishes and statoliths in cephalopods) received much less attention. Nevertheless they may prove to be a source of important information on paleoecology and paleogeography of these two groups in sediments where other fossils are rare or absent. Otoliths are calcium carbonate structures in the inner ear of all vertebrates. In fishes they are arranged in three pairs (sagittae, lapilli and asterisci) and large enough to be easily identified. Their fossil record is not yet fully exploited. Relatively much is known on otoliths of Cenozoic fishes (Nolf 2013) but knowledge on their more ancient counterparts is less (Schwarzhan 2018). Increasing amounts of evidence allows attributing the majority of those otoliths to respective families, genera and even species.

Statoliths are well developed structures occurring in cephalopods which are roughly analogous to fish otoliths. We investigated otoliths from Cassian formation (Late Triassic) in Northern Italy, which most likely belong to very young lepisosteiform fish (compare Long and Snow, 2016). No Triassic statoliths are known to date. The investigated associations of Jurassic “ear stones” display low diversity of otoliths and an ubiquity of cephalopod statoliths (see also Hart, et al. 2016). Subsequently, we investigated a rich Valanginian (Early Cretaceous) otolith-based ichthyofauna from Wąwał, central Poland. This unique assemblage shows a considerable teleost diversity, immediately preceding The Great Fish Radiation (Cavin, 2008). This fossil association also reveals a significant shift in the abundance ratio of fish otoliths vs. cephalopod statoliths in fully marine deposits, with otoliths much more abundant than the statoliths. Cephalopod statoliths from the Early Cretaceous, are unique microfossils that fill the gap in the fossil record between Jurassic and Cenozoic forms and they are more similar to the Jurassic statoliths. The comparison of the Mesozoic forms to the statoliths of the Recent and Cenozoic decabrachians shows that they are most similar to the Recent *Idiosepiidae*, it might be therefore suggested that the Mesozoic cephalopod statoliths belong to the basal decabrachians and their most closely related group are *Idiosepiidae*.

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Keywords: Otolith, statolith, Teleostei, Decabranchia, *Idiosepiidae*, Mesozoic,





Deep sea chondrichthyan egg capsules in fossil record

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Extant chondrichthyans are either oviparous, viviparous, or ovoviviparous. Oviparous chondrichthyans lay fertilized eggs, encased in large, collagen-rich capsules which are either attached or unattached to the bottom. The function of the capsule wall is to protect the developing embryo until it hatches up to four years after the capsule was laid. Extant oviparous chondrichthyans belong to several groups, including chimaeras (Chimaeriformes, Holocephali), skates (Rajiformes, Elasmobranchii), catsharks (Scyliorhinidae, Carchariformes; Elasmobranchii), bullhead sharks (Heterodontiformes; Elasmobranchii) and nurse sharks (Orectolobiformes; Elasmobranchii) (Fischer et al. 2014). Only the three former groups live and reproduce in deep waters where they contribute to formation of sometimes spectacular egg case accumulations on raised seabed features, like deep-water coral reefs or cold seep carbonates. Unlike the former, both bullhead and nurse sharks are mostly shallow water, tropical groups and do not lay their eggs in deep-waters. In addition to extant elasmobranchs, extinct groups for which oviparity and capsule laying has been suggested include various Holocephali, or xenacanthiform and hybodontiform elasmobranchs. Oldest possible chondrichthyan capsules (*Palaeoxyris* Brongniart, 1828) are Carboniferous (Mississippian) in age and could have been laid by hybodontid sharks, whereas other Palaeozoic, Triassic or Jurassic capsules were likely laid by unidentified Holocephali, hybodontiform or xenacanthiform elasmobranchs.

A characteristic feature of pre-Cretaceous capsule records is that they all come from shallow marine, brackish or freshwater deposits. The oldest capsules known from deep-sea settings are Cretaceous in age and come from both Early and Late Cretaceous seep deposits from California, Arctic Canada and Japan. They are most similar to Eocene (e.g. *Scyliorhinotheca* Kiel, Peckmann and Simon, 2013) and Recent scyliorhinid egg capsules, for example those laid by the species of deep-sea catshark *Apristurus* Garman, 1913, although skate affinity is also possible for some Late Cretaceous specimens. Cenozoic egg capsules of Eocene or Miocene deep sea seep deposits are also known, and these are also likely laid by deep-sea catsharks. We suggest that the observed onset of deep-sea chondrichthyan egg capsule reproduction during the Cretaceous is an actual phenomenon as indicated by similar age of modern deep-sea fauna (e.g. Kiel & Little, 2006; Thuy et al. 2014) and that capsule-laying among the chondrichthyans followed a general onshore-offshore pattern as did the general evolution of marine fauna (Jablonsky et al. 1983). Once established in the deep sea during the latter part of the Mesozoic, oviparous elasmobranch reproduction survived there in very similar form until Recent, in spite of K/Pg mass extinction, Oceanic Anoxic Events during the Cretaceous and Eocene, and other oceanographic perturbations.

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Keywords: chondrichthyans, carbonate cementation, cold seeps, deep sea, egg cases, reproduction



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Fish evolution through the Mesozoic and Cenozoic



Tracing the trophic ecology of extinct elasmobranchs using the calcium record of their teeth

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Among the big five, the K/Pg crisis is well known to have caused the extinction of the non-avian dinosaurs. It is also responsible for strong disturbances and faunal turnover in marine ecosystems leading to the extinction of several marine organisms including elasmobranchs (sharks and rays). Study of taxonomic turnovers is the main approach used to highlight these disturbances but other approaches are powerful as the monitoring of trophic chain instability through a crisis. The development of trophic analysis based on the isotopic composition of oxygen, carbon or nitrogen has opened new alternatives to the study of feeding behaviors in terrestrial and marine vertebrates. The stable isotopes of calcium (⁴⁴Ca, ⁴²Ca, ⁴⁰Ca) measured in the enamel of vertebrate teeth have been correlated to their trophic level. It is estimated that calcium isotope fractionation between the food source and the predator is reflected along the food chain by a decrease in $\delta^{44/42}\text{Ca}$ values with increasing trophic position, thus allowing the discrimination of trophic ranks, ranging from primary producers to apical predators, in the analyzed specimens. Elasmobranchs represent a very good model for testing this method as they occupy all the trophic levels in the marine food web and display a relatively abundant fossil record in marine deposits due to the permanent renewal of their teeth. This leads to an abundance of available specimens for geochemical analysis in neontological and paleontological collections.

Here we present the interest and limits of this method, performed on several sharks and rays teeth from the K/ Pg deposits from Morocco, in the study of food chains of fossil elasmobranchs : 1) the characterization of the functional resilience of elasmobranch communities through a major biological crisis despite evidenced taxonomic turnover and 2) the characterization of diet in elasmobranchs at the specific level, highlighting the presence of singular feeding habits such as scavenging in the taxon *Squalicorax pristodontus* which occupied worldwide coastal waters at the end of the Cretaceous. Understanding the trophic changes among fossil elasmobranch faunas is a major challenge both for the study of the ecology of extinct taxa as well as for current conservation issues.

Keywords: Trophic level, elasmobranchs, calcium, K/Pg boundary, Morocco





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Fish evolution through the Mesozoic and Cenozoic

Early and Middle Triassic fossils illuminate the endoskeletal anatomy and interrelationships of †Perleididae (Actinopterygii).

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Neopterygii nowadays encompass the vast majority of ray-finned fish species. Following a somewhat cryptic early evolutionary history during the late Paleozoic, Neopterygii and their closely related taxa produced impressive radiations in the aftermath of the End-Permian Mass Extinction, which are well documented by fossils. †Perleididae comprises relevant fossil examples from different landmasses, which radiated in mostly durophagous niches during the Triassic. Historically viewed as primitive neopterygians, †perleidids play a central role in discussions on the early evolution of the clade. Yet, important aspects of the anatomy (e.g., the cranial endoskeleton) of †perleidids remain poorly known or characterized, while the monophyly and systematics of the group, and especially of its namesake genus †*Perleidus*, remain unclear. To address this gap of knowledge, we reappraise the anatomy and interrelationships of one of the oldest known representatives of the family and genus, as well as of the type species of †*Perleidus*. Our survey of numerous two-dimensionally preserved fossils of ‘†*Perleidus*’ *woodwardi* from the Early Triassic (early Olenekian) of Spitsbergen illuminated previously unknown anatomical aspects of the species, such as the presence of epaxial rudimentary and principal rays in the caudal fin, or the composition of the snout and cheek. In addition, our μ CT-aided study of an uncrushed skull of ‘†*P.*’ *woodwardi* led to the most complete reconstruction of the cranial and pectoral endoskeleton of a stem-neopterygian known to date. ‘†*P.*’ *woodwardi* exhibits many unprecedented endoskeletal features, such as the presence of a maxilla that is loosely integrated—but not fully mobile—into the cheek, or the presence of perforate suprapharyngobranchials associated with the first branchial arch. Our re-examination of the type series of †*Perleidus altolepis* from the Middle Triassic (late Ladinian) revealed the presence of two morphotypes that can be distinguished largely on the basis of caudal fin anatomy. The results of our phylogenetic analyses, including data from our observations on ‘†*P.*’ *woodwardi* and †*P. altolepis*, reinforce the recently proposed monophyly of †Perleididae, to the inclusion of both Early and Middle Triassic species. However, the monophyly of the Early Triassic genus †*Teffichthys* is challenged.

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Keywords: Actinopterygii, Neopterygii, Triassic, μ CT, endoskeleton, phylogeny



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Fish evolution through the Mesozoic and Cenozoic



New fossil coelacanths from the Middle Triassic of Alsace, France

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Four specimens of fossil coelacanths, exceptionally preserved in 3D, have recently been found in Middle Triassic deposits near Saverne (Alsace, France) and have become part of the collection of the Museum of Natural History of Geneva. Morphological studies have started in 2021, with different imaging tools, most notably MicroCT. A first series of CTscans revealed an innumerable amount of bony elements embedded in the rock matrix. A specimen of the extant coelacanth *Latimeria chalumnae* (Smith, 1939) was also CTscanned as a reference for anatomical comparisons. Most of the neurocranial and branchial elements, rarely preserved in fossil coelacanths, were identified in these four specimens. The postcranial skeleton, including vertebral elements, fin rays, and an ossified lung are also observable. Segmentation was performed with Dragonfly 4.1 (ORSsystems), then isolated bones were rendered in Amira 9 (ThermoFisher). The bones of the skull were rearranged in Blender 3.1. For further morphological studies, we scanned the fossils a second time with a microtomography beamline at the European Synchrotron Radiation Facility in June 2022 (DOI:10.15151/ESRF-ES-788657609). Synchrotron scans are currently being segmented, revealing very fine anatomical details, which may establish these fossil coelacanths as some of the best preserved ever. Preliminary observation of the neurocranium, skull roof, jaw and cheek bones of 2 specimens show some resemblance with the genus *Whiteia*, which currently includes five species from Madagascar, Greenland, South Africa, Indonesia, Canada (Yabumoto et al, 2019). If our preliminary inference is confirmed, it may be the first record of *Whiteia* from Europe.

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Fish evolution through the Mesozoic and Cenozoic



A new amiiform fish (Holostei, Halecomorpha) from the Early Cretaceous of Thailand, with comments on the Asian Sinamiidae

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The Sinamiidae are a family of halecomorph fish (Holostei) from the Early Cretaceous first discovered in China, then in Thailand and Japan. The three recognized genera, *Sinamia* Stensiö, 1935, *Siamamia* Cavin et al., 2007 and *Ikechaoamia* Liu, 1961, are characterized, among other characters, by an unpaired parietal. Here we describe a new sinamiid taxon based on a single specimen from the Aptian Khok Kruat Formation of Ban Krok Duean Ha, Nakhon Ratchasima, Thailand. The 3D preserved specimen shows characters that allow recognizing a new genus diagnosed by four pairs of extrascapulars and tall cylindrical teeth with a conical enamel stalk marked by thin ridges and with an arrowhead-shaped acrodine cap with cutting carinae, among other characters. Another sinamiid taxon, *Siamamia naga*, has been found in the older Barremian Sao Khua Formation. Isolated remains of this family are fairly common in the Early Cretaceous deposits of Thailand, but absent from the Jurassic-Lower Cretaceous Formation of Phu Kradung. A review of this family shows that in China and Japan its fossil record appears to be restricted to the Early Cretaceous as well, and always found in freshwater deposits. Several cranial and post-cranial features indicate that these fish were piscivorous predators showing a morphological evolution parallel and coeval to another clade of amiiform fishes, the Calamopleurini of western Gondwana (South America and Africa).

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Keywords: Sinamiidae, Halecomorphi, Khok Kruat Formation, Early Cretaceous



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Fish evolution through the Mesozoic and Cenozoic

New material of Tselfatiiformes, weird group of Cretaceous ray-finned fishes, elucidating their inter- and intra-relationships

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Tselfatiiformes is an enigmatic group of ray-finned fishes with a relatively short stratigraphic range extending from the Albian to the Campanian. This clade shows its highest diversity during the Late Cretaceous in the Western Interior Seaway of North America. Haqel and Hjoula, two Lebanese Cenomanian localities that represent the richest Mesozoic fish assemblages worldwide, also yield a number of tselfatiiforms. Despite being the focus of investigation since the 19th century, the phylogenetic position of these fishes is still disputed and the intrarelations within the clade are far from being resolved. To tackle this issue, we studied new material of Tselfatiiformes from the Cenomanian of Lebanon as well as representatives of this clade from other localities in Europe, Morocco and the Western Interior Seaway of North America. These form the basis for osteological, phylogenetic and palaeobiogeographical analyses. The new Lebanese material consists of several exceptionally preserved specimens. Two of which are complete and were assigned to two different genera within the Lebanese endemic family Protobramidae, one to the genus *Protobrama* and one to the genus *Eusebichthys*. Two additional specimens were placed in two different newly erected taxa. One of them is incomplete, characterized by a long rostrum and shows more affinities with the younger North American genus *Martinichthys* of the family Plethodidae rather than previously known Lebanese genera. Whereas the other specimen was placed in a newly erected taxon *incertae sedis* within the Tselfatiiformes. This material shows the diversity of morphotypes and the implied different ecological niches they have occupied during the Cretaceous. We used this data to include the Tselfatiiformes in a first computer-based phylogenetic analysis using a newly created synthetic matrix. This will allow us to evaluate the position of tselfatiiforms among teleosts, resolve the intrarelations within the group and test the monophyly of this weird group of fishes.

Keywords: Tselfatiiformes, Cenomanian, Cretaceous, Lebanon, Western Interior Seaway, morphotypes, phylogeny, monophyly

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Fish evolution through the Mesozoic and Cenozoic



Fossils reveal marine long-distance dispersal in bonytongue fishes (Osteoglossomorpha), an iconic example of vicariance

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While the importance of fossils in biogeographic inference has been recognized since the early days of evolutionary biology, the impact of palaeontological relative to neontological data for the reconstruction of the biogeographic history of extant clades remains mostly unexplored. Bonytongue fishes (Osteoglossomorpha)—popularly seen as an example of continental vicariance caused by the progressive breakup of Pangaea—represent an ideal study case in this respect, as their fossil record is relatively abundant and geographically widespread. While living species are restricted to freshwater settings in mostly tropical environments, several fossil bonytongues are known from early Cenozoic marine deposits worldwide, making this group particularly fitting to study freshwater-to-marine ecological transitions in a biogeographical context. However, the lack of a phylogenetic framework for marine bonytongues has previously precluded this research avenue. Here, we inferred ancestral geographic ranges and environments using phylogenetic models of biogeographic evolution applied on a total-evidence, time-calibrated Bayesian phylogeny of 60 extant and 32 extinct bonytongue species, including 8 from marine deposits. We find that fossil marine bonytongues do not form a clade to the exclusion of freshwater forms. Instead, they are represented by several lineages that consistently cluster within Osteoglossidae (arapaima, arowanas and relatives). Trait-dependent dispersal models—where freshwater/marine ecology is treated as a binary trait affecting dispersal ability—strongly support a marine origin for osteoglossid bonytongues. Extant osteoglossids likely derived from marine ancestors that dispersed globally and entered freshwater environments multiple times independently, resulting in their disjunct geographic distribution we observe today. Therefore, the current distribution of bonytongues and apparent agreement with patterns of continental fragmentation represents an instance of pseudo-congruence. Ignoring fossil taxa in the biogeographic analysis results in a completely different scenario that largely corresponds to continental vicariance. Our study provides a striking case of how fossil data can overthrow biogeographic and ecological patterns that are apparent from the examination of extant species alone, and highlights the perils of ignoring palaeontological evidence when inferring ancestral conditions for living organisms.

Keywords: biogeography, teleost fishes, Bayesian phylogenetics, fossilized birth-death, Paleogene, long-distance dispersal, Osteoglossomorpha, trait-dependent dispersal



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Fish evolution through the Mesozoic and Cenozoic



A fossilized birth-death phylogeny of early Late Cretaceous spiny-rayed fishes (Teleostei: Acanthomorpha)

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Spiny-rayed fishes (acanthomorphs) account for approximately 30% of all living vertebrate species (Dornburg & Near, 2021). Their exceptional morphological disparity and ecological diversity are a focus of large-scale comparative studies of phenotypic evolution in both extant and extinct taxa, though such studies remain hindered by the lack of an accurate evolutionary timescale incorporating the earliest members of the clade. Exemplifying this problem, although the earliest fossil acanthomorphs are roughly 101 million years old (López-Palomino *et al.*, 2021), recent node-dated molecular phylogenies suggest acanthomorphs originated roughly 140–145 million years ago (Hughes *et al.*, 2018).

We build upon recent works that have incorporated early fossil acanthomorphs into extant morphological matrices (e.g., Davesne *et al.*, 2014; Cantalice *et al.*, 2021). We focus on adding characters to further the inclusion of members of ‘Berycimorpha’. This group accounts for nearly 50% of all early Late Cretaceous acanthomorph genera (Murray, 2016), yet its intrarelationships have not received the same attention as other acanthomorph lineages with Late Cretaceous fossil representatives (Davesne *et al.*, 2014; Delbarre *et al.*, 2016; Murray *et al.*, 2020).

We combine our expanded morphological dataset with published molecular alignments (e.g. Rabosky *et al.*, 2018) and use the ages of the fossil taxa within the analysis to infer a tip-calibrated topology of acanthomorph fishes under the fossilized birth-death framework. We generally find low support for the monophyly of fossil ‘berycimorphs’ and fail to infer a younger age for total-group acanthomorphs than those previously recovered by node-calibrated molecular phylogenies. These results highlight a greater need to examine the phylogenetic affinities of fossil non-acanthomorph neoteleosts, such as the ctenothrissiforms, and suggests a greater need to scour the late Early Cretaceous fossil record for acanthomorph taxa.

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Delbarre, D.J. et al. 2016. Anatomy and relationships of †*Aipichthys pretiosus* and †*Aipichthys nuchalis* (Acanthomorpha: Lampridomorpha), with a review of Late Cretaceous relatives of oarfishes and their allies. *J. Syst. Palaeo.* 14: 545–567.

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Hughes, L.C. et al. 2018. Comprehensive phylogeny of fishes (Actinopterygii) based on genomic and transcriptomic data. *Proc. Natl. Acad. Sci. USA* 115: 6249–6254.

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Murray, A.M. 2016. Mid-Cretaceous acanthomorph fishes with the description of a new species from the Turonian of Lac des Bois, Northwest Territories, Canada. *Vert. Ana. Morph. Paleo.* 1: 101–115.

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Keywords: acanthomorphs, fishes, phylogenetics, fossilized birth-death, total evidence



Session 25 - POSTER

Fish evolution through the Mesozoic and Cenozoic

Ariidae (sea catfish) remains from Borneo (Sarawak, Malaysia)

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The island of Borneo has a high potential for diverse marine fish habitats due to its geographic position and proximity to the Coral Triangle, where today's highest marine biodiversity occurs. However, the fossil fish record is very sparse and understudied in the region. The here investigated fossil fish fauna is a part of a recently discovered Pleistocene/Holocene reworked and mixed vertebrate assemblage from central Sarawak (East Malaysia). The fossils were found washed up on the beaches along the coastline near the Rajang River delta. This study mainly focuses on the family Ariidae commonly known as sea catfishes. To describe and identify more precisely the ariid remains, specimens from the modern taxa have also been collected in Brunei and Sarawak. Altogether, skeletal remains (mainly heads) of 14 modern siluriform taxa (10 ariids) have been prepared and added to our comparative collection. The fossil ariid material includes over 200 bones with many cranial elements, which are the most characteristic parts for identifying the remains at the species level. In some specimens, even the otoliths (lapilli) were recovered. Post-cranial elements, such as pectoral and dorsal spines, and vertebrae were commonly found. Our preliminary identifications of these Ariidae fossils indicate the presence of at least four species, of which *Hexanematichthys sagor* is the most abundant, followed by *Plicofollis nella*, *Nemapteryx nenga* and *Arius* cf. *maculatus*: they are still extant in the Indo-Western Pacific. The rare remains of eeltail catfishes (Plotosidae) have also been recovered. Relationship between total body length (TL) and the size of selected bones of the modern specimens allowed establishing the TL range of the fossil specimens. This pilot study illuminates similarities to the modern size distribution of these catfishes, as *P. nella* being the largest species in our record. The modern ariids have a broad habitat range, as some are known to travel between marine and nonmarine environments during their lifetime. Therefore, based on the fossil fauna ideally the palaeoenvironment can be reconstructed. The vertebrate assemblage as a whole consists of reworked material and of mixed marine and nonmarine faunas, including fully marine fish taxa (e.g., shark teeth: *Galeocerdo*) and few terrestrial mammal remains (e.g., deer and pig teeth). The fish remains dominate, and the ariids are the most common ray-finned fish. The fossil ariid fauna of Sarawak would be best linked to coastal marine environment alongside with estuaries, something similar to that of today in the transitional environment around the Rajang River delta. In such a setting the presence of marine and nonmarine vertebrate fossils is not surprising, even if the exact stratigraphic origins of the fossils are not known yet (i.e., the source deposits).

Keywords: sea catfish, fossil bones, otolith, allometry, palaeoenvironment, Borneo, Rajang River

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Fish evolution through the Mesozoic and Cenozoic

Development and replacement of the marine and brackish water teleostean fish faunas throughout the Oligocene and Miocene of the Eastern Paratethys

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At the beginning of the Oligocene, an intracontinental basin, the Paratethys, separated from the Tethys. The most diverse assemblage of marine fish in the territory of the former USSR is confined to the Rupelian of the North Caucasus and its analogues in Abkhazia and Azerbaijan. Of the 76 taxa of bony fishes reliably recorded from the Rupelian of the Eastern Paratethys, 51 belong to the acanthopterygians, but most commonly collected fishes are clupeids. The co-dominants are scabbardfish *Anenchelum*, *Palimphyes*, *Protobrotula*, etc. The composition of the fish fauna indicates a subtropical climate of the Pshekha time, and the appearance of *Aeoliscus*, *Fistularia* and *Bregmaceros* marks warming in the middle of the Rupelian time. The anaerobic environment at the bottom of the Early Maikop Sea began deep; at least 300–400 m of the upper water column were suitable for fish life. In the second half of the Early Oligocene, the Eastern Paratethys closed and desalinated, but in the late Oligocene this basin is again characterized by marine conditions. However, there has not been a complete restoration of fish biodiversity: to date, no more than 30 bony fish taxa have been identified from the Upper Oligocene of the North Caucasus. In the upper Aquitanian – lower Burdigalian a rich and rather diverse assemblage of marine fishes was found in the Caucasus and Crimea, from which at least 49 taxa were noted, of which 36 belong to acanthopterygians. Pelagic, mainly neritic fishes predominate here (clupeids predominate in the number of finds), and typical meso- and bathypelagic fishes are almost absent. In the early Miocene fauna, for the first time for the Eastern Paratethys, bottom dwelling Blenniidae and Gobiidae appear, flounders become relatively numerous, which, however, are mainly represented by their pelagic larvae. Subsequently, the Eastern Paratethys desalinated, and in the Tarkhanian and the early half of the Chokrakian (early Middle Miocene), this basin is again characterized by a marine regime; due to the Tarkhanian transgression, marine biota was restored. Mesopelagic lightfishes *Vinciguerria* appear in the Tarkhanian of the northern Caucasian basin for the first time after the Lower Oligocene, which indicates a significant lowering in the border of the anoxic zone. In the Tarkhanian and Chokrakian 32 species of bony fishes were noted, most of which belong to stenohaline genera and could not tolerate significant desalination. By the end of the Chokrakian, the salinity of the Eastern Paratethys decreased again (Karaganian time), and afterwards, only in the Konkian time, the characteristics of the basin approached the normal sea. The Sarmatian (late Middle to Upper Miocene) fishes of the Eastern Paratethys are better known than the Karaganian and Konkian ones, herewith two rich localities of early Sarmatian bony fishes, differing in composition, are known: one from northern Moldova, and the other from the North Caucasus. In total, more than 40 forms of teleosts were noted in these two localities, of which the vast majority belong to the acanthopterygians. While herrings predominate in the North Caucasus in terms of the number of finds, in Moldova predominate *Atherina*, and herrings, gobies and porgies are co-dominant. Sarmatian Moldovan gobies are extremely diverse in their systematic composition. At the beginning of the Late Miocene the Eastern Paratethys was completely closed, and in the early Maeotian it was again episodically connected with the open waters. Maeotian fishes have been studied very poorly so far. Marine fish faunas are not known from the younger deposits of the Eastern



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Paratethys. A brackish-water fish assemblage consisting of 11 species has been recorded from the terminal Miocene of Abkhazia. Thus, fluctuations in climate and eustatics in the Cenozoic, and changes in the hydrological regime of the late Tethys and Paratethys over time caused the extinction of fish faunas with their subsequent incomplete restoration.

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Keywords: Bony fishes, ichthyofaunas, Eastern Paratethys, marine, brackish water, Oligocene, Miocene



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Fish evolution through the Mesozoic and Cenozoic

Preliminary morphological studies of Ariidae (sea catfish) otoliths from Northern Borneo

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Morphological study of sea catfish otoliths (Ariidae, Siluriformes) along with their basic systematic and taxonomic knowledge in Borneo is rather sparse. In this work, we provide morphological information on lapilli otoliths of several modern ariid species with the aim to evaluate their taxonomic application and to study fish diversity of past fish assemblages. Ariid otoliths have a rather complex and almost indistinguishable morphological features, especially at lower taxonomic level. Therefore, the analysis was not limited to the otolith's general shape and its sulcus morphology (its unique "pattern" or "fissure"), but their other intricate details such as its *prominentia marginalis* (the translucent part of the otolith visible on its ventral face) was also examined. A total of 82 modern otoliths belonging to 10 ariid species were collected in various fish markets in Brunei and Bornean Malaysia. Additionally, the work of Ohe (2006) was used for extending the modern database, which investigated and illustrated the otoliths of 16 ariid species (7 overlaps with our record). The obtained morphological characteristics were then compared to 164 fossil Ariidae otoliths found in late Miocene deposits of Brunei Darussalam. Altogether, 7 Ariidae species were distinguished in the fossil record, in which *Nemaphryx nenga* (thickspined catfish) is the most abundant. The recovered taxa suggest a generally shallow marine coastal environment, although the faunal composition among the fossil sites varies, which may indicate subtle environmental differences. These disparities could possibly appear as a consequence from coastal processes and related salinity gradient between fully marine and deltaic/estuarine brackish conditions.

It must be mentioned that fossil otoliths were first studied in the region by Fred C. Stinton in 1962. He reported a total of 20 ariid otoliths from the Miri Formation and Seria Formation, from the same lithostratigraphic units where our materials were collected. Stinton described 4 new fossil species based on his material. Upon inspection of his illustrations, and the type specimens deposited in the Natural History Museum in London, our preliminary results indicate that the otoliths of the fossil taxa could not be distinguished from the otoliths of certain extant species. Therefore, we also suggest a revision of Stinton's ariid species.

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Keywords: Sea Catfish, Lapilli Otolith, Otolith Morphology, Palaeoenvironment



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Fish evolution through the Mesozoic and Cenozoic

A new exceptionally preserved basal actinopterygian fish in the juvenile stage from the Upper Triassic Amisan Formation of South Korea

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The study of the large paraphyletic group of extinct palaeoniscoid fishes has shed light on the diversity and evolutionary history of basal actinopterygians. However, only a little ontogenetic information about palaeoniscoids is known because palaeoniscoids in the early stages of development are very rare. Here we report a new basal actinopterygian fish in the juvenile stage from the Upper Triassic Amisan Formation of South Korea. Fourteen specimens, including five counterpart specimens, represent a new taxon showing exceptional preservation with the eyes possibly containing the crystalline lens, the otoliths, and the lateral line canals without covering scales. The new taxon has the typical body plan of palaeoniscoids by having an elongate fusiform body, a large gape, a strongly heterocercal caudal fin, and a series of dorsal and ventral scutes on the caudal peduncle. However, a unique combination of features (the large protruded eyes, a single rectangular branchiostegal ray with a posterodorsal spine, and a large dorsal fin opposite the pelvic fin in the middle of the body) makes the new taxon distinguishable from other basal actinopterygians. Several morphological features reflect the surviving strategies in the early developmental stage of the new taxon. The eyes are quite large and protrude anteriorly beyond the margin of the snout. It would make binocular vision possible and largely contribute to targeting and catching prey. The initially developed dorsal and ventral scutes on the caudal peduncle and the development of squamation from posteriorly to anteriorly would indicate the stiffness of the tail. The increased stiffness of the tail would improve swimming capability by increasing thrust and swimming speed. Furthermore, all specimens show initial ossification of the upper and lower jaws and the cleithrum, where the muscles that enable the pectoral fin to move are attached. These characteristics would be linked to the adaptation of young individuals to increase their viability by preferentially acquiring the ability to feed and swim.

Keywords: Basal Actinopterygii, Palaeoniscoidae, Juvenile, Late Triassic, Amisan Formation, South Korea





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Fish evolution through the Mesozoic and Cenozoic

Otolith-based ichthyofauna from Cassian Formation (Carnian), Northern Italy

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The fossiliferous beds of Late Triassic Cassian Formation (Northern Italy, Southern Alps) is renowned for hosting the most diverse early Mesozoic marine invertebrate fauna known worldwide. It is also known to yield some well-preserved vertebrates fossils, in particular from the base of the formation (Bizzarini et al. 2001). The upper part in turn provided only a few chondrichthyan and actinopterygian teeth and scales (Bernardi et al. 2011). The otoliths in the Cassian Formation are excessively rare and only one specimen found at Settsass-Scharte locality has been reported as a possible palaeoniscid by Nützel & Kaim (2014). Our subsequent investigations resulted in the find of a fragmentary fish skull and additional otoliths in the same locality and several specimens in Picolbach and Misurina Skilift localities in the same formation. We compared the Cassian otoliths to their recent and Mesozoic counterparts. We argue that most of the otoliths from Picolbach and Misurina belong to very young, or even larval lepisosteiform neopterygian (compare Long and Snow, 2016). Otoliths from Settsass Scharte are more reminiscent of sphaeronchid teleost rather than palaeoniscid. Therefore, the otolith fauna from the Cassian Formation represents neopterygians early domination, and the early stage in teleost diversification.

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Keywords: Otolith, skull, Neopterygii, Teleostei, Cassian Formation, Carnian, Norian





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Fish evolution through the Mesozoic and Cenozoic

New data on Barbinae fish from the Pliocene of the Camp dels Ninots site (Girona, Spain)

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The Upper Pliocene volcano-sedimentary site of Camp dels Ninots (located in the village of Caldes de Malavella, Girona, Catalonia, Spain) preserves sediments of an estimated age around 3.3–3.1 Ma. The locality is considered a fossil Konservat-Lagerstätte preserving a wide range of fossil remains, including flora, mammals, reptiles, amphibians and fishes, including remains of genus *Luciobarbus* Heckel, 1843 (Gómez de Soler et al., 2012; Claude et al., 2014; Příkryl et al., 2016). Contemporary representatives of this genus are species-diversified, inhabiting freshwater and brackish sites of Europe, Asia and Africa (Froese and Pauly 2022).

Number of Barbinae fossil remains have been described from pharyngeal elements and teeth only and their comparison with more completely preserved taxa is often difficult. The specimens from the Camp dels Ninots site represent middle sized fish (the standard length of the largest recorded specimen is slightly more than 400 mm), with the pharyngeal formula showing condition of 4-2-1 or 4-3-2. The teeth show positional heterodonty, with mamilliform to spatulate morphology, reflecting individual position within the pharyngeal bone. The available specimens allow reconstructing the general morphology of the skull and detailed morphology of selected cranial and postcranial bones. Data are used for a detailed comparison with other fossils and contemporary Barbinae taxa to determine affinity of the fossils under consideration. This study is part of the projects GAČR 21-33751S (Czech Science Foundation).

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Keywords: Europe, Iberian Peninsula, Pliocene, osteology, Cyprinidae, *Luciobarbus*



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Fish evolution through the Mesozoic and Cenozoic

Early Pleistocene fish assemblages from the Orce Archeological Zone (Iberian Peninsula; Spain)

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The Orce Archeological Zone (province of Granada, southeastern Spain) includes several fossiliferous sites of Late Pliocene and Early Pleistocene age. Two of them, Barranco León (1.4 Ma) and Fuente Nueva 3 (1.2 Ma) have provided some of the oldest hominin evidence from southwestern Europe (Toro-Moyano et al., 2013) and this fact put the area to center of a scientific interest with various aspects of research. In particular, paleoecological reconstructions before and after this first hominin dispersal into Europe has been one of the main lines of the last Orce Research Project. The area is characterized by a lacustrine-palustrine environment (Oms et al., 2011) with shallow lakes, ponds and wetlands. The archeo-paleontological sites are situated on what was the marginal area of the large saline Baza Lake (Anadón et al., 1987). During periods of lake expansion, saline conditions extended throughout the basin, but when the lake receded, the basin margins were fed by freshwater inputs of thermal origin and precipitation runoff (Anadón et al., 2015).

Besides the large mammals unearthed from the sites, the faunal collections also include rich microvertebrate assemblages comprising fish remains. Detailed examination of the separated skeletal remains allows delimiting distribution of the fish remains to within layers D1, D2 and E of the Barranco León site. The absolute majority of the fish remains is represented by bones and bony fragments of the family Cyprinidae. For the moment, it is possible to recognize the presence of *Squalius* and Barbinae (*Barbus* or *Luciobarbus*) individuals identified based on pharyngeal elements (teeth and fragments of the pharyngeal arches). Furthermore, several specimens of non-cyprinid fish in layers D1 and D2 were identified. These specimens are represented by three fragments of dentaries and several abdominal vertebrae. These remains are preliminary identified as belonging to Gobiidae, but definitive determination is conditioned by more detailed comparison. Some paleoenvironmental issues are briefly discussed, such as the absence of fish remains in Fuente Nueva 3 that could be explained by the colder and drier conditions evidenced at this site (Sánchez-Bandera et al., 2020).

This study is part of the Leakey Foundation project "Early hominin climate envelope: the lower vertebrate perspective", and the General Research Project "Primeras ocupaciones humanas y contexto palaeoecológico a partir de los depósitos Pliopleistocenos de la cuenca Guadix-Baza. Zona Arqueológica de la cuenca de Orce" (ref. BC.03.032/17) funded by the Consejería de Cultura, Junta de Andalucía.



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Keywords: Europe, Iberian Peninsula, Pliocene-Pleistocene, osteology, Teleostei





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Fish evolution through the Mesozoic and Cenozoic

A Putative spadefish (Acanthomorpha: Ephippidae) from the Indo-Pacific region and its implications for marine fish biogeography in the Paleogene

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Ephippidae (spadefishes) is a clade of marine fishes containing 15 extant species divided among 8 genera. Found on coral reefs and in open waters worldwide, ephippids are laterally compressed fishes with small, non-protrusive mouths and often bear striking, dark vertical bars of pigmentation on their flanks. Apart from so-called “Tilly bones,” fossil hyperostotic elements attributed to ephippids and other tropical fishes, the paleontological record of ephippids is poor. Articulated remains of putative ephippids derive almost exclusively from the early Eocene (Ypresian, ca. 49 Ma) deposits of Bolca, Italy, and include two extinct genera: *Eoplatax* and *Archaeophippus* (Blot 1980). Today the greatest diversity of extant spadefish species is in the Indo-West Pacific, yet there are no known fossil ephippid remains from this region. Here we report the first fossil spadefish from the Indo-Pacific, from the middle Eocene (Lutetian, ca. 47 Ma) Habib Rahi Formation of western Pakistan. Preserved as an impression on a limestone slab, this single articulated individual does not preserve definitive synapomorphies of ephippids, such as the branchial skeleton, dentition, and pelvic girdle (Cavalluzzi, 2000). However, intact portions of the skeleton correspond closely to the anatomy of *Eoplatax* from Bolca. Major similarities include a nearly circular body, greatly elongated dorsal- and anal-fin rays, and a very deep caudal peduncle. The discovery of an *Eoplatax*-like fossil in the middle Eocene of Pakistan could have important implications for marine fish biogeography in the Paleogene. At this time, Indo-Pakistan is thought to have been outside the margins of an ancient biodiversity hotspot centered in the West Tethys. The presence of similar faunal elements in the ancient Indo-Pacific can help to constrain models of shifting biodiversity hotspots during the Cenozoic. Such hotspot migration is supported by fossil evidence as well as patterns of relationships among some extant groups. Integration of putative fossil ephippids, including the new form from Pakistan, into a phylogenetic framework with living examples will be critical for determining what—if any—bearing spadefishes might have on these broad biogeographic questions.

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Keywords: Biogeography, Acanthomorpha, Indo-West Pacific, Ephippidae





Session 26 - KEYNOTE

Palaeozoic fishes and the first tetrapods

Life on the cusp of apocalypse? A new terrestrial biota from the latest Devonian of Greenland

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The end-Devonian mass extinction, representing the final episode of the Hangenberg Crisis, is commonly regarded as an important milestone in the early evolution of tetrapods. It is held to mark the beginning of "Romer's Gap", a 20 million year hiatus in the tetrapod fossil record, and when tetrapods again emerge into visibility after this gap they appear very different: more advanced, with higher diversity and disparity, and including early members of the crown-group lineages. The proposed explanation is that tetrapods were severely affected by the end-Devonian extinction and then rebounded with a new radiation of more derived forms. This has also been linked to the transition from an essentially aquatic lifestyle to full terrestriality. In fact, none of these claims has strong evidential support. Romer's Gap is gradually beginning to fill up with new Early Carboniferous discoveries from Britain and Canada, which show that tetrapod faunas of quite high diversity existed already during the Tournaisian. Fragmentary remains of tetrapods resembling the Carboniferous genus *Whatcheeria* have been recovered from Late Devonian localities in the United States and Belgium, suggesting that this diversification had begun before the end-Devonian extinction. Furthermore, and crucially, there has until now been no significant tetrapod record from the latest Devonian, and thus no information about the tetrapod faunas that encountered the extinction event. Only *Tulerpeton* from Russia is of probable terminal Famennian age; all other late Famennian tetrapods, such as *Acanthostega* and *Ichthyostega* from Greenland, and *Ventastega* from Latvia, are slightly older. Here I present a first report on a new end-Devonian fossil assemblage from the top of the Stensiö Bjerg Formation of North-east Greenland, collected during July and August 2022, that fills this gap. The bulk of the material comes from a 7.5m thick floodplain sequence, with additional specimens from over- and underlying fluvial to lacustrine sandstones. At least 3, but more probably 4-5 tetrapods are present, all except possibly one new to science. For comparison, the previous 90 years of collecting in the Devonian of Greenland has produced only 4 tetrapods (*Ichthyostega*, *Acanthostega*, *Ymeria* and *Brittagnathus*). They are accompanied by rare lungfish and acanthodian remains but no other fish. Phylogenetically, some appear to be '*Ichthyostega*-grade' while others are substantially more crownward. The body fossils, which are perfectly three-dimensional and include partly articulated individuals as well as isolated bones, are accompanied by tetrapod coprolites (the only known Devonian examples), footprints and body resting traces. There are also abundant plant remains, including in-situ arborescent lycopods, and large arthropod fragments. The assemblage appears to represent a thriving tetrapod-dominated ecosystem, quite different from the prevailing idea of Devonian tetrapods as a rare, low-diversity component of fish-dominated faunas.

Keywords: Devonian, Famennian, Tetrapoda, Greenland, Hangenberg Crisis



Session 26 - ORAL

Palaeozoic fishes and the first tetrapods

Quantifying convergence and innovation in fossil fish ecomorphology across time and space

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Biomechanical studies routinely link fish form with functional and ecological demands, including hydrodynamics and feeding mechanics. The reality of this phenomenon is also shown by the numerous cases of convergence in body form among fishes and other vertebrates (e.g. whales, ichthyosaurs), and even invertebrates (e.g. sea slugs), past and present. Anomalous, single-origin forms like seahorses are the exception that proves the rule. However, body form has never been quantified across the 500-million-year fish record and/or their 34000+ living species, let alone the extent and correlates (ecological and structural) of convergence across time and space. Construction of the requisite ‘morphospace for all fishes’ was limited by a lack of homologous structures for geometric morphometrics, and the apparent complexity of their traits. Here, we show results from a new reductionist approach using discrete coding to captures the form of functionally-relevant, analogous features, such as “median hydrofoils,” regardless of their construction. This has permitted the creation of a single morphospace encompassing Paleozoic jawed and jawless fishes as well as modern tropical fishes from the Great Barrier Reef. Akin to ‘Raup Space’ for mollusks, this fish space allows explicit testing of the scope and stability of links between specific forms for functional traits, relationships between form, or form diversity, and other ecological variables (e.g. benthic assemblage zone, tooth form, salinity, or known/inferred diet), and changes in ecotype occupation and clustering across time and space, allowing us to address long-standing hypotheses of ecological diversity.





A morphofunctional analysis of jaws and feeding in Devonian antiarchs

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Antiarch placoderms, known from the Silurian to end Devonian represent the second most successful group of placoderms after the arthrodires. Their body morphology has traditionally been considered conservative, characterised by a boxy dermal armour, highly modified pectoral fins, a specialised neck joint and modified jaws. The antiarchs were thought to lack a number of characters considered key gnathostome features; however, discoveries of basal antiarchs from China have now shown the presence of pelvic fins and girdles (Zhu et al., 2012) and confirmed the presence of dentine in the dermal armour (Giles et al., 2013) indicating that their evolution is characterised by a series of “losses”. Although the excellent preservation, including soft tissue, present in multiple species has provided a wealth of information, considerable controversy remains in respect to the orientation and function of the jaw elements.

Our recent study (Lebedev et al., 2022) utilising CT scanning has enabled the reconstruction of the jaw apparatus in antiarchs and has demonstrated that although antiarch jaws follow the same basic pattern there is considerable variety of morphologies between families. The porous nature of the jaw elements suggests that blood supply extended to the surface of the bone and, in order to have been effective in food manipulation and processing the jaw elements must have been covered by an epidermal layer (Lebedev et al., 2022). It was determined that the suborbital–infragnathal morphofunctional unit in antiarchs could be divided into four distinct morphotypes. These differences in structure suggest differences in the shape of the mouth between antiarchs and are therefore considered to indicate different methods of food processing and thus different prey.

This hypothesis is supported by the occurrence of prey items in the mineralised intestine of *Bothriolepis* which included the valves of conchostracans (Cloutier 2013) and detritic-like bone material in the stomach region of *Asterolepis* (Upeniec, 2001; 2011). The long spiral valved intestine of *Bothriolepis canadensis* supports at least partial herbivory with digestion aided by bacteria in a reducing environment. In addition, this reducing environment would have also facilitated the preservation of the soft anatomy.

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Keywords: Antiarch, biomechanics, feeding ecology, tomography, Devonian





Session 26 - ORAL

Palaeozoic fishes and the first tetrapods

New discoveries of exceptionally well-preserved fishes from the Late Devonian Gogo Formation of Western Australia

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Fish fossils from the Frasnian Gogo Formation of Western Australia are found as uncrushed, 3D-preserved remains ranging from complete individuals to isolated single bones. Some have soft tissue preservation with muscles and even soft organs preserved. Gogo is one of the most diverse vertebrate assemblages of this age with over 50 species of placoderms, osteichthyans and sharks that once inhabited the algal-stromatoporoid reef environment. Recent collecting from the sites keeps producing new taxa from the formation as well as more complete representation of species originally described from incomplete type material. New placoderm specimens include more remains of the incompletely known forms *Bullerichthys* and *Kimberleyichthys* as well as new taxa of torosteid and eastmanosteid arthrodires. One of these is a new large predatory genus related to *Eastmanosteus* but bearing well-developed pointed teeth on all gnathal plates. New smaller taxa of torosteid arthrodires indicate that micro-predatory niches were occupied by fishes on the reef system. New material of ptyctodontid placoderms reveals insights into feeding mechanics and endocranial features. The antiarch *Bothriolepis* sp. from Gogo is undescribed but is now represented by many new specimens and is currently under focus by research teams in Australia and the UK. New osteichthyan remains include a strange oticooccipital unit with the posterior half of the skull roof intact, at first thought to represent a porolepiform, but now shown to be a basal sarcopterygian allied to coelacanths but lacking the typical postparietal shield pattern seen in most coelacanths. A new Gogo coelacanth known from two specimens is currently under study and shows many features that have enabled us to do a thorough phylogenetic analysis of the group. Lungfishes are well-represented at Gogo with some 12 taxa, but some earlier named forms thought to represent existing European genera are now known to represent new taxa (eg *Griphognathus*, *Chirodipterus*). New research on dipnoan feeding biomechanics has begun. Chondrichthyans were initially unknown from the fauna for many decades, in the past decade a stem-shark (*Halmacanthodes*) and a selachian (*Gogoselachus*) were described and a new, slender scaleless and edentulous form is currently under investigation. New research projects will focus on the palaeoecology of the Gogo Formation and will allow us and our team of collaborators to undertake detailed studies of trophic interactions between fishes and invertebrates of the ancient reef and to model the robusticity of the ecosystem and compare it with modern reefs.





Session 26 - ORAL

Palaeozoic fishes and the first tetrapods

An exceptional new coelacanth from the Devonian of Australia, and rates of morphological evolution in Actinistia

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Coelacanths (Actinistia) are a clade of lobe-finned fish that have a lineage stretching back some 400 million years to the Devonian Period. Together with lungfish and tetrapods they comprise the extant piscine Sarcopterygii (lobe-finned fish). Although the lineage was thought long extinct since the end of the Mesozoic, an extant species of coelacanth (*Latimeria chalumnae*), was recognised to science in the 1930s. *Latimeria* has been long-proclaimed as a “living fossil” due to its supposed primitive anatomy and purported low rates of morphological evolution.

The fossil record of coelacanths is considerable with over 100 species described, although only 12 of these are of Devonian age. 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 (although the posterior body is missing). Micro-CT is used to elucidate internal cranial anatomy of the new taxon and provides insights into the early palaeoneurological evolution of the group.

Maximum parsimony, Bayesian and Bayesian tip-dating analyses provide insight into the latest phylogenetic relationships for the Actinistia as well as calculating rates of phenotypic evolution. All analyses produce similar topologies using our greatly expanded character matrix comprising 268 discrete, 14 meristic and 40 continuous morphometric characters and 87 coelacanth taxa. All trees produce congruent topologies with the new taxon recovered as a basal member of the actinistian total group as sister taxon to *Gavinia*. *Latimeria* displays extraordinary evolutionary conservatism with little innovation in the last 100 million years, although continuous adjustment of meristic and morphometric traits indicates that although it may have stopped producing morphological novelties, the lineage does continue to evolve and should thus not be considered a “living fossil”.

Keywords: Gogo Formation, Devonian, Palaeozoic, Sarcopterygii, Actinistia, rates of morphological evolution, tomography, palaeoneurology.



Session 26 - ORAL

Palaeozoic fishes and the first tetrapods

Diversification of jaw geometry during the initial radiation of lobe-finned fishes (Osteichthyes: Sarcopterygii)

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The origin of crown sarcopterygians around 420 Ma proceeds the emergence of major lineage specializations, including contrasts relating to morphology of the feeding apparatus. Key examples include dental plates in lungfishes, reduction of marginal jaw bones in coelacanth, and elaboration of fangs in a variety of porolepiforms and tetrapodomorphs. Such putative ecological divergence, alongside evidence that individual lineages show high rates of evolutionary change early in their history, mark this event as a possible episode of adaptive radiation. Here, we explicitly test this hypothesis using mandibles as a taphonomically robust, taxonomically diagnostic trait intimately associated with ecology. We assembled a dataset of over 30 three-dimensionally preserved jaws of total-group Sarcopterygii obtained by CT scanning or photogrammetry. Most are dipnomorphs or tetrapodomorph fishes, plus a smaller sample of stem sarcopterygians and taxa of less certain placement. We developed a basic landmarking scheme (6 fixed landmarks, 8 curves with sliding semilandmarks) capturing overall jaw shape and orientation, including aspects of the glenoid and adductor fossa. We paired these data with a composite phylogenetic tree with branch durations informed by the ages of fossil tips. We examined the fit of three basic models of trait evolution to these shape data in a multivariate framework: Brownian motion (BM; diffusive evolution at a constant rate), early burst (EB; diffusive evolution with a declining rate over time, corresponding to theoretical predictions for adaptive radiation), and Ornstein-Uhlenbeck (OU; constant rates of change with a central tendency limiting the accumulation of variation over time). Our results indicate that EB is the best-supported model for jaw shape evolution, corroborating our hypothesis. This implies that high initial rates of phenotypic evolution complemented the extensive exploration of shape space early in the history of lobe-finned fishes.

Keywords: jaws, Sarcopterygii, 3D geometric morphometrics, adaptive radiation, Paleozoic



Session 26 - ORAL

Palaeozoic fishes and the first tetrapods

Unexpected discrepancy between bone microanatomy and presumed lifestyle revealed in Carboniferous tetrapods

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The terrestrialisation of vertebrates is a major evolutionary event that effects drastic changes in the limb bones. It has been an area of great interest in the palaeontological community. However little focus has been put on the patterns of ossification of these bones, probably because of the scarcity of the fossil material. This study aims to map in detail the diversity of bone patterns in the humeri of a wide variety of stem tetrapods from the Carboniferous, based on a non-destructive method: high-resolution propagation phase-contrast synchrotron microtomography. We have observed the internal bone architecture of the following Carboniferous genera: *Baphetes*, *Pederpes*, *Ossinodus* and *Crassigyrinus*. We have investigated, among others, their ossification pattern, compactness profile, and bone microstructure. Unexpectedly, our results reveal that they all retain a very spongy microanatomy, regardless of their varying lifestyles (from aquatic to terrestrial). They all have an unossified anterior margin where muscles are expected to connect and play a major role, even in terrestrial locomotion. This discrepancy between bone compactness, ossification pattern and lifestyle suggests that cartilaginous entheses probably played a function in the adaptation of Carboniferous tetrapods to land. This further indicates that a shift in microanatomy towards a more tubular long-bone structure in terrestrial locomotion is probably a more derived feature than expected.

Keywords: Carboniferous, stem tetrapods, humeri, synchrotron scanning, microstructure





Session 26 - POSTER

Palaeozoic fishes and the first tetrapods

Van Wees JD, Stephenson RA, Ziegler PA, Bayer U, McCann T, Dadlez R, et al. 2000. On the origin of the southern Permian Basin, Central Europe. *Marine and Petroleum Geology*, 17(1), 43–59.

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Keywords: Chondrichthyes, Osteichthyes, Poland, Baltic countries, Permian, Zechstein Basin



Session 27 - ORAL

Metazoan diversifications from Early Palaeozoic Lagerstätten (IGCP 735)

Ontogenetic factors controlling preservation bias in the shrimp, *Palaemon varians*

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The arthropod life-cycle in the fossil record is highly biased towards the later ontogenetic stages of their development, with larvae and other early post-embryonic stages being rarely preserved. Amongst the Burgess Shale-type (BST) Lagerstätten, only the Haiyan locality in China and the Fezouata Shale in Morocco yield abundant early developmental arthropod stages. Similarly, the Orsten biota yields almost exclusively larval and juvenile euarthropods, without preserving the later developmental stages. Such ontogenetic data offers invaluable information about the evolution of the development of metazoan clades, but the taphonomic biases controlling preservation of juvenile forms remains poorly understood. Here we conducted taphonomic experiments to investigate the preservation potential of the common marine shrimp *Palaemon varians* at six stages of its development, from eggs in an ovigerous female, through larval stages up to the juvenile, and adult. Individual developmental stages showed differential preservation in line with other studies, with morphologically informative characters being lost through decomposition. Disarticulation patterns appear markedly distinct especially between larvae and adult specimens. The ontogenetic differences, especially in the cuticle structure between the adult shrimps, and larvae control the overall breakdown of the carcass and could explain absences in the fossil record of some developmental stages in certain taxon. These experimental results provide important information on the relationship between ontogeny and taphonomy, allowing us to start to outline the variation in preservation in the arthropod life-cycle at different Lagerstätten.

Keywords: Ontogeny, experimental taphonomy, *Palaemon varians*, Lagerstätten



Session 27 - ORAL

Metazoan diversifications from Early Palaeozoic Lagerstätten (IGCP 735)

The lower Cambrian Sirius Passet Lagerstätte (North Greenland) is a natural laboratory for investigating primary ecological and taphonomic patterns

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Burgess Shale-type Lagerstätten provide some of the best opportunities to study the Cambrian Explosion. They record distinct depositional environments, each with different limitations for understanding ecosystem dynamics, such as low fossil densities (Caron et al., 2014), temporally punctuated records (Caron and Jackson, 2006; Zhao et al., 2009; Nanglu et al., 2020), and filtration by biased preservation (Saleh et al., 2020, 2021) and mixing of faunas by transportation (Bath Enright et al., 2021). The lower Cambrian Sirius Passet Lagerstätte (North Greenland) is distinct in this context: it preserves primary taphonomic and ecological signals with minimal secondary filtering. These are a consequence of preservation within a stacked succession of dilute gravity flows which captured a continuous sequence of high-density, *in situ*, fossil assemblages. The fossils include both pelagic and benthic organisms that are predominantly fully articulated and often retain internal tissues such as guts, muscles, and nervous systems. Together, this suggests that the organisms experienced minimal decay or transportation prior to burial. Phosphatization of labile soft tissues is extraordinarily frequent across several taxa, permitting a unique opportunity to test existing hypotheses for the underlying mechanism(s). Ecological bed-by-bed patterns reveal temporal population dynamics, with some bedding surfaces containing disproportionately high numbers of small (juvenile) *Isoxys volucris* suggestive of mass spawning events. Additionally, gut contents, preserving direct predator-prey interactions, show that *Isoxys volucris* was an important prey item within the biota's food web. Altogether, Sirius Passet presents a unique natural laboratory to understand Cambrian ecosystem dynamics at a biologically meaningful scale.

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Session 27 - ORAL

Metazoan diversifications from Early Palaeozoic Lagerstätten (IGCP 735)

Zhao, F., Caron, J.-B., Hu, S., and Zhu, M., 2009, Quantitative analysis of taphofacies and paleocommunities in the Early Cambrian Chengjiang Lagerstätte: *Palaios*, v. 24, p. 826–839.

Keywords: Sirius Passet, Burgess Shale-type Lagerstätten, taphonomy, phosphatization, paleoecology, ecosystem dynamics



Session 27 - ORAL

Metazoan diversifications from Early Palaeozoic Lagerstätten (IGCP 735)

The Chengjiang Biota inhabited a deltaic environment

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The Chengjiang Biota is the earliest Phanerozoic soft-bodied fossil assemblage offering the most complete snapshot of Earth's initial diversification, the Cambrian Explosion. Although palaeobiologic aspects of this biota are well understood, the precise sedimentary environment inhabited by this biota remains debated. Herein, we examine a non-weathered core from the Yu'an-shan Formation including the interval preserving the Chengjiang Biota. Our data indicate that the succession was deposited as part of a delta influenced by storm floods (i.e., produced by upstream river floods resulting from ocean storms). Most Chengjiang animals lived in an oxygen and nutrient-rich delta front environment in which unstable salinity and high sedimentation rates were the main stressors. This unexpected finding allows for sophisticated ecological comparisons with other Burgess Shale-type deposits and emphasizes that the long-held view of Burgess Shale-type faunas as snapshots of stable distal shelf and slope communities needs to be revised based on recent sedimentologic advances.

Keywords: Exceptional preservation, China, sedimentology, taphonomy, Palaeozoic

Session 27 - ORAL

Metazoan diversifications from Early Palaeozoic Lagerstätten (IGCP 735)

The oldest hurdiid radiodont in China known from complete specimens

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The Qingjiang Biota is a recently described Burgess Shale-type fossil Lagerstätte from the Cambrian Series 2, Stage 3 of South China, preserving an early Cambrian community characterised by cnidarians, kinorhynchs, sponges, algae and nektobenthic arthropods (Fu et al., 2019). Here we describe the first known radiodont from the Qingjiang Biota, based on articulated specimens. It has a body bearing wide lateral flaps and dorsal setal blades, and a head consisting of stalked eyes, a tetradial oral cone, and a pair of frontal appendages with five elongated endites. Details of the digestive tract, the nervous system, and potentially the circulatory system are visible. It has a unique head organisation with a single dorsal carapace covering three prominent head segments, as well as visible glands in the midgut, and a body termination consisting of a central spine flanked by two rounded tail flukes. Phylogenetic analyses identify the Qingjiang radiodont as belonging to the Hurdiidae.

Hurdiids are rare in the Cambrian Series 2, known only from isolated carapaces and frontal appendages (Guo et al., 2019; Wu et al., 2022). The Qingjiang radiodont thus greatly expands our knowledge of early hurdiid evolution and allows for comparison of its detailed anatomy with other contemporaneous radiodonts in China, and with the abundant and diverse hurdiids that are globally distributed in younger strata.

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Key words: Radiodonta, Hurdiidae, Qingjiang Biota, Lagerstätte, South China, Cambrian



Session 27 - ORAL

Metazoan diversifications from Early Palaeozoic Lagerstätten (IGCP 735)

New insights into the three-dimensional ventral morphology of early Cambrian euarthropods from the Chengjiang biota, South China

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The early Cambrian (Stage 3) Chengjiang biota in South China contains the oldest exceptionally preserved metazoan-dominated biota in the Phanerozoic, and thus represents a valuable window into the biodiversity and ecology of the biosphere during the Cambrian Explosion. The fauna preserved in Chengjiang is dominated by euarthropods, animals with jointed appendages and hardened exoskeletons, which vary enormously in terms of their relative abundance and quality of fossilization. Consequently, whereas many Chengjiang euarthropods are well known in terms of their morphology and functional ecology, others are exceedingly rare or simply too poorly preserved for a comprehensive description. The recent application of micro computed tomography (micro-CT) imaging for visualizing Chengjiang fossils has opened a new dimension for the study of these extinct organisms, and revealed new insights about their anatomical and functional complexity. Micro-CT allows to examine fine morphological structures that are either concealed by rock matrix or too small for manual preparation, thanks to the extensive pyritization of Chengjiang fossils. We demonstrate that ventral appendage heteronomy is likely an ancestral trait for members of Artiopoda. Our data challenges the long-held view that the largely homonomous biramous appendages of trilobites reflect a primitive condition, and instead show that early-branching artiopods had various degrees of appendage differentiation, and likely performed different functions throughout the body. The use of micro-CT also casts new light on the ventral morphology of the head in *Leanchoilia illecebrosa* and *Jianfengia longicaudata*, and demonstrates the presence of a labrum in these great appendage euarthropods, with implications for the evolution of the euarthropod head problem.

Keywords: Micro computed tomography, exceptional preservation, Trilobitomorpha, Megacheira, pyritization





Session 27 - ORAL

Metazoan diversifications from Early Palaeozoic Lagerstätten (IGCP 735)

Frontal appendages from the Early Ordovician Fezouata Biota (Morocco) reveal high diversity and ecological adaptations in radiodonts after the Cambrian.

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The Fezouata Shale Formation (Early Ordovician, Tremadocian) of Morocco yields exceptionally preserved remains of marine organisms that highlight the transition between the Cambrian Explosion and the Great Ordovician Biodiversification Event (GOBE) (Saleh et al. 2020). Arthropods are abundant in this *Lagerstätte*, especially the remains of radiodonts (informally known as anomalocaridids) (Van Roy et al. 2015a). Radiodonta is a clade of stem-lineage arthropods characterised by a segmented body with wide swimming flaps, and a head bearing a pair of appendages, a pair of eyes on stalks, and a mouth surrounded by spiny plates. Their frontal appendages are sclerotized and have a high preservation potential, meaning they are often found in isolation, providing both taxonomic identification and palaeoecological information on feeding behaviour (Daley & Budd 2010), even in the absence of complete bodies. We examined 105 radiodont specimens in the collections of the Musée Cantonal de Géologie de Lausanne and the Yale Peabody Museum, allowing us to revise *Aegirocassis*, (Van Roy et al. 2015b), the first and only named radiodont yet described from the Fezouata Shale, and to identify several new taxa, most belonging to Hurdiidae. The enigmatic fossil *Pseudoangustidontus* (Van Roy & Tetlie 2006), previously described as a single spinose fragment of an unknown raptorial appendage, is also identified as a hurdiid radiodont. Using computer tomography (CT-scanning), we were able to reconstruct a specimen showing several *Pseudoangustidontus* spinose fragments articulated together as endites attached to podomeres of an appendage with an arrangement typical for hurdiids. Radiodonts in the Fezouata Shale were highly diverse and employed a variety of different feeding strategies. Suspension feeding is interpreted as the feeding strategy for 96 specimens, whereas there are only 9 sediment sifters. This abundance in suspension feeding may be linked to the “Ordovician Plankton Revolution”, which saw a huge radiation in plankton diversity during the GOBE (Perrier et al. 2015). The study also points the decline of active raptorial predation in radiodonts, as suggested by their absence, so far, in the Fezouata Shale Formation.

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Perrier, V., Williams, M., & Siveter, D.J. 2015: The fossil record and palaeoenvironmental significance of marine arthropod zooplankton, *Earth-Science Reviews*, 146, 146-162.

Saleh, F., Antcliffé, J.B., Lefebvre, B., Pittet, B., Laibl, L., Perez-Peris, F., Lustrì, L., Gueriau, P., & Daley, A.C. 2020: Taphonomic bias in exceptionally preserved biotas, *Earth and Planetary Science Letters*, 529, 1-6.

Van Roy, P., Briggs, D.E.G., & Gaines, R.R. 2015a: The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician, *Journal of the Geological Society*, 172, 541-549.

Van Roy, P., Daley, A.C., & Briggs, D.E.G. 2015b: Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps, *Nature*, 522, 77-80.

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Keywords: Arthropoda, Great Ordovician Biodiversification Event, radiodonts, Fezouata Shale, Early Ordovician, palaeoecology, feeding strategy.



Session 28 - ORAL
Freedom to Breathe (IGCP 668 and 735)



Assessing drivers for Earth system evolution and animal diversification during the early Paleozoic

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The early Paleozoic encapsulates some of the most profound changes to the biosphere in Earth history, particularly the initial diversification of the animals via the Cambrian ‘explosion’ the Great Ordovician Biodiversification Event (GOBE). This interval also included numerous extinction events throughout the Cambrian and the first of the “Big 5” mass extinctions at the end of the Ordovician. These shifts in Earth’s biota occurred in tandem with major shifts in Earth’s surface environment in terms of climate and oceanic oxygenation, and the relationship between these remains debated. In this talk I will discuss recent work that considers the timing the of these biodiversification and extinction events in relation to changes in environmental conditions. Moreover, I will discuss potential drivers for these shifts in Earth’s surface system with an emphasis on the evolution of solid Earth processes that are linked to the carbon and oxygen cycles.

Keywords: Cambrian, biodiversity, mass extinction, climate change, tectonics



Session 28 - ORAL
Freedom to Breath (IGCP 668 and 735)



Early heliolitine tabulate corals from the Sandbian (Upper Ordovician) in the Yunnan-Sichuan border area, SW China

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Heliolitine tabulate corals are extremely rare in pre-Katian (Upper Ordovician) rocks worldwide, hindering understanding of their origin and early evolution. Here, we systematically study new heliolitine material from the Sandbian part of the Huadan Formation in the Yunnan-Sichuan border area, SW China, which include *Protaraea ningnanensis*, *Lelehusites kiaeri*, *Wormsipora* sp. and *Heliolites spinosus*. Comparison of these corals with faunas previously recognised elsewhere in South China indicates a simultaneous appearance of the three heliolitine clades during the Sandbian, thus supporting their independent origins. The findings also indicate that *Protaraea* and *Lelehusites* are ancestral forms of coccoserids and plasmoporellids, respectively.

Cui, Y.-N., Wang, G.-X. 2021. Revision of late Katian (Late Ordovician) heliolitine corals from northern Kuruktag in northeastern Tarim Basin of China. *Alcheringa* 45(2), 178–194.

Cui, Y.-N., Wang, G.-X., Percival, I. G. 2022. Early heliolitine tabulate corals from the Sandbian (Upper Ordovician) in the Yunnan-Sichuan border area, Southwest China. *Palaeoworld*. doi: 10.1016/j.palwor.2022.01.004

Keywords: heliolitine corals; Sandbian; Late Ordovician; early evolution; South China





Chronology and demise of Palaeozoic carbonate platforms in SE Asia

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Well-developed carbonate platforms are known in the Palaeozoic of mainland South East Asia south of the Song Ma suture.

4. Ratburi. Kungurian to late Permian. Sibumasu Terrane
3. Saraburi – Khammouan. Viséan to late Permian. Indochina Terrane
2. Nalou – Phabing. Givetian to Tournaisian. Truong Son Terrane
1. Thung Song – Setul. Tremadoc to Devonian/Carboniferous. Sibumasu Terrane

The Thung Song-Setul platform developed on eroding remnants of a Cambrian collisional orogen along the peri-Gondwana margin. The underlying fossiliferous Furongian to Tremadoc Tarutao – Machinchang Group sandstones developed in a lagoonal – off-shore bar complex and were succeeded by middle Tremadoc peritidal carbonates. Shallow water carbonates containing a mainly Australian – North Chinese molluscan, conodont fauna followed until deepening in the Darriwilian and a replacement by a South China cooler/deeper water fauna characterised by *Sinoceras chinense*, often psychrospheric trilobites and ‘North Atlantic’ type conodonts.

In contrast, the Ordovician in Laos is characterised by unfossiliferous siliciclastics and minor fossiliferous carbonates until the Dapingian. The earliest platform carbonates are Givetian and are mainly shallow water until the Tournaisian when uplift and erosion led to an influx of often coarse siliciclastics across the whole of the newly amalgamating Indochina Terrane. Subsequent erosion led to the Saraburi- Khammouan carbonate platform developing across the whole of the Indochina Terrane from the Viséan until the latest Permian. The Ratburi carbonate platform developed across Sibumasu after the melting of the Gondwana ice-cap in the Kungurian and as Sibumasu rifted from N.W. Australia and drifted into progressively warmer Tethyan seas.

Small carbonate build-ups of Tournaisian to late Permian age are well known in the Inthanon Terrane and have been interpreted as allochthonous volcanic islands or atolls deposited in a large ocean basin. An alternative interpretation is that they are isolated carbonate build-ups such as those found in the Cenozoic of the eastern Mediterranean.

Controls on carbonate platforms were mainly tectonic with their demise mainly due to continental/terrane collisions in the mid- Carboniferous and Triassic. The demise of the Thung Song-Setul was mainly due to the uplift and erosion during the late Carboniferous associated with the Gondwana ice sheets.



Session 29 - ORAL

From platforms to reefs-faunas and floras from the Archean to the Recent (IGCP 700)

Conodont diversity of Paleozoic platforms: a case study from Peninsular Malaysia

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Based on major stratigraphic, geological, geophysical and tectonic phenomena, the Peninsular Malaysia is divided into Western, Central, and Eastern tectono-stratigraphic belts (Metcalf, 2013). Within the Western Belt, the Kinta Limestone is a capacious succession, representing 65% of the Paleozoic era in the Kinta Valley, Perak. Owing to structural and tectono-thermal complexities of the carbonates; sedimentological and paleontological works have proven to be problematic. In addition, establishing precise age constraints has been far from complete and understanding the sedimentation history was also tenuous as most primary sedimentary/geochemical features are obliterated. This condition has thwarted studies on stratigraphy, sedimentology, paleontology, and petroleum exploration in this basin. Thus, the current study has integrated sedimentological, paleontological, and geochemical datasets to characterize the lithofacies, depositional environments, and to determine the age, and the extent of alterations of the carbonates, and associated shale beds in the basin. Field observations integrated with 360 m cores of the Kinta Limestone provide a better understanding of the basin filling in the Paleozoic. Core description, geophysical logging, petrography, micropaleontological, mineralogical, and organic carbon content and maturation indices have provided clues on the sedimentation history and potential for sedimentary history of the basin. The results indicate that the Kinta Limestone is composed chiefly by carbonate mudstone, siltstone, shale, and minor chert units. The dominance of fine-grained texture, lack of detrital siliciclastic grains, and preserved sedimentary structures, with bedded cherts, and presence of high organic carbon content and lack of benthic fauna may suggest deposition in low energy and low oxygen slope environment with considerable contribution from hemipelagic to pelagic sediments. Although the Kinta Limestone lacks benthic calcareous fossils but contained a diverse abundance of conodont faunal represented by 8 diagnostic conodont genera and 32 diagnostic conodont species. The identification of the diagnostic taxa such as *Polygnathus longiposticus?* *Bispathodus* sp., *Pseudopolygnathus triangulus triangulus*, and *Declinognathodus noduliferus noduliferus* indicated the succession is Upper Devonian-lower Carboniferous, *i.e.*, Famennian-Bashkirian age (Haylay Tsegab et al., 2017). This has improved the biostratigraphy and may suggest the prevalence of continuous carbonate deposition during this time. The identification of diagnostic conodonts species improved the biostratigraphic resolution and establishes depositional continuity of the Kinta Limestone, which enabled correlation with globally established geological events, which may provide clues for paleogeographic reconstruction and paleodepositional conditions in the Palaeo-Tethys such as anoxic conditions.

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Keywords: Kinta Valley, Conodont, lithofacies, alteration, paleo-Thethys

Session 29 - ORAL

From platforms to reefs-faunas and floras from the Archean to the Recent (IGCP 700)

Permian gastropods from limestone conglomerates of the Upper Triassic Khao Nam Yot Formation, Northeastern Thailand

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The Upper Triassic Khao Nam Yot Formation (Carnian–Norian) of Wichian Buri District, Phetchabun Province, Northeastern Thailand contains mainly conglomerate interbedded with sandstone. The conglomerate is poorly sorted and consists mainly of limestone pebbles which are up to 1 m large and of sandstone, siltstone and mudstone pebbles. The matrix of the conglomerate is a reddish, iron-rich sandstone. Composition, poor sorting, large grain size, and the reddish sandstone matrix indicate proximal deposition of the conglomerate under arid conditions. The limestone pebbles have yielded an abundant and diverse silicified marine invertebrate fauna representing mostly gastropods, bivalves, brachiopods, corals, bryozoans, ammonoids, crinoids, fusulinids and sponges. Brachiopods and fusulinids from the limestone clasts are indicative of a Carboniferous to Middle Permian age. Gastropods are especially abundant and diverse representing at least 30 species. Although the silicification is rather coarse, many of the gastropods are reasonably well-preserved for taxonomy and systematic classification. In several cases even protoconchs are preserved. The gastropod species belong mostly to typical Late Palaeozoic cosmopolitan genera with caenogastropods being most diverse. On the genus level, the studied gastropod assemblage from the Khao Nam Yot Formation is similar to Middle Permian gastropod faunas from other Permian deposits of Thailand e.g., the Tak Fa and the Khao Khad formations of the Saraburi Group which consists of deposits of vast late Palaeozoic carbonate platforms. The gastropod-bearing limestone pebbles is probably derived from several formations of the Saraburi Group of the Indochina Terrane of Southeast Asia. The new fauna shares no or few species with already known Permian gastropod faunas from Southeast Asia. This corroborates the view that this region was a diversity hotspot in the Late Palaeozoic that is still poorly sampled.

Keywords: Gastropoda, Indochina, Phetchabun, Phu Nam Yot, silicification

Session 29 - ORAL

From platforms to reefs-faunas and floras from the Archean to the Recent (IGCP 700)

Late Paleozoic and early Mesozoic radiolarians from chert conglomerate embedded in the Kaeng Raboet Formation (Late Mesozoic continental red-beds), Kanchanaburi Province, western Thailand

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Continental clastic red-beds including red and variegated, fine to medium-grained sandstone, pebbly sandstone and conglomerates are distributed in the Sai Yok area, western Thailand. This rock sequence has been established as the Jurassic Kaeng Raboet Formation by Bunopas (1981). A similar clastic rock succession of about 200 meters thick, outcropping at Wat Phu Toey was investigated. The section studied was located approximately 10 kilometers to the east of Ban Kaeng Raboet, the type locality of the rock formation. Detailed stratigraphy in ascending order is coarser-grained chert conglomerate graded into medium-grained chert conglomerate, medium- to coarse-grained pebbly sandstone with chert fragments, medium-grained sandstone with cross lamination with red sandstone and shale intercalations. We collected 5 chert conglomerate samples from this section for micropaleontological analysis. Chert conglomerates consist of angular to subrounded chert clasts whose maximum diameter less than 3 cm, within matrices of silt-sized chert grains and clay minerals. We discriminated early Carboniferous (Tournaisian) to late Middle Triassic (Ladinian) radiolarian-bearing chert clasts from five levels of chert conglomerate. Although preservation of radiolarians is generally not good, we identified 37 species including 25 genera with one radiolarian gen. et sp. indet. Exact age of the Kaeng Raboet Formation is still equivocal. Bunopas (1981) estimated the age of this formation to early Jurassic, however, Hong et al. (2021) assigned the age of the red-beds distributed in the type locality to Cretaceous based on the presence of Jurassic limestone clast in the conglomerate embedded in the formation. Furthermore, Sashida et al. (2022) reported the occurrence of Permian and Triassic radiolarians from chert breccia in the Nong Prue area, western Thailand and proposed the origin and depositional setting of radiolarian-bearing chert clasts. The present chert conglomerate including radiolarian-bearing chert clasts is sedimentary origin and clasts are interpreted to have been derived from the grained siliceous rock bodies cropped out at the surrounding area near the fluvial depositional basin in Cretaceous.

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Hong, P., Putthapiban, P., Trakunweerayut, K., Jitsawat, K., Pakchin, C., Sashida, K. 2021. Kaeng Raboet Formation: A re-investigation of the continental red beds at Sai Yok, western Thailand. Programme and abstract book of the Geothai Webinar 2021, 93-95.

Sashida, K., Ito, T., Salyapongse, S., Phutthapiban, P. 2022. Permian and Triassic radiolarians from chert breccia in the Nong Prue area, western Thailand: its origin and depositional setting in the Paleotethys. *Palaeoworld*, 31, 103-115.

Keywords: chert conglomerate, clast, Kaeng Raboet Formation, radiolarians, red-beds, Sibumasu



Session 29 - ORAL

From platforms to reefs-faunas and floras from the Archean to the Recent (IGCP 700)

Microbial fossil examples from Doi Long Formation, Lampang area, central north Thailand – a preliminary study

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Microbial fossils were studied in the Doi Long Formation of the Lampang Group, northern Lampang, central northern Thailand. Identifications could be made from thin-sections and field observation and texture characteristics. Moreover, the preservation is sufficient to reliably identify some taxa and to establish general attributes of the fauna. The overall characteristics of the fauna is characterised by an abundance of including microbes, oncolites, structureless coatings, *Tubiphytes*, various types of tubules (*Girvanella* and *Microtubus*), and cell assemblages (*Bacinella*), that would now be considered microbial in origin. The binding textures are formed by *Tubiphytes*, calcimicrobes, and minor skeletal organisms such as foraminifers, and algae. These attributes have also been noted in samples assignable to reef environment and carbonate platform setting (Klovan, 1964; Flügel et al., 1993) that correspond to the Standard Microfacies Types 7 (SMF 7: Organic boundstones) (Flügel, 2004). Microbial fossils occur at important sequence stratigraphic and paleoecologic horizons indicating changes in sea level, nutrient supply, and biotic assemblages (Whalen et al., 2002).

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Keywords: Microbial, Fossils, Doi Long, Lampang, Northern Thailand, Reef





Session 29 - ORAL

From platforms to reefs-faunas and floras from the Archean to the Recent (IGCP 700)

New Mesozoic smaller foraminiferal localities of Kanchanaburi, western Thailand

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Carbonate rocks of the upper Paleozoic and Mesozoic ages are widely distributed in Kanchanaburi Province, western Thailand. Previous studies have shown the occurrence of smaller foraminiferal faunas and other micro fossils such as conodonts and algae which suggest the presence of the Triassic and Jurassic carbonate rocks in the narrow area from Thong Pha Phum to Sai Yok Yai, and Si Sawat area (Hagen & Kemper, 1976; Kemper et al., 1976; Fontaine & Suteethorn, 1988).

We are presenting herewith five more new localities of the Mesozoic carbonate rocks based on smaller foraminifers from the following areas; Ban Lin Tin (Thong Pha Phum district), Khao Nong Puk, Ban Phu Takian and Mahidol University Kanchanaburi Campus (Sai Yok district) and Ban Kang Luang (Muang district), Kanchanaburi Province. The results of the lithostratigraphy and biostratigraphy of these foraminiferal findings are as follows: 1) Middle Triassic, based on the rare occurrence of smaller foraminifers *Citaella* – *Hoyenella*? from well bedded grey dolomitic limestone at Mahidol University. 2) Upper Triassic, characterized by dark grey dolomitic limestone that exposed at Ban Pu Takien and Ban Lin Tin. The foraminiferal fauna consisting of *Sigmoilina*, *Duostomina*, *Trochammina* and micro-problematic *Microtubus communis* is assigned to the Norian to Rhaetian. 3) Lower to Middle Jurassic mud-limestones exposed at Khao Nong Puk, 45 km northwest from Sai Yok and at Khao Keang Luang, 10 km southeast from Kanchanaburi Town. These localities have yielded a Toarcian to Aalenian smaller foraminiferal fauna of the *Gutnicella* – *Haurania* assemblage and algae *Holosporella*. In addition, the occurrence of the foraminiferal genus *Gutnicella* which was found from Kanchanaburi and Surat Thani, southern Thailand (Dill et al., 2004) reveals the distribution of shallow marine environments during Jurassic. Our findings are crucial for a better understanding of the depositional environment of the shallow seas on the Sibumasu Terrane during Mesozoic time.

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Keywords: Smaller foraminifers, Triassic-Jurassic, Western Thailand, Sibumasu





Session 29 - POSTER

From platforms to reefs-faunas and floras from the Archean to the Recent (IGCP 700)

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Keywords: Cenozoic, shallow-water carbonates, CLIP, Beata Ridge, Nicaragua Rise, Bahoruco



Session 29 - POSTER

From platforms to reefs-faunas and floras from the Archean to the Recent (IGCP 700)

Upper Palaeozoic platform, slope and basin in Loei-Phetchabun Fold Belt, Indochina Terrane

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Loei-Petchabun Fold Belt is a 1500-1100 km long, 100-150 km wide foldbelt, consisting of Silurian to Triassic, igneous, metamorphic and sedimentary rocks which were deformed in the Late Triassic and possibly in earlier periods. The foldbelt forms the western margin of the Khorat Plateau and extends from Thailand into western Lao PDR, probably extends northwards into China and may curve south-eastwards into Cambodia

Along the western margin of the Khorat Plateau in Thailand, Carboniferous to Permian limestones and associated siliciclastics and volcanoclastics of the Khao Kwang Platform were separated to the east from the Pha Nok Khao Platform by deeper water basins such as the Nam Duk Basin. However, this palaeogeographic scenario is probably in need of revision as it is likely that these long elongate carbonate platforms consist of many, sometimes structurally superimposed, smaller carbonate platforms separated by sometimes wide, deep-water basins.

The oldest sedimentary-volcanic sequence known so far in the Khao Kwang Platform area is gently dipping to 75° 'early' Carboniferous probably early Viséan in age. These oldest rocks consist of unfossiliferous (so far), thinly bedded, chert and volcanoclastics and, although outcrops are scattered, appear to be overlain by a succession of limestones from early Viséan to middle Permian containing dateable foraminiferans and corals.

Some of this Viséan limestone appears to be deposited as mud mounds. Potentially economically important deposits of 45 m of gypsum/anhydrite is probably interbedded in the Carboniferous sequence, appears to be coeval with reddish siliciclastics and, on the basis of seawater isotope composition and overlying fusuline-bearing carbonates, was deposited by "hypersaline seawater on a shallow lagoon or shelf on the Khao Khwang Platform during the Serpukhovian" (or late Mississippian).

Early to middle Permian carbonate sequences are well exposed in the central part of the Phetchabun-Lamnarai to Saraburi area. Biostromes and coral reefs are well exposed in some intervals with obvious massive and fasciculate rugose corals and other associated faunas. Allogenic limestone sequences -the evidence of slope facies - are often observed between this platform facies and the basin deposits which is mainly characterised by successions of shale-chert. Conodonts are observed in the turbidite successions and indicate a late early Permian (Kungurian) age for at least parts of the slope deposits. Late middle Permian carbonates were eroded and unconformably overlain by carbonate breccias and polymictic conglomerates. These breccias and conglomerates are pronounced at the Khao Somphot and Khao Paeng Ma sections in Lopburi. This rock assemblage is also observed at Khao Amon Rat and Phu Nam Yot as well as the sequences in the Phra Phutthabat and other areas along the Loei-Phetchabun terrane. This might be correlative to a major subaerial exposure event and the consequent demise of the Upper Palaeozoic platform in this region related to an early phase of the Indosinian Orogeny.

Keywords: Platform, Reef, Indochina, Palaeozoic



Late Ediacaran to earliest Cambrian algae from Mongolia: their low diversity compared with Chinese Ediacaran algal flora

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As for the floral diversity during the Ediacaran, there is clear contrast between China and Mongolia. The Ediacaran of China, such as Lantian and Doushantuo, hosts highly diversified algal flora. Instead in Mongolia, only two species of macroalgae, *Chinggiskhaania bifurcata* and *Zuunartsphyton delicatum* were previously described from a single locality of the upper Ediacaran of Zuun Arts, Zabkhan Province (Dornbos et al., 2016). Our newly conducted survey of the Ediacaran and Cambrian formations in wider area in western Mongolia provided additional three localities of algae but also revealed that only one species of alga, *Chinggiskhaania bifurcata* is more widely distributed both geographically and stratigraphically, resulting that the floral diversity contrast between China and Mongolia becomes more pronounced. This may not be attributed to the collection bias.

In addition to the locality of *Chinggiskhaania bifurcata* and *Zuunartsphyton delicatum* in Zuun Arts (Dornbos et al., 2016), *Chinggiskhaania bifurcata* was newly discovered from three additional localities (Bayan Gol, Taishir and Khukh Davaa) in Govi Altay Province, western Mongolia. Among these three localities, two (Bayan Gol and Taishir) are from the same stratigraphic level with the original locality of Zune Arts, namely the lower part of the Zune Arts Formation (upper Ediacaran). In Khukh Davaa, however, *Chinggiskhaania bifurcata* occurred abundantly from the lower part of the lower Cambrian Bayan Gol Formation. Thus *Chinggiskhaania bifurcata* is considered as a characteristic algal species in western Mongolia from the late Ediacaran to the early Cambrian. The reason for the low diversity in western Mongol remains unsolved, but this may due to high sedimentation rate that prohibited invasion of other algal species.

Dornbos, S.Q., Oji, T., Kanayama, A. and Gonchigdorj, S. 2016. A new Burgess Shale-type deposit from the Ediacaran of western Mongolia. Scientific Reports 6, 23438. Doi. 10.1038/srep23438

Keywords: Algae, Ediacaran, Cambrian, biogeography





Conservation of spatial data via soft sediment stabilisation constrains the role of decay in early geochemical phase changes within “Ediacaran-style” taphonomic experiments

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The ubiquitous exceptional preservation of Ediacaran macroorganisms has been interpreted to reflect a “lost” taphonomic window of high-fidelity mouldic preservation that is broadly absent in the Phanerozoic geologic record. Several underlying mechanisms have been implicated for such “Ediacaran-style” preservation, from microbially-induced precipitation of pyrite (Gehling, 1999) or amorphous silica (Tarhan et al., 2016; Slagter et al., 2022), to simple differences in sediment rheology (Bobrovskiy et al., 2019), yet consensus remains elusive. Previous attempts to experimentally replicate Gehling’s (1999) theoretical pyrite death mask in the modern do not confirm the formation of a continuous veneer but arguably lack the spatially constrained resolution of phases necessary to do so in artificial Ediacaran taphonomic conditions (Darroch et al., 2012; Gibson et al., 2018).

We employ a novel approach to rapidly stabilise and consolidate whole taphonomic experiments, allowing the spatial component of decay-induced mineral phase changes in decay experiments to be constrained. Continuous, molecular sieve-driven replacement of hydrous pore fluids within unconsolidated sand with anhydrous acetone promotes rapid dehydration of biological samples, permitting resin impregnation and thin-sectioning. Consolidation of these decay experiments effectively halts further decay-related phase changes and prevents remobilisation of phases during investigation and analysis.

This new technique enables us to recognise evidence for iron mineral phase changes directly associated with the microbially-induced decay of *Actinia equina* tissues. We note that burial within a sterile ferrihydrite-supplemented quartz sand is not itself conducive to Ediacaran-style mouldic preservation of *A. equina* tissues. Nonetheless, without controlled inoculation of the sediments with microbial consortia, we observed rapid reduction of bioavailable ferrihydrite and precipitation of reduced authigenic minerals proximal to the *A. equina* carcass. Our results highlight the importance of considering the 3-dimensional spatial distribution of palaeoredox conditions surrounding decaying carcasses when attempting to elucidate the mechanisms underpinning exceptional preservation. We argue that the application of novel stabilisation methods to taphonomic experiments strengthens their explanatory power when considering both spatial *and* temporal effects on decay processes.

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Darroch, S.A.F., Laflamme, M., Schiffbauer, J.D. and Briggs, D.E.G., 2012. Experimental formation of a microbial death mask. *Palaios* 27(5), 293-303.

Gehling, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics; Ediacaran death masks. *Palaios* 14(1), 40-57.

Gibson, B.M., Schiffbauer, J.D. and Darroch, S.A., 2018. Ediacaran-style decay experiments using mollusks and sea anemones. *Palaios* 33(5), 185-203.

Slagter, S., Hao, W., Planavsky, N.J., Konhauser, K.O. and Tarhan, L.G., 2022. Biofilms as agents of Ediacara-style fossilization. *Scientific reports* 12(1), 1-9.

Tarhan, L.G., Hood, A.V., Droser, M.L., Gehling, J.G. and Briggs, D.E., 2016. Exceptional preservation of soft-bodied Ediacara Biota promoted by silica-rich oceans. *Geology* 44(11), 951-954.

Keywords: Taphonomy, Ediacaran, Stabilisation, Resin Impregnation, Phase Changes





Community development in the Ediacaran of Avalonia

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Community composition varies over time in response to differential patterns in biotic and abiotic variables. Pathways of succession in the benthic communities in the Avalonian Ediacaran (~580-560 Ma) have been suggested with certain taxa associated with different phases of community development; e.g. *Fractofusus* is often associated with early succession, whereas large frondose taxa are placed in later stages of community development. In order to investigate how Avalonian communities mature, we mapped out the position of specimens using laser-scan and photogrammetric data from 10 bedding planes from Newfoundland, Canada. The *in-situ* preservation of these sessile organisms provides a near census of communities at this time, enabling modern ecological methods to be used to investigate their community ecology. These maps were used to calculate species densities and aerial coverage, as a proxy for biomass. Rank abundance and k-dominance curves of abundance-aerial coverage comparisons were calculated to estimate relative levels of disturbance and community succession. Early successional communities are expected to show a steep biomass-density-based k-dominance relationship which becomes less steep later in succession. The W-statistic was applied to determine demonstrable differences between communities. These analyses enabled us to establish how community development contributes to observed variation in these Avalonian benthic communities.





Session 31 - POSTER
Insights into Ediacaran life

Ediacaran-like modular body plan revealed in a Cambrian problematic mackenziid

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Most members of the Ediacaran macrobiota, such as erniettomorphs, exhibit a body composed of self-repeating units akin to quilted pneu structures that have functioned as a hydrostatic skeleton (Seilacher, 1989). Such a modular body plan disappeared with the exception of a few putative surviving forms in the Cambrian. *Mackenzia* from the Burgess Shale (Miaolingian Epoch, Wuliuan Age) has a cylindrical body up to 200 mm in height (Walcott, 1911). It has in the past been speculated as a holothurian, actiniarian or Ediacaran-like organism. In our recent paper (Zhao *et al.*, 2022), we reported a new mackenziid, *Paramackenzia canalifera*, from the Cambrian Chengjiang biota (Epoch 2, Age 3). *Paramackenzia* resembles *Mackenzia* in the body architecture, but with a prominent stalk. Specimens of *P. canalifera* reveal lines of evidence that the cylindrical body consists of longitudinal tubular modules. Thin lamellar sheets, previously known as longitudinal septa, are present between two adjacent modules. Regularly arranged sediment infilling and/or dark stains are evidence of a pore-canal system within the lamellar sheets. The modular structures and their anatomy together reject a cnidarian affinity for the mackenziids and any more derived taxon within Bilateria. The serial arrangement of tubular modules in *Paramackenzia* is reminiscent of that in *Ernietta*, an iconic Ediacaran macro-organism. The pore-canal system may be functionally similar to that in sponges and archaeocyathids, but a homologous origin remains to be assessed. Mackenziids are most likely to be a blastic or diploblastic grade of stem eumetazoans, providing novel insights into the possible evolution of modular Ediacaran macro-organisms after the Precambrian.

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Walcott, C. D. 1911. Cambrian Geology and Paleontology II: No. 3-Middle Cambrian holothurians and medusae. *Smithsonian Miscellaneous Collections*, 57, 41-68.

Zhao, Y., Vinther, J., Li, Y.-J., Wei, F., Hou, X.-G. & Cong, P.-Y. 2022. An early Cambrian mackenziid reveals links to modular Ediacaran macro-organisms. *Papers in Palaeontology*, 8, e1412.

Keywords: mackenziid, pneu structure, pore-canal system, eumetazoan, Ediacaran-like fossil





Impact of Lau bioevent (Upper Silurian) on ostracods (Crustacea, Ostracoda)

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Lau bioevent (420 million years ago) was one of the most important geobiological events which affected biota in the dynamic Silurian period. At that time it had a major effect on the conodont fauna and other important Ludfordian fauna groups. Regardless of the significance of this event it is not much known about the impact of this event on to the benthic biota like brachiopods or ostracods. Similar to the previously studied Mulde/ *lundgreni* event (Lower Silurian) (Rinkevičiūtė et al., 2022) this event coincided with a global sea level fall that immediately was followed by an excursion in geochemical isotopes, named the mid-Ludfordian carbon isotope excursion (CIE) by Kaljo et al. (1997), and this excursion has been considered the largest carbon isotope excursion throughout the entire Phanerozoic.

Ostracods are one of the most important component of level-bottom communities and the ostracodes of the Silurian period are insufficiently investigated on the global scale. The aim of this study is to investigate changes in the ostracod group during the Lau bioevent.

In order to achieve this goal detailed sampling (77 samples, spl. int. 0, 25 m) was performed from the Bebirva-110 core section (South Baltic, Lithuania), with later processing of samples and extraction of ostracod shells. Additionally their taxonomic identification was accomplished.

Ostracods acts similar to brachiopods through this bioevent and its scientifically understandable as both groups are benthic (Mergl et al., 2018). In the data we can see reorganization of the major groups: species that occurred before Lau event was replaced by others with some minor loses. After a recovery period after the Lau bioevent ostracod fauna again became an important part of faunal communities.

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Mergl, M., Frýda, J., & KubaJKo, M. (2018). Response of organophosphatic brachiopods to the mid-Ludfordian (late Silurian) carbon isotope excursion and associated extinction events in the Prague Basin (Czech Republic). *Bulletin of Geosciences*, 93(3).

Rinkevičiūtė, S., Stankevič, R., Radzevičius, S., Meidla, T., Garbaras, A., & Spiridonov, A. (2022). Dynamics of ostracod communities throughout the Mulde/*lundgreni* event: contrasting patterns of species richness and palaeocommunity compositional change. *Journal of the Geological Society*, 179(1).





Session 33 - ORAL
The 4th Asian Ostracod Meeting (AOM4)

Devonian ostracod assemblages at Ban Pa Samed section, Satun Province, Thailand: Palaeoenvironment implication

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Paleozoic ostracods have been intensively studied worldwide for the past decades, but in Southeast Asia only few results have been reported. In this study, ostracods are recovered from limestones of the Upper Silurian to Lower Devonian section of the Kuan Tung Formation located at about 10 kilometers from La-Ngu city, Satun Province, southern Thailand. The section consists of limestone in the lower part, alternations of limestone and dark grey muddy limestone in the middle part and changes to black shale at the top of the section. Ostracods are classified to 11 families, 25 genera, and 39 species. The assemblage comprised of adult and juvenile carapaces suggests a calm and low-energy environment. The assemblage is dominated by smooth shell Podocopina (63-81%) accompanied by Metacopina (11-30%), Palaeocopina (3-10%) and few Platycopina. The dominance of smooth shell Podocopina corresponds to the Eifelian assemblage III (Casier 2017, Song et al., 2018) and suggests well oxygenated and normal salinity sea water (Casier et al., 2011). However, the deep-water habitant such as genus *Ampuloides* is also found that may represent deeper setting, resembles the Thuringian assemblage (Crasquin and Horne, 2018). The palaeoenvironment should be an offshore open carbonate slope shelf under a storm wave base, relatively deep. The changes in lithology and ratio between the Podocopina and Metacopina (the former decreases while the latter increases) suggest a sequence of transgression, from the limestones in the lower part to the black shale in the upper part of the section where ostracods are barren.

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Crasquin, S. and Horne, J. 2018. The palaeopsychrosphere in the Devonian. *Lethaia* 51, 547-563. <https://doi.org/10.1111/let.12277>.

Song, J., Crasquin, S. and Gong, Y. 2018. Late Devonian benthic ostracods from western Junggar, NW China: Implications for palaeoenvironmental reconstruction. *Geological Journal* 54, 91-100 <https://doi.org/10.1002/gj.3156>

Keywords: Devonian, Kuan Tung Formation, Ostracod, Palaeoenvironment, Satun Geopark





Non-marine Ostracod fauna from the Xiagou Formation (Jiuquan Basin): Taxonomy, Biostratigraphy and palaeoenvironment implication

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The Jiuquan Basin, which is situated to the juncture of the north Qilian orogenic belt, the Altyn block and the Alashan block of the northwest China, is one of the earliest studied Early Cretaceous basins for oil exploitation (e.g. Chen et al., 2014). During the Early Cretaceous rifting stage of the Jiuquan Basin, the depositional processes of this basin were mainly controlled by the activities of a series of tensional and NE-NNE torsional growth faults (Chen et al., 2014). And the Xinminpu Group (which is also translated as Xinminbao Group and is equal to the Huihuiipu Series) was deposited during this period. The Xinminpu Group consists of three formations in ascending order: the Chijinpu (which is also translated as Chijinbao Group), Xiagou and Zhonggou formations. Among them, the Xiagou Formation hosts abundant fossil invertebrates, vertebrates, and plants, which have long been of interest to paleontologists. Here we re-study the non-marine “Wealden type” ostracods from the Xiagou Formation of the Jiuquan Basin, based on our newly collected material. This non-marine ostracod fauna consists of 14 species belonging to 9 genera: *Bisulcoocypridea astute*, *C. koskulensis*, *C. yumenensis*, *C. latiovata*, *Cypridea* sp., *Lycopterocypris debilis*, *Mogolianella gigantea*, *Rhinocypris jurassica*, *Ziziphocypris costata*, *Alicenula* sp., *Limnocythere xiagouensis*, *L. subpeculiaris*, *Candonia* spp. It is dominated by *Cypridea* species as well as shows a high diverse of non-*Cypridea* species. In this ostracod fauna, the species *Bisulcoocypridea astute* is also found in the Barremian to Aptian Jingchuan Formation (Wang et al., 2012). *C. koskulensis* is widely distributed in Barremian to Aptian strata of Mongolia and China (Hou et al., 2002). *C. latiovata* may belong to *Cypridea valdensis-parallela* group of Wolburg (1959), which indicates the Early Cretaceous. *Lycopterocypris debilis* is widely distributed in Hauterivian to Albian non-marine strata of east Asia (Wang et al., 2016). *Rhinocypris jurassica* has a long stratigraphic range (Late Jurassic to Barremian), and *Ziziphocypris costata* was found in Aptian to Maastrichtian strata of east Asia (Wang et al., 2016). Our ostracod biostratigraphic data and correlations indicate that this ostracod fauna can be assigned to the Aptian to Albian *Cypridea (Morinina)-Bisulcoocypridea-Mongolocypis* ostracod assemblage of Wang et al. (2012). This result, combined with the updated Early Cretaceous chronostratigraphic framework from the Jiuquan Basin, indicates that the Xiagou Formation is Aptian. Based on ostracod taxonomic and taphonomic as well as sedimentological analysis, the depositional environment of the Xiagou Formation is interpreted as lacustrine to fluvial (fluvial-deltaic).

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Wolburg, J., 1959. Die Cyprideen des NW-deutschen Wealden. *Senckenbergiana Lethaea* 40, 223-315.

Keywords: *Bisulcoocypridea*, *Cypridea*, northwest China, ostracod biostratigraphy, Aptian





Ostracod community composition in the channels of an artificial wetland system, Tancat de la Pipa (Albufera de Valencia – Spain)

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L'Albufera de Valencia is the largest natural lagoon on the Spanish Mediterranean coast, it is surrounded by rice fields but also by a densely populated area with about 1500000 inhabitants, including the conurbation of Valencia. The lake is very shallow and traditionally has been an important habitat for waterfowl but also for human activities, chiefly fishing, rice culturing and hunting. Since the 60's the lake experienced severe eutrophication, attaining a hypereutrophic state during the last decades. In 1986, the area was protected as a Natural Park, and several programs have been implemented to improve its ecological quality. Our study was done in "Tancat de la Pipa", an old set of rice fields, located at the north shore of the lake, which has been transformed into a restored wetland. It includes a network of interconnected channels and shallow ponds which function as green filters to improve the water quality of the lake. In the Albufera Natural Park, channels have been less studied than other environments, such as rice fields, ponds or the lake itself, so we aimed at improving our knowledge on these systems. The main objective of the study was to evaluate the seasonal diversity of ostracods throughout an annual cycle (2020 - 2021) in the channels of the study area. Three main channels of the system were sampled and monitored in spring (May/20), summer (June/20), autumn (November/20) and winter (February/21). We used a 250- μ m hand net for collecting the samples, corresponding to 6 m long trawls in each channel. The samples were fixed in 96% ethanol for later identification of ostracod species in the laboratory. Water temperature, dissolved oxygen, pH, and conductivity were also recorded. In our preliminary results we found a total of 14 ostracod species, out of which 10 species (6 native and 4 exotic) were found alive, and the rest were shell remains. In general, the input and output channels of the system presented the highest abundances for both living ostracods and shells, and for all seasons. The highest abundances were recorded in spring, reporting 9 living species of which the most abundant was *Physocypria* sp. s.l., an exotic new species, and *Cypridopsis vidua*, a native one. Regarding the proportion between living ostracods and valves, the lowest percentage of living ostracods was recorded in winter. With these results we show that the diversity of ostracods in the artificial channels can be relatively high, being winter the season with the lowest ostracod species richness.

Keywords: Ostracoda, richness, diversity, channels, restored wetland.





Session 33 - ORAL
The 4th Asian Ostracod Meeting (AOM4)

3D exploration of the pores of recent and fossil ornate Bairdiidae (Ostracoda)

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Ostracods from the family Bairdiidae have been components of marine ecosystems since the Ordovician. In their long history, the Triassic was a major turning point with the explosive diversification of ornate forms: ornate Bairdiidae are still present in modern environments but the phylogenetic link between Triassic and modern taxa remains unresolved. The classification of fossil Bairdiidae has not evolved since the 1960s and the use of ornamentation in the systematic of ornate taxa remains highly debated. The significance of pores in the taxonomy and phylogeny of ostracods is widely acknowledged but has never been investigated in the case of Bairdiidae. Here, we present the first results of an investigation of Recent and Triassic ornate Bairdiidae by X-ray computed tomography (CT) to observe and describe their pore systems. This investigation further highlights the implications of new imaging techniques in diverse fields of ostracodology, even in the absence of soft parts preservation.

Keywords: Bairdiidae, Recent, Triassic, CT-scan, 3D analysis, pores





Session 33 - POSTER
The 4th Asian Ostracod Meeting (AOM4)

A new genus of Cypridopsinae (Crustacea: Ostracoda) from the Lower Songkhram River Basin, Thailand

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A new genus and species of subfamily Cypridopsinae is discovered from the Lower Songkhram River Basin, Thailand. The prominent diagnostic characters of the new genus mainly exist in antenna (A1), antenna (A2) and third thoracopod (T3): the 6-segmented A1, the strongly serrated claw G2 on the female A2, the large aesthetasc Y with remarkably large and striated third section and the completely separated terminal segment of T3. The A1 with 6 segments has been recognized for the first time in the Cypridopsinae. The new genus is similar to *Paranadopsis* but they cannot be confused because the soft parts morphology of *Paranadopsis* is exceptional which displays reductions of segmentation and chaetotaxy of limbs (Almeida et al., 2021) while such aspect not exists in the new genus. The new genus also resembles *Brasilodopsis*; it can be distinguished mainly by the larger overlapping anteriorly, the presence of anterior inner list on the RV, the widely inwardly displaced posterior selvage on the RV, the strongly serrated claw G2 on female A2, the completely separated terminal segment of T3, the number of post-labyrinthal spermiduct loop (1 in the new genus, 2 in *Brasilodopsis*) and the smaller number of spiny whirles of Zenker organ (8 in the new genus, 10 in *Brasilodopsis*). The T3 with separated terminal segment is a tribe character of Cyprettadopsini. However, there are several other features of the new genus which are not congruent to the characteristics of Cyprettadopsini, such as the absence of marginal septa, the 6-segmented A1 and the divided penultimate segment of T2. The completely separated terminal segment of the T3 can also be seen from *Neocypridopsis* (see e.g. Klie 1940), a genus in the tribe Cypridopsini. Taxonomic position of *Neocypridopsis* is uncertain (see e.g. Meisch et al., 2019) and the revision is strongly needed. Some differences between the new genus and *Neocypridopsis* can be recognized in the A1 segmentation (6 in the new genus, 7 in *Neocypridopsis*) and the morphology of Hp. In conclusion, the new genus has several unique features, together with the shared characters of several tribes, and it cannot be assigned to any tribe. Therefore, a new tribe should be established to accommodate this new taxon. Although the species number of Thai cypridopsinae is somewhat low (11 taxa, including the new species - see Savatnalinton & Suttajit 2016; Savatnalinton 2017, 2018, 2020), these representatives show the wide range of diversity as six of seven tribes have so far been recorded from Thailand.

Almeida, N.M., Higuti, J., Ferreira, V.G., Martens, K. 2021. A new tribe, two new genera and three new species of Cypridopsinae (Crustacea, Ostracoda, Cyprididae) from Brazil. *European Journal of Taxonomy* 762, 1–48.

Klie, W. 1940. Süßwasserostracoden aus Nordbrasilien. 6. Cyprinae mit geißelförmiger Furka. *Zoologischer Anzeiger*, 130, 59–73.

Meisch, C., Smith, R.J., Martens, K. 2019. A subjective global checklist of the extant non-marine Ostracoda (Crustacea). *European Journal of Taxonomy*, 492, 1–135.

Savatnalinton, S., Suttajit, M. 2016. A checklist of recent non-marine ostracods (Crustacea: Ostracoda) from Thailand, including descriptions of two new species. *Zootaxa*, 4067 (1), 1–34.

Savatnalinton, S. 2017. *Siamopsis* gen. nov. and five new species of the subfamily Cypridopsinae Kaufmann, 1900 (Crustacea: Ostracoda) from Thailand. *European Journal of Taxonomy*, 384, 1–39.

Savatnalinton, S. 2018. New genus of subfamily Cypridopsinae Kaufmann, 1900 (Crustacea: Ostracoda) from Thailand. *European Journal of Taxonomy*, 487, 1–17.

Savatnalinton, S. 2020. A new cypridopsine genus (Crustacea, Ostracoda) from Thailand. *European Journal of Taxonomy*, 631, 1–16.

Keywords: taxonomy, crustacean, Cyprididae, Song Khram River





Session 33 - POSTER
The 4th Asian Ostracod Meeting (AOM4)

A new species of *Gurayacypris* (Crustacea: Ostracoda: Notodromadidae) from Thailand

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A new species of a rare genus *Gurayacypris* is found in a rice field in Maha Sarakham Province, Thailand. *Gurayacypris* is more closely related to *Notodromas* than other genera of the subfamily Notodromadinae. Its outstanding valve features are the scallop line of concrescence and the improminent eye tubercles which are different from *Notodromas* (see Smith & Kamiya, 2014). *Gurayacypris* comprises only one species, *G. kangraensis* which was described from a permanent waterbody in India (Battish, 1987) and since then, it has not reported from anywhere in and outside of India. Hence, its status as endemic genus and species of the country and also of the Oriental region has existed for a long time. The present discovery of *Gurayacypris* n. sp. is thus the first record of this genus in Thailand and Southeast Asia. *Gurayacypris* n. sp. can be mainly distinguished from *G. kangraensis* by the more rounded carapace in lateral view, the triangular protrusion on the postero-ventral part of the female left valve (small blunt-tipped protrusion in *G. kangraensis*), the absence of pointed protrusion on distal margin of the basal segment of the left prehensile palp and the triangular distal lobe of the hemipenis. Thus far, only three species of Notodromadidae have been reported from Thailand (Savatnalintont, 2015; Savatnalintont & Suttajit, 2016): *Notodromas sinensis*, *Oncocypris rostrata* and *Gurayacypris* n. sp.

Battish, S.K. 1987. A new recent genus and species of notodromadinid ostracod from India. *Researches on Crustacea* 16, 127–134.

Smith, R.J., Kamiya, T. 2014. The freshwater ostracod (Crustacea) genus *Notodromas* Lilljeborg, 1853 (Notodromadidae) from Japan; taxonomy, ecology and lifestyle. *Zootaxa* 3841, 239–256.

Savatnalintont, S. 2015. On three new species of non-marine ostracods (Crustacea: Ostracoda) from Northeast Thailand. *Zootaxa* 3914 (3), 275–300.

Savatnalintont, S., Suttajit, M. 2016. A checklist of recent non-marine ostracods (Crustacea: Ostracoda) from Thailand, including descriptions of two new species. *Zootaxa* 4067 (1), 1–34.

Keywords: Notodromadinae, taxonomy, microcrustacean, rice field, Southeast Asia





Session 34 - ORAL
Open Session - Arthropods

Cephalic shape has little association with trilobite moulting behaviour

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Trilobites had strongly biomineralised exoskeletons with a diversity of morphological adaptations to different ecological niches across the Palaeozoic. Like all euarthropods, trilobites moulted their exoskeletons repeatedly throughout their lives to grow and develop. Exoskeleton moulting behaviour in trilobites appears to have been uniquely variable compared to modern arthropod groups, partly because of their cephalon morphological diversity. Previous work has suggested that trilobites were both highly inter- and intraspecifically variable in moulting behaviour, producing a variety of moult configurations preserved in the fossil record (Drage et al., 2018a). For some species this was related to morphology at ontogenetic stage (Drage et al., 2018b). Variation in moulting during adulthood might be expected to be related to morphometry; the shape and proportions of exoskeleton sclerites. However, proportions appear largely unrelated to moulting behaviour both interspecifically and intraspecifically in at least one species (submitted, Drage et al.).

We tested for an association between cephalic shape and moulting behaviour to confirm whether broad-scale trilobite moulting variability was indeed unrelated to morphometry. Cephalic shape has been shown to relate to variation in other trilobite behaviours, such as enrolment (Suarez & Esteve, 2021). We used a dataset of cephalon outline semi-landmarks of ~200 trilobite species with moulting behaviour information to test this potential association.

Elliptical Fourier Analysis suggests cephalon shape has little impact on moulting behaviour, with different behavioural groups almost entirely nested in morphospace. Species showing the Sutural Gape mode of moulting, using only the facial and/or rostral sutures, occupy the greatest amount of morphospace, though this is unsurprising given the facial sutures were likely adaptive for moulting and are found throughout the trilobite orders. Perhaps trilobites indeed demonstrated high phenotypic plasticity in moulting across the group that cannot be explained by individual variables or evolutionary drivers such as morphometry or development.

Drage, H. B., Holmes, J. D., García-Bellido, D. C. and Daley, A. C., 2018a. An exceptional record of Cambrian trilobite moulting behaviour preserved in the Emu Bay Shale, South Australia. *Lethaia* 51, 473-492.

Drage, H. B., Laibl, L. and Budil, P. 2018b. Postembryonic development of *Dalmanitina*, and the evolution of facial suture fusion in Phacopina. *Paleobiology* 44, 638-659.

Drage, H. B., Holmes, J. D., García-Bellido, D. C. and Paterson, J. R. submitted. Associations between trilobite intraspecific moulting variability and body proportions: *Estaingia bilobata* from the Cambrian Emu Bay Shale, Australia.

Suárez, M.G. and Esteve, J. 2021. Morphological diversity and disparity in trilobite cephalata and the evolution of trilobite enrolment throughout the Palaeozoic. *Lethaia* 54, 752-761.

Keywords: Trilobita, Palaeozoic, moulting, outline morphometry, behaviour





Session 34 - ORAL
Open Session - Arthropods

Recapitulating pygidial spine evolution during regeneration in Devonian scutelluid trilobites

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Despite the heavy biomineralization of their dorsal exoskeleton, trilobites have been preyed upon by predators since their origin in the early Cambrian, as attested by multiple discoveries of injured specimens of that age. Analysis of such specimens show that attacks affecting the pleural regions of the thorax and pygidium were not necessarily lethal. As in modern arthropods, the injured parts were healed and eventually fully replaced via regeneration after several moulting cycles.

In the Devonian, the diversification of large marine predators, such as ammonoid cephalopods and jawed fishes, is associated with enhanced defensive strategies in trilobites. Body enrolment – a strategy key to the success of the group, albeit severely constraining its morphological evolution – is complemented in many taxa by the spectacular development of spinosity. This phenomenon is particularly well exemplified by thysanopeltine scutelluids, which evolve spines all around the pygidial margin. Tiny and numerous in early forms, these marginal spines progressively increase in size, while decreasing in number in later representatives; ultimately, the number (16) and distribution of the marginal spines parallel those of the pygidial ribs. This evolutionary trend involves the fusion of neighbouring spines, as attested by the presence of bifid spines in intermediate representatives.

The discovery of two remarkable specimens featuring partially healed pygidia provides strong evidence for the recapitulation of this evolutionary trend during regeneration. Indeed, the regeneration of the marginal spines of the injured area, which starts before the pygidium has regained its normal size and shape, proceeds through three stages: 1) the regeneration of numerous minute spines; 2) their increase in size; and 3) their reduction in number by fusion of neighbouring spines. All three stages are illustrated by different parts of the healing margin in one of the two specimens, as if spine regeneration started anteriorly first and then progressed posteriorly. We hypothesize that this rare example of recapitulation of evolution during regeneration in trilobites results from the fact that the sequence of reactivation of morphogenetic processes during healing mirrored their historical sequence of acquisition.

Keywords: Trilobita, Scutelluidae, Regeneration, Spinosity, Devonian





Session 34 - ORAL
Open Session - Arthropods

The function of enrolment and flexures in the trilobite *Strenuella polonica* Czarnocki, 1926 from the Cambrian of Poland

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Enrolment in trilobites has been theorized to be a protective response against predation, or extreme environmental conditions (Babcock and Speyer, 1987; Pompeckj, 1892). Other postures, such as dorsal flexures, may assist with the moulting process, by facilitating the breakage of sutures that allowed the trilobite to exit from its old exoskeleton (McNamara and Rudkin, 1984). In some cases, these positions could also have positioned pleural spines to strengthen anchorage during the moulting process (Drage et al., 2018).

In this study, we investigate if moults of the ellipsocephalid trilobite *Strenuella polonica* Czarnocki, 1926 are more often found in postures theorized to help with moulting, and correspondingly if carcasses are more often found in postures associated with protection. Our sample comprises 85 specimens of *S. polonica*, from the Cambrian Series 2 of the Holy Cross Mountains in Poland (Żylińska, 2013). Each specimen in this study was categorized into one, or a combination of the following posture categories: thorax enrolled, outstretched, cranidium flexed, and pygidium flexed. We also identified each of these specimens either as a moult or a carcass.

The moults of *S. polonica* were mainly recognizable because of their detached librigenae, meaning this species predominantly moulted through an opening at the anterior end of the cephalon. We also describe some parts of the morphology of *S. polonica*, such as the axial spines and the hypostome. The preliminary results indicate an association, but not a perfect correlation, between the different postures and their proportions in moults and carcasses. We found more carcasses in postures with the thorax enrolled, and more exuvia in the outstretched and flexed postures. This suggests a possible evolutionary link between enrolment and moulting.

Babcock, L. E., & Speyer, S. E. 1987. Enrolled trilobites from the Alden Pyrite Bed, Ledyard Shale (Middle Devonian) of western New York. *Journal of Paleontology*, 61(3), 539-548.

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McNamara, K. J. & Rudkin, D. M. 1984. Techniques of trilobite exuviation. *Lethaia*, 17(2), 153-173.

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Keywords: Trilobites, Poland, Cambrian, Paleozoic, Moulting, Enrolment





The evolution of compound eyes across extant and fossil crabs

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Image-forming compound eyes are such a valuable sensory adaptation that similar visual systems have evolved independently multiple times across panarthropods. However, the origin and evolution of different compound eye types remain poorly constrained, and the eyes of most extant families are understudied. Moreover, fossils preserving compound eyes—especially internal neural tissues—generally are rare, and information about visual systems is seldom placed in a broader phylogenetic and evolutionary context. Here, we investigated the utility of compound eye structures and ommatidia morphology of true crabs, or Brachyura—one of the few panarthropod groups where all main types of compound eyes occur—for assessing the ecology and resolving phylogenetic relationships, by integrating new data from fossil and extant taxa across the crab tree of life. The exceptional preservation of compound eyes in several Cretaceous and Cenozoic crabs from different families and ontogenetic stages (Luque et al. 2019a; Jenkins et al. 2022), highlights the advantage of mapping optical characters in a phylogenetic context at different taxonomic and time scales to investigate the origins of visual systems. The preservation of external corneal eye lenses together with soft neural tissues (e.g., retinotopic neuropils) is rare among fossil arthropods and largely restricted to a few Cambrian taxa. The exceptional preservation of delicate corneal lenses together with corneagenous cells and retinotopic neuropils in the Cretaceous *Callichimaera perplexa* is the first example of such a combination of preservational styles discovered in a post-Paleozoic marine arthropod (Luque et al. 2019b; Jenkins et al. 2022), and illuminates the roles of development and ecology as important drivers of the evolution of visual systems among higher taxa. Ongoing work aims at shedding light on whether particular selection pressures account for convergent origins and/or losses of different eye types among true crabs and other decapod crustaceans through deep time. Funding: National Science Foundation (NSF), DEB grants #1856667 and #1856679 (USA).

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Keywords: Apposition, Brachyura, Cretaceous, exceptional preservation, phylogeny, superposition, vision





A novel form of biphasic moulting in cirolanid isopods

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Isopods are a diverse group of extant crustaceans with a long evolutionary history. They occupy a range of modern ecological niches in marine, freshwater, and terrestrial environments, and perform important ecosystem roles like intensive scavenging. The fossil record of Isopoda begins in the Carboniferous, though it is sparse and highly incomplete. Isopods, extant and extinct, are characterised by a unique biphasic moult cycle. Like other euarthropods, they moulted their protective exoskeletons repeatedly throughout their lifetimes to grow and develop, but first shed the posterior section, and, following a variable delay, the anterior section. The two sections are often found separately because it is usually hours to days before the anterior section is moulted. This biphasic moulting is likely an adaptation to various ecological modes, such as compartmentalised biochemical processes supporting parasitism (Sahadevan et al., 2022).

Cirolanidae is a derived isopod family with a reasonably diverse fossil record of predatory and scavenging species. New specimens of the extinct cirolanid species *Cirolana feldmanni* (Miocene, Slovakia) and '*Palaega*' *collinsi* (Eocene, UK) show a novel deviant style of biphasic moulting seemingly unique to Cirolanidae. The exoskeleton disarticulates into posterior and anterior sections, as in other isopods, but the anterior section is consistently found overturned, with both sections orientated towards the anterior. Further, both sections are preserved in close association, with little to no sediment between them, suggesting moulting of both sections close to simultaneously (almost monophasic).

This style of moulting is alike Salter's configuration in trilobites, with the cephalic sclerite disarticulated and overturned (Drage et al., 2018), though the consistent anterior orientation is the inverse to Salter's configuration. Otherwise, this is unique amongst isopods and euarthropods generally. However, extant cirolanid moulting is poorly understood. Is this moulting style wider spread within Cirolanidae and observable in extant representatives? Is it an ecological adaptation, such as to burrowing or scavenging, rather than parasitism?

Drage, H. B., Holmes, J. D., García-Bellido, D. C. and Daley, A. C., 2018. An exceptional record of Cambrian trilobite moulting behaviour preserved in the Emu Bay Shale, South Australia. *Lethaia* 51, 473-492.

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Sahadevan, A.V., TA, J.P. and Kappalli, S. 2022. Biphasic moulting in isopods confers advantages for their adaptation to various habitats and lifestyle. *Biologia*, 1-15.

Keywords: Isopoda, Cirolanidae, moulting, Eocene, Miocene, *Cirolana*





Research progress on Mesozoic stick insects

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Phasmatodea (stick and leaf insects) is a rather small insect order with more than 3000 known species. Extant stick and leaf insects exhibit a wide array of exaggerated morphologies mimicking twigs or leaves. However, the fossil records of Phasmatodea are relatively sparse, and only about 100 species are reported until now. Mesozoic is an important period for the morphological and behavioral evolution of stick insects, and more than 80 species are discovered. Most species of Susumaniidae from Yanliao and Jehol Entomofauna of northeastern China with fully-developed wings different from extant stick insects are considered as the stem-groups of living stick and leaf insects. Among them, *Aclistophasma echinulatum* from the Middle Jurassic of China was supposed to be the earliest evidence of mimicry and defense within Phasmatodea, exquisitely preserving abdominal extensions and femoral spines (Yang et al., 2021). *Cretophasmomima melanogramma* from the Early Cretaceous of China showed the peculiar wing markings resemble ginkgo leaf (Wang et al., 2014). Recently, many stick insects with similar morphological characters of living species are reported from mid-Cretaceous Kachin amber of northern Myanmar. The earliest timematids revealed diverse tarsal pads of stick insects, which might have increased friction and helped them to climb more firmly on various surfaces (Chen et al., 2019). Pterophasmatidae intermingle plesiomorphic traits from Susumaniidae with modern derived features of extant species, was regarded as a transitional group from ancient to modern stick insects (Yang et al., 2019). In addition, several twig-like stick insects from Kachin amber revealed that the different body parts of stick insects became distinctly elongate during early evolution, bringing about a long twig body form to mimicking twigs. It is remarkable that the lateral lamellae on thorax, femora and abdomen used to improve crypsis for stick or leaf insects when they sprawled on twigs or leaves (Chen et al., 2018). All these fossils suggested that the morphological and behavioral specializations about Phasmatodea were already established in the Mesozoic.

Chen, S., Deng, S.W., Shih, C.K., Zhang, W.W., Zhang, P., Ren, D., Zhu, Y.N., Gao, T.P. 2019. The earliest Timematids in Burmese amber reveal diverse tarsal pads of stick insects in the mid-Cretaceous. *Insect Science* 26, 945–957.

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Keywords: Phasmatodea, evolution, morphology, mimicry, defense, fossil, amber, China



Session 34 - ORAL
Open Session - Arthropods



A new chaerilid scorpion from early Late Cretaceous Burmese amber (Arachnida: Scorpiones: Chaeriloidea)

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Extant scorpions of the small family Chaerilidae are very sparse, and they are poorly documented in the fossil record. Here we describe a new chaerilid species, *Electrochaerilus cretaceus* sp. nov., from early Late Cretaceous Burmese amber. We have revealed the high-resolution morphological information of new specimen by the combination of stereo microscope, green fluorescence microscope, confocal laser scanning microscope, and X-ray microtomography. The new specimen can be unambiguously assigned to the extant family Chaerilidae based on their complete type B trichobothrial pattern, very broad anterior margin of maxillary lobes I, and crenulated ventral denticle of cheliceral movable finger. However, *E. cretaceus* has some characters distinctly differing from those of the extant taxa, such as the anterior margin of carapace broadly concave, the posterior edge of carapace with a small notch, and the median eyes situated in anterior quarter of carapace. The Oriental-endemic Chaerilidae remains enigmatic, as its precise phylogenetic position within the tree of scorpions is unsettled (Sharma et al., 2015; Santibáñez-López et al., 2022). The discovery of a new fossil species, *Electrochaerilus cretaceus*, provides valuable information about the early diversity of this family. It also could be selected as a crucial fossil calibration for dating the molecular phylogenetic tree of scorpions. *Electrochaerilus cretaceus* sp. nov. is the second fossil record of Chaerilidae, suggesting that the chaerilids have been established since the early Late Cretaceous.

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Keywords: Chelicerata, Arachnida, Burmite, Fossil, Endemic



Session 34 - ORAL
Open Session - Crinoids



Crinoid columnals from the Hitachi metamorphic complex, eastern Japan

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Tiny but relatively well-preserved columnals were found from the Kanayama Limestone of the Akazawa Formation in the Hitachi metamorphic complex, eastern Japan. Fossils are embedded in laminated or thinly-bedded, relatively weakly metamorphosed part of the limestone, with fine-grained recrystallized calcite crystals. The limestone also retains original bedding such as cross stratification and convolute bedding with water escape structure. Our preliminary result of U-Pb age obtained from detrital zircons shows that the limestone would be Ordovician, but precise dating awaits further examinations. Columnals are rounded in outline, range 1 to 2 mm in diameter, with axial canals that generally show stellate to pentagonal morphology in cross section. Most of these columnals are isolated but some specimens show a series of columnals still attached. Previously small amygdaloidal clusters were found from a different but nearby locality and possible biogenic affinity was discussed (e.g., Tagiri, 2021). If the Kanayama Limestone with these crinoids will be assigned to the Ordovician, these fossils may represent one of the oldest fossils from Japan. The present discovery of crinoid fossils from the metamorphic complex also implies that paleontological information can be obtained not only from sedimentary rocks but also from weakly metamorphosed rocks, expanding the future possibility of new discovery from metamorphic complexes.

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Keywords: Crinoid, Ordovician, Hitachi metamorphic complex





Early life record from the late Paleoproterozoic Changcheng Group in North China and their implications for early eukaryote evolution

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The Eukaryota comprises all complex life characteristic of sophisticated cellular architecture and organismal complexity on Earth. Yet, the timing of its origin and early innovations fundamental to present-day biosphere are poorly understood. Organic-walled microfossils from several paleocontinents (Yin, 1997; Javaux et al., 2004; Prasad et al., 2005; Miao et al., 2019) point to the unambiguous existence of eukaryotes as early as ca. 1.65 Ga, including evidence for subcellular complexity and certain biological innovations. Among these records, microfossils from the Changzhougou and Chuanlinggou formations, lower Changcheng Group in the Yanshan Range, North China, are geochronologically well constrained to be ca. 1.67–1.64 Ga and contain the very early eukaryotic remains that are crucial to our understanding of early eukaryote evolution. Our new palynological study reveals a diverse and continuous record of microfossils from transgressive shallow marine mudstone and shales of the two rock units in three localities. The results are broadly consistent with previous studies but also uncover new form taxa. Fossils from Changzhougou Formation in the Pangjiapu section are dominated by sphaeromorphs (largely smooth-walled *Leiosphaeridia* spp.) with diameter reaching 230 µm, including *Valeria lophostriata* with sculpture of concentric striations interpreted to be eukaryotic. Microfossils from the lower Chuanlinggou Formation in northern Tianjin area, show a similar but more diverse assemblage containing more eukaryotic taxa such as *Dictyosphaera macroreticulata*, *Germinosphaera alveolata* and *G. bispinosa*, in addition to *Valeria*. A low diversity of cellular aggregates with distinct cell-arrangement pattern and small cell sizes (<10 µm) of possible prokaryotic affinity are also abundant components. Unlike these two assemblages from intertidal deposits, microfossils from subtidal shales of upper Chuanlinggou Formation in the Kuancheng area are taxonomically different and comprise a variety of filamentous forms with minor acritarchs. Majority of these filaments can be morphologically compared with sheaths and trichomes of prokaryotes. Large uniseriate filaments with width up to 195 µm show morphological complexity and intracellular sphere, are interpreted to be multicellular eukaryotes comparable to certain extant algal filaments. Although rare, spinose acritarchs with randomly distributed tubular processes and neck-like extension ascribed to *Tappania plana* which is widely accepted as unicellular eukaryotes are here first discovered in Yanshan area, extending its geographic distribution. The new fossil records in lower Changcheng Group provide one oldest conclusive evidence for the presence of both unicellular and multicellular eukaryotes diversified in late Paleoproterozoic.

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Yin, L., 1997. Acanthomorphic acritarchs from Meso-Neoproterozoic shales of the Ruyang Group, Shanxi, China. *Review of Palaeobotany and Palynology* 98, 15-25.

Keywords: eukaryotic evolution, microfossil, Proterozoic, Changzhougou Formation, Chuanlinggou Formation





The first fungus vegetation of Earth' land, a 425 Ma case from South China

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From 450 to 400 Ma, it is a rapid decline processes of the relative concentration of atmospheric CO₂ (Bernier, 2006), and a rising processes of atmospheric oxygen (O₂) (Lenton et al., 2016). What factors generate the change of earth's atmosphere, especial during late Silurian? The late Silurian marine organisms keep the relatively stable populations, the fauna presented mostly cosmopolitans. The marine organisms might make less contribution to atmospheric change and the terrestrial organisms play the important roles. Around or before ~420 Ma, the known vascular land plants are the small plants with the sparse distribution (Libertin et al., 2018), i.e. *Cooksonia*, that are only less than 10 cm high. To the earth terrestrial ecosystem, the impact of early vascular plants is negligible. Which land plants affect atmospheric change? Is there a group of unknown land plants? Did these plants control and effect the terrestrial ecosystem, increase the storage of organic carbon, and cause the atmospheric change? It is very necessary to find new evidences to confirm the existence of the unknown land plants.

Here, we report one special ~425 m.y. old land plant in South China. The plant fossils are found from the Xiaoxi or Chejiabaformations (Wang et al., 2017), among 17 localities in South China, that belong to three distribution regions, and the area total is about near 10000 Km². These formations consist mainly of the clastic rocks. The plant fossils are collected from the gray-yellowish siltstone or mudstone.

Plant diagnosis: Terrestrial plant, mainly consisted of one erect trunk, less with the lateral branches or bifurcating system. The trunk, with a swollen base, about at least 62 mm in diameter; and a tongue top, less than 5 mm in diameter. Plant, about over 1000 mm high. Surface of trunk, with longitudinal ridge along the longitudinal direction, and transversal nodes along the traverse direction. On surface of over 30 mm in diameter, the transversal nodes being fragment, and below 30 mm, being totally across the trunk. Trunk composed of smooth tubes, 35-37 μm in diameter and at least 1000 μm long.

Age and horizon: Late Silurian (Ludlow-Pridoli, ~425 Ma), the Xiaoxi and Chejiaba formations.

Based on the fossils from 17 localities within 10 thousand Km² preserved area, the plant communities are mainly consisted of this plant. The existing vegetation covering the Earth's land surface is mainly consisted of this plant. Based on this plant likely belonging to the fungi, around 420 Ma, the Earth's land surface is controlled by fungi. The Earth's terrestrial biosphere was under the domination of fungi. During late Silurian, This plant is the 'bigmac' plant in terrestrial ecosystem, exactly increased the organic carbon burial, and effects on the biogeochemical cycles. The widely distribution and flourish might quicken the decline of RCO₂, and rising of atmospheric oxygen (O₂). The level of atmospheric oxygen might begin to create the modern levels.

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Session 34 - ORAL

Open Session - Palaeoenvironments

Near-equatorial paleoenvironmental reconstructions of the Eocene Bengal Bay: insights from Burmese sedimentary archives and implications for past monsoonal evolution

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Some of the earliest pieces of evidence for monsoonal activity in the Bengal Bay come from the middle and Upper Eocene sedimentary series of Myanmar. Recent paleogeographic reconstructions have yet relocated Myanmar close to the equator during the Eocene, which questions the relevance of Burmese material to study past South Asian monsoonal activity. In this talk, we present existing and new paleobotanical, paleontological, and isotopic data from the Eocene of Myanmar in the light of the new paleogeographical reconstructions. We show that the numerous pieces of evidence for a long dry season indicate a wide migration of the intertropical convergence zone, supporting models for proto-monsoons driven by land-sea temperature contrasts. Paleobotany-based proxies yet suggest unrealistic cooler-than-today temperatures near the Equator, as found at other Paleogene low-latitude locations in South Asia. These results indicate that Eocene ecosystems and proto-monsoonal climate have no adequate modern analogue and call for caution when interpreting monsoonal proxies.

Keywords: Eocene, Monsoon, Myanmar, Paleobotany, Isotopes





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Open Session - Palaeoenvironments

Controls on Fluvial Architecture and Avulsion of The Liang Formation, Barakas Area, Brunei Darussalam

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J.J. Lambiase and A.B. Cullen (2013) suggested that Middle Miocene to Pliocene sedimentation on the NW Borneo margin has been interpreted as the product of one relatively large deltaic system, the Champion Delta. However, several lines of evidence indicate that the Champion system was not a simple, large delta; its drainage basin was too small, shallow marine depositional systems and fluvial outcrops indicate multiple, relatively small rivers and outcrop studies indicate the same facies associations as the diverse, modern depositional systems. Anticlinal ridges and rapidly subsiding synclines related to inversion and shale withdrawal significantly alter sediment dispersal patterns by deflecting multiple, relatively small fluvial systems. Predecessors of the Padas, Limbang and Trusan Rivers apparently are important sources of sand within the Champion system.

Limbang River flows into the Barakas syncline that composed of shallow marine and fluvial deposits formed as the uppermost part of Liang Formation during late Miocene to Pliocene. The exposed thickness of 14-16m, clean Sandstone with low angle to horizontal cross-bedding current structures and abundant burrows of foreshore environment during transgression. That was overlain by fluvial deposits and shows paleoflow from west to north-northwest with fining upward braided river and meandering river deposits.

In braided river system, consists the thick conglomerate facies of lenticular and erosional sandstone braided bars associated with sandstone and mudstone facies of channel bars. The planar cross bedded sandstone point out that obliquely to nearly the main flow direction represents to cross-channel bars.

Conversely in the meandering river system, composes of fine-medium grained sandstone with lateral and vertical accreted point bars and mudstone channel fill represent to oxbow lake clay plugs and mudstone channel fill of crevasse deposits.

A relative sea level fall formed a braided river and that was diverted to a meandering river system after a decrease in slope gradient at the next sea level rise and flooded time that meant switched to the river course and flow regime gave way to avulsion and diversion of fluvial architectures during relatively stable tectonic period.

Valenza J. M. et al. (2020) signified that one of the most dramatic events in river environments is the natural diversion, or avulsion, of a channel across its floodplain. Though rarely witnessed, avulsions can cause massive floods, and over geologic time they create most of the fluvial stratigraphic record. Avulsions exhibit behavior ranging from reoccupying abandoned channels to constructing new channels and splay complexes.

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Keywords: Brunei, Liang Formation, Barakas, Fluvial Avulsion



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Open Session - Palaeoenvironments

Palaeobiogeography of the NE Atlantic archipelagos during the Last Interglacial (MIS 5e): a molluscan approach to the conundrum of Macaronesia as a marine biogeographic unit

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The Last Interglacial (LIG) was one of the warmest interglacials of the last 1 million years. How species have behaved during this period in the Macaronesia geographical region has been intriguing scientists for years. The main goal of this study is to examine the status of Macaronesia as a marine biogeographic unit during the LIG. A large molluscan dataset was compiled containing 1,233 species-level taxa from shallow-water settings of the Atlantic and Mediterranean. Shallow-water marine molluscan occurrences from the LIG were obtained from field surveys undertaken in the Azores, Canary Islands and Cabo Verde archipelagos, and from Masseria S. Pietro (Taranto, Italy). This dataset was coupled with data taken from the literature, covering the Azores, Madeira, Selvagens, Canary Islands, Cabo Verde, NW Atlantic African Coasts, the Mediterranean, NE Atlantic American Coasts, Brazil, Uruguay, and Argentina. Dendrograms depicting the LIG palaeobiogeographic similarities between areas were compared with those obtained for present-day data, to pinpoint changes in biogeographic affinities. The analysis shows that during the LIG, the molluscan faunas of the Canary and Cabo Verde archipelagos were part of the same tropical Late Pleistocene Mediterranean West-African Province, whilst those in the Azores, Madeira and Selvagens archipelagos would be included in the subtropical Late Pleistocene French-Iberian Province. This contrasts with the present-day situation, where the subtropical/warm temperate Azores and “Webbnesia” marine ecoregions (Lusitanian province) are biogeographically separated from the Cabo Verde biogeographic subprovince, which in turn belongs to the West African Tropical biogeographic province. This study therefore provides another line of evidence of how climate change may impact



Session 34 - ORAL

Open Session - Herpetology

The first 70 Ma (Triassic-Early Jurassic) of terrestrial Pan-Aves evolution

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Pan-Aves corresponds to the entire branch of bird-line archosaurs, in opposition to its sister-clade, the crocodile-line archosaurs. It comprises dinosaurs (with birds included) and pterosaurs, as well as other taxa not usually nested within those groups, but commonly referred to as their precursors, i.e., aphanosaurs, lagerpetids, and silesaurids. With its oldest osteological records coming from poorly dated Middle Triassic beds of Russia and India, pan-avians have an evolutionary history of almost 250 Ma, spanning most of the Mesozoic and Cenozoic eras. This remarkable radiation has its roots deep in the Triassic, but flourished after the extinction event at the end of that period. In fact, the first 70 Ma of pan-avian geologic history is marked by important environmental changes, which shaped the evolution of the group. Focussing on terrestrial pan-avians (excluding pterosaurs), we quantitatively characterized the diversification and body size evolution of the group during the Triassic and Early Jurassic. Raw species richness and phylogenetic diversity (from time-calibrated phylogenies) were quantified as diversity metrics, but we also analysed net diversification rates using different methods/models and through-time patterns of body size evolution and evolutionary rates. Macroevolutionary shifts estimated from occurrence data were placed more recently in time than those from phylogenetic-based approaches. This includes various shifts during the Carnian, corroborating the hypothesis that the “Carnian Pluvial Episode” was key for the early radiation of Pan-Aves (Bernardi et al. 2018). Instead, phylogeny-based analyses identified higher diversity/diversification rates in the Norian, when several dinosaur groups attained a more global distribution (Kent & Clemensen 2021). In fact, several of the analysed metrics behave differently before and after the middle Norian, suggesting that dinosaur populations with a more global distribution, in opposition to faunas clustered in the southern Pangaea temperate belt, were more resilient to major environmental events. As an example, no meaningful macroevolutionary shifts were identified across the Triassic-Jurassic boundary, which is marked by the emplacement the ‘Central Atlantic Magmatic Province.’ Although it is likely that the end-Triassic mass extinction emptied ecospace into which dinosaurs expanded during the Jurassic (Brusatte et al. 2008), such diversification was not as fast nor as homogeneous for the entire group as previously thought. During the Early Jurassic, a reduction in body size near the Pliensbachian-Toarcian boundary may be related to the “Jenkyns” oceanic anoxic event, but macroevolutionary patterns should be interpreted with caution towards the verges of the analysed timeframe, as they may be biased by an “edge effect.”

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Keywords: Pan-Aves, Dinosauria, Triassic, Jurassic, diversity, macroevolution



Session 34 - ORAL

Open Session - Herpetology

New material of *Phuviangvenator* and the early evolution of Megaraptora

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Megaraptora is a clade of medium to large-sized highly pneumatized theropods with a long-snout, large-manual claws, and long and gracile metatarsals. The basal members were reported from the Barremian of Japan and Thailand. A more derived clade, the Megaraptoridae, is known from the Cenomanian to Santonian rocks of Gondwana. Here, we reported new skeletal material of *Phuviangvenator yaemniyomi*, an early branching megaraptoran from the Lower Cretaceous Sao Khua Formation of Khon Kaen, Thailand. The new material is assigned to be the same individual as the holotype of *Phuviangvenator* based on size, shape, and shared phylogenetic affinities. This material was recovered at the same quarry as the holotype and consists of an incomplete fibula, left and right metatarsals. A new autapomorphy observed from the new material is the presence of a long, deep fossa between the lateral and medial distal condyles of the metatarsal II that extends to the distal articular facet and visible in anterior view. The metatarsal III of *Phuviangvenator* is relatively short, more similar to the proportion present in the basal carcharodontosaur *Concavenator* than in the more derived megaraptorans (e.g., *Australovenator* and *Fukuiraptor*), but more gracile than other basal allosauroids (e.g., *Sinraptor* and *Allosaurus*). Its hindlimb proportions are similar to the basal carcharodontosaur *Neovenator* than other Gondwanan megaraptorids (e.g., *Australovenator*) and some coelurosaurs (e.g., *Garudimimus*). *Phuviangvenator* shows a combination of features shared with allosauroids and basal coelurosaurs and appears to be “intermediate” between non-megaraptorid and megaraptorid theropods. The present work provides information on the early evolution of the Megaraptora. The Early Cretaceous megaraptoran fossil record has been recovered from Asia, Australia, and South America. This shows a high diversity and a wide distribution of the megaraptorans during the Early Cretaceous. The clade then became more provincial in the Late Cretaceous of Gondwana.

Keywords: Dinosauria, Theropoda, Megaraptora, evolution, systematic

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Hatchlings of Tyrannosauridae and the evolution of dinosaur reproductive strategies

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Tyrannosaurs were giant predatory dinosaurs occupying the apex of Late Cretaceous food chains. Little is known about their early life due to the rarity of juveniles, however, and the earliest ontogenetic stages are virtually unknown. We describe hatchling remains (< 1 yr) of Tyrannosauridae weighing ~2.5 kg, <0.1% adult mass. Clutches were likely large (est. 25-60 eggs) suggesting tyrannosaurs used an *r*-selected reproductive strategy with limited investment in many small offspring. Synchrotron scans reveal remodeling and intensive loading, showing tyrannosaurs moved soon after hatching. Hatchling tyrannosaurs' small size and precociality suggest limited parental care. Tyrannosaurs had proportionately larger offspring than ancestral Archosauria, but relatively smaller hatchlings than Maniraptora, suggesting a reproductive strategy intermediate between basal archosaurs and birds. Multiple dinosaur lineages independently evolved large eggs and hatchlings, culminating in the large eggs and small clutches of modern birds. These patterns, paralleled in other groups, suggest a possible evolutionary trend towards increased parental investment in vertebrates.





Pliosaurid (Reptilia: Sauropterygia) remains from the Upper Cretaceous of Japan

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The Pliosauridae (Reptilia, Sauropterygia) represent one of the three lineages of the Plesiosauria known from the Upper Cretaceous. They are characterized by the short neck and massive skull with stout teeth, and although it is hard to give a reliable estimation of the body size based on often fragmentary remains, some Late Jurassic and Early Cretaceous forms are assumed to have reached over 10 m long (e.g., Knutsen et al., 2012). The youngest pliosaurid materials confidently diagnostic at lower taxonomic levels came from the Turonian of North America (Schumacher et al., 2013), and the group appears to have disappeared much earlier than other two Cretaceous plesiosaurian lineages, i.e. long-necked Elasmosauridae and short-necked Polycotylidae, whose stratigraphic ranges reach to the uppermost Cretaceous (Campanian-Maastrichtian) (Fischer et al., 2018; Otero et al., 2018). Despite their ecological significance as a possible top predator, extinction of the Pliosauridae seems to have attracted little attention in the study of Mesozoic vertebrates.

In this presentation we describe/re-describe pliosaurid specimens (skull, dental, and postcranial elements) from the Yezo Group in Hokkaido, northern Japan. They came from four different localities, and their stratigraphic origins range from the Cenomanian to the Turonian. Although their fragmentary nature does not allow identification at genus or species levels, estimated skull sizes approaches to those of contemporaneous large pliosaurids known from North America. In the Japanese Upper Cretaceous, elasmosaurid remains are fairly common but two short-necked lineages are represented by much smaller number of specimens (e.g. Sato et al., 2012). The described pliosaurids demonstrate that all three plesiosaurian clades of the Late Cretaceous survived the Cenomanian-Turonian boundary in this region.

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Keywords: Mesozoic marine reptiles, Plesiosauria, Japan, Cenomanian-Turonian boundary



Session 34 - ORAL

Open Session - Mammals

New Fossils from Hasnot (Late Miocene), Pakistan: *Bramatherium* and *Merycopotamus*

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The article describes fossils of two artiodactyl species *Bramatherium megacephalum* and *Merycopotamus* sp. which were found during 2010 to 2014 in the Late Miocene-Early Pliocene of Hasnot, Potwar Plateau of northern Pakistan. The material is, in terms of morphology and dimensions, referred to *Bramatherium megacephalum* and *Merycopotamus* sp. These species represent in the coeval deposits of the Dhok Pathan type locality of Dhok Pathan Formation, Pakistan, dating back to ca. 7 Ma. The zoogeographic affinities of the taxa are similar to those of other Dhok Pathan Formation localities of Pakistan.

The Hasnot outcrops range 7 – 5 Ma in age and correspond to the fauna of the Late Miocene-Early Pliocene of Eurasia and Africa. The artiodactyl community structure of the Hasnot Late Miocene – Early Pliocene is suggestive for establishing a vast open land environment depicting sporadic dry and flood seasons forcing a mosaic of ecotonal habitats with countless number of niches and parallel adaptations. Its paleoclimatic reconstruction is represented an aridity however supporting pockets of areas are covered by forests and wetlands as measured by its taxonomic composition. The assemblages proposed a mosaic of both more open and forested landscapes which comprised of heavy cover and, to some extent less significantly, forested, and wetlands.

Keywords: Giraffidae, Anthracotheriidae, Pliocene, Siwaliks, Potwar Plateau





Session 34 - ORAL

Open Session - Methodology

digital data within the review process, digitization projects in developing countries, digitization of private collections, to the creation of NFTs, etc. Additionally, we want to highlight the importance of digital collection curators/managers, their role, and how to efficiently manage digital collections with regard to their future-proofing and updating. Finally, we are working on adequate definitions/terms for identifying specific types of 3D models and accompanying files following the recommendations from international nomenclature codes. Thereby, we aim to delineate the way(s) in which digital collections are curated (i.e., evaluated, stored, hosted) and, throughout their life cycle, managed within the ever-evolving digital landscape. We invite anybody interested in these ongoing discussions to join and participate in the 3DigiPal group.

Keywords: 3D models, cyber-taxonomy, digitization, museum collections, digital curation



Session 34 - ORAL

Open Session - Methodology

A new R package to spatially subsample taxon occurrences for fair comparisons of biodiversity across time, clades, and environments

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The published fossil record is unevenly distributed over space and time, due to variation in taphonomy, sedimentation, outcrop exposure, collection effort, and research attention (e.g. Kiessling 2005, Patzkowsky and Holland 2012, Vilhena and Smith 2013, Raja *et al.* 2022). The degree of geographic coverage of fossil occurrences affects estimates of biodiversity and biogeography parameters in deep time; for instance, observed richness increases with geographic extent of sampling, due to the species–area effect (Connor and McCoy 1979). Spatially-uncorrected results may be uninformative at best and confidently wrong at worst. Therefore, we advocate that data treatment and analysis should account for variation in geographic coverage (Benson *et al.* 2021), irrespective of richness rarefaction methods that are widely used to account for variation in sampling intensity. Standardisation should be incorporated from the start of a project workflow, rather than as a refinement after initial data exploration.

There are many viable ways to control for unequal spatial coverage across a dataset. One versatile solution is to spatially subsample the data *a priori*, then estimate parameters and fit models on those subsamples. Several subsampling methods exist to standardise geographic area and extent, dispersion, or latitudinal breadth of localities (Marcot *et al.* 2016, Antell *et al.* 2020, Close *et al.* 2020, Flannery-Sutherland *et al.* 2022). Most methods iteratively cut samples from a dataset by first restricting occurrences to a bounding extent and then selecting an equal number of sites within that regional scope.

We present a new R package, ‘divvy’, which implements three methods of spatial subsampling, each with customisable parameters, in addition to related analysis functionality. ‘divvy’ operates on any dataset with taxonomic spatial occurrences, such as downloads from the Paleobiology Database, NEOTOMA, or GBIF. We review theoretical background, use cases, and examples of integrating spatial standardisation into analytical workflows using the ‘divvy’ package.

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Keywords: quantitative palaeobiology, spatial analysis methods, community database occurrences, sampling standardisation, species–area effect



Session 34 - ORAL

Open Session - Methodology

U-Pb Dating of Fossils: Toward Practical Paleontological Chronometry

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A better understanding of the status of our planet and future climatic conditions, depends on how well we understand the nature of past events. For example, extinctions of species have occurred throughout the history of life on Earth and must have been driven by geological events such as volcanic eruptions leading to climate changes. We can study extinction events in many different ways but one of the most important tools is uranium-lead (U-Pb) geochronology because it allows us to establish the order and duration of events and processes preserved in sedimentary rocks. Sedimentary rocks are the archives of life, climate, and environmental change. Fossils can be preserved in sedimentary rocks and are obvious targets for dating because they represent the very archive that records evolution and extinction events. Up to now, dating of fossils was almost impossible because fossils usually contain very low uranium, which makes them inapplicable for U-Pb dating techniques. New laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) data using improved processing methods provide early diagenetic U-Pb ages of fossils and constrain the mechanisms of trace element mobility during late-diagenesis. Testing of our dating technique has allowed the first accurate U-Pb age on fossilized soft tissue from a Pliocene mold of a bivalve yielding an age of 3.16 ± 0.08 Ma that is consistent with its late Pliocene stratigraphy whereas coexisting shark teeth from the same unit are variably reset by late-diagenesis. U-Pb dating on Cretaceous belemnites and Devonian rugose corals can be dated to reasonable precision and accuracy ($\pm 1-2$ Ma) using LA-ICPMS even when calcite invertebrate fossils show low U content (< 1 ppm). In some cases, examining LA-ICPMS data at the single cycle level can allow separate regression of totally reset and partially reset domains thus resolving ages of early and late diagenesis. LA-ICPMS U-Pb dating of apatite and calcite fossils offers an important technique to date the timing of deposition but there are several challenges that limit age interpretations.

Keywords: U-Pb dating, fossils age dating, LA-ICPMS dating



Session 34 - ORAL
Open Session - Methodology



Improving palaeoclimatic reconstructions with ecological data: How hot was the early Eocene?

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Geochemical data such as oxygen isotopes ($\delta^{18}\text{O}$), tetraether indices (TEX_{86}) and magnesium calcium ratios (Mg/Ca) are routinely used to reconstruct ocean temperatures in deep time. However, limited spatial coverage and disagreements between geochemical proxies compromise the accuracy of these reconstructions. Geological data such as coral reefs, mangroves, and evaporites have the potential to supplement geochemical data by improving spatial coverage and constraining temperature estimates. Historically, these data have been used to qualitatively inform upon palaeoclimatic conditions at broad spatial scales, yet no transfer functions exist to convert geological data into temperature estimates. Quantitative temperature reconstructions have therefore not made use of these data. Here, we present a Bayesian hierarchical model to integrate geological data—with established temperature proxies—into a unified quantitative framework. We apply this approach to the early Eocene climatic optimum (EECO), the interval with the warmest sustained temperatures of the Cenozoic. Assuming the conservation of thermal tolerances of modern coral reefs and mangrove taxa, we establish broad sea surface temperature ranges for EECO coral reef and mangrove sites. We integrate these temperature estimates with the EECO geochemical shallow marine proxy record to model the latitudinal temperature gradient and its uncertainty. Our results confirm the presence of a flattened latitudinal temperature gradient and unusually high polar temperatures during the EECO. We show that the inclusion of ecological data can substantially reduce the uncertainty on temperature estimates in climate zones lacking geochemical data.



Session 34 - ORAL

Open Session - Methodology

A novel analytical pyrolysis technique for the assessment of chitinous traces in putative fungal fossils

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The oldest undisputed fungal fossils date back to the Ordovician, yet display a large diversity and possess noticeable organizational development. On the other hand, molecular clock studies estimate the separation of the fungal clade from basal metazoans during the Cryogenian (Berbee and Taylor, 2010). Some recent studies (Loron et al., 2019; Bonneville et al., 2020) have proposed that the fungal fossil record may be extended to the Neoproterozoic, based on assignment of fungal affinity to putative fossils, prominently focusing on identification of chitinous residues as the basis for the assignment of fungal character. These studies, along with others from more recent fossils (e.g. Speranza et al., 2015) have primarily employed staining methods using agents that are neither exclusive nor specific to chitin (Nakashima et al., 2018), hence necessitating the need for independent and chitin-specific techniques. Here, we propose a method using comprehensive two-dimensional gas chromatography coupled with time-of-flight mass spectrometry (Py-GC×GC-TOFMS). We analyse using this technique fungal fossils from the Pliocene and report the presence of a suite of nitrogen-bearing compounds in their pyrolysis products, suggesting that some chitinous moieties could still be preserved. From these we identify, based on comparisons with standard chitin, 3-acetamidopyrones and their methylated homologues as potentially unique markers for chitinous origin. We also compare the observed distribution with cell wall peptidoglycan from *Bacillus subtilis*, a biopolymer which shares the N-acetylglucosamine moiety with chitin, and find that the previously identified markers remain specific to chitin. We also find that chitin can be differentiated from peptidoglycan based on the overall distribution of compounds, as peptidoglycan produces a series of fatty acids as well cyclic 2,5-diketopiperazines. Identification of chitinous origin is an important pre-requisite in the assignment of fungal affinity to putative fossils, particularly in cases such as Pre-Cambrian fossils, where the mycelial morphology displays equivocation between a bacterial or fungal origin, and we believe that Py-GC×GC-TOFMS offers a robust technique that can be employed along with, or independent of, staining methods, provides reliable proxies for assignment of chitin and/or chitinous residues, and could have great potential applications in future analyses of fossils from deep time.

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Keywords: Pyrolysis, Py-GC×GC-TOFMS, chitin, fungi, deep time



The elusive ancestors of Neogastropoda—where we stand?

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Gastropods are the most successful class of molluscs, which conquered majority of the available habitats and display rich fossil record throughout the Phanerozoic. The evolutionary history of several groups, however, is difficult to decipher since the shells of the gastropods are commonly poorly preserved due to their prevailing aragonite mineralogy and numerous convergences in morphology. A good example are Neogastropoda, which nowadays is most successful and highly diversified group of marine gastropods. Neogastropods are active predators and their hunting innovations are considered a crucial factor in their rapid radiation in the mid-Cretaceous. The phylogeny of living neogastropods is well resolved now due to the molecular studies and their monophyly confirmed (e.g., Osca et al., 2015). The identification of neogastropod stem group in the fossil record is much more challenging since it is based solely on comparative shell morphology of extinct taxa. Three families of Purpurinidae, Pseudotritonidae and Maturifusidae were so far proposed as possible neogastropod stem groups (Taylor et al., 1980, Bandel, 1993, Kaim, 2004). The relationship between and possible synonymy of Triassic Pseudotritonidae and Jurassic Maturifusidae still remains a matter of debate (Nützel, 2010). Anyway, Maturifusidae were proposed to be ancestors of Neogastropoda (Taylor et al., 1980) while Purpurinidae as ancestors of Tonnoidea (Bandel, 1993). These assumptions are based on shell morphology and in particular on larval shell (protoconch) characters. The latter are crucial for the familial identification but regrettably only rarely preserved in fossils and not always documented in the recent taxa. Neogastropods typically have unusually big and highly conical multispiral protoconchs, which differ from obtusely conical purpurinid protoconchs. The members of Maturifusidae also have highly conical multispiral protoconchs, which are ornamented with two strong spiral ribs. The latter, however, are typically absent in living neogastropods and extinct purpurinids. On the other hand, maturifusid larval shell characters resemble somewhat those known from herbivore cerithiid gastropods and therefore they might be also interpreted as their extinct branch. The oldest record of purpurinids is known from the Late Triassic (Carnian) (Münster, 1841), maturifusids appeared in the Early Jurassic (Toarcian) (Schulbert & Nützel, 2013), while the oldest record of the true neogastropod was described from the Early Cretaceous (Valanginian) (Kaim 2004). Other Early Cretaceous neogastropods were recorded from the Aptian-Albian of Mexico – 1 species (Allison, 1955) and Albian of England – 6 species (Tracey, 2010). The material from the Albian of France (d'Orbigny's collection) requires revision due to doubtful stratigraphic references. We have examined two extensive undescribed collections of Cretaceous gastropods: one from the Barremian of Bulgaria (114 species) and the other from the Cenomanian of India (118 species). Only one neogastropod shell was identified in the Bulgarian collection, which is 0.9% of the total number of species, while 7 species were determined from the Indian collection so their contribution increased to 5.1% of the entire number of species. Thus, it can be assumed that the key period for radiation of the group was Aptian-Albian when their explosive diversification took place. This research is supported by the NCN grant number: 2018/31/D/ST10/03817.

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Gastropods in ancient hydrocarbon seeps – a state of art

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Gastropods are one of the most important groups of organisms adapted to chemosynthesis-based communities. The fossil record of gastropod occurrences in the ancient hydrocarbon seeps shows that the trochomorph gastropods are already known from Paleozoic seeps and vents though they are poorly preserved and thus researched. In the Late Triassic seeps from Turkey, gastropods are well diversified, including the first possible abyssochrysoidea. The Jurassic and Cretaceous were times of abyssochrysoidea dominance in seep and vent gastropod communities not only in number of taxa but also in number of individuals. The Jurassic and Early Cretaceous seeps were dominated by Hokkaidoconchidae and Paskentanidae while in the mid-Cretaceous Provannidae and Desbruyeresidae appeared. Abyssochrysoidea, Rubyspiridae and Alviniconchinae are only Cenozoic/Recent groups. The oldest report of neomphalid gastropods in seeps is from the Jurassic though their diversity is restricted to small-sized *Retiskenea*-like taxa and apparently they are absent at Mesozoic vents. Most likely, the neomphalid radiation in vents came much later. Limpet-shaped gastropods occur at seeps already in the Jurassic but became common only in Late Cretaceous. Similarly, colloniid vetigastropods appear in large quantities only in Late Cretaceous seeps although they were present already in the Early Cretaceous. Eucyclid seguenziids are extremely common in Jurassic seas and they apparently migrated to Jurassic seeps while cataegids appeared in the Cretaceous and still occur at seeps today. Stem and/or sister groups of neogastropods (Purpurinidae and Maturifusidae) first appeared at seeps in the Jurassic, while true neogastropods are nearly absent in Mesozoic seeps, apart from a single poorly preserved specimen in a Campanian (Late Cretaceous) seep in Japan. Otherwise, neogastropods appear in larger numbers in Oligocene seeps. Cephalaspids are recorded at seeps from the Triassic but never occur in larger numbers, being apparently only opportunistic in these environments.

Keywords: Gastropoda, Abyssochrysoidea, Neomphalida, hydrocarbon seeps, hydrothermal vents, chemosynthesis-based communities, evolution





Session 34 - ORAL
Open Session - Museums

The relocation of the paleontology collections of the National Museum of Natural History, Paris

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The relocation of the paleontology collections of the National Museum of Natural History, Paris (MNHN) responded to several fundamental challenges. The first was the direct threat of a hundred-year flood of the Seine River, which would flood 75% of the collection. The second was to gather all the paleontology collections in the same place by 2022. This was a major task since it involved organizing and re-organizing the fossils in a rational and sustainable way for future generations. In the future, it will make it possible to have a high-performance tool that meets the demands of French and international researchers, but also requests from decision-makers and calls for tenders: directorates, ministries, national and international programs. The third issue was the possibility of allowing the MNHN to undertake a renovation of the comparative anatomy and paleontology galleries. In preparation for many years (preventive conservation, sorting of collections and cartography) and initiated internally by the removal of the d'Orbigny's collection in June 2019, the phase 1 of the transfer of the paleontology collections officially began in August 2019. Three sectors were moved: fossil invertebrates, micropaleontology, fossil fish. The data confirm the pharaonic nature of this operation: 4 to 5 million specimens, 15,000 European standard bins, 50 linear meters of non-standard specimens, installation of a new storage dedicated for types and figured specimens of fossil invertebrates (45,000 samples – 120 cabinets), installation of a new micropaleontology room (100 m²). Beforehand, during the first half of 2019, four rooms in the new building were equipped with a mobile cabinet system and a 100 m² room was equipped with semi-heavy fixed shelving for the non-standard (too large, too heavy) specimens of phase 2. This phase 2 concerned collections of fossil mammals (500,000 samples) and fossil reptiles, amphibians and birds. It took place between winter 2020 and summer 2021 and resulted in the displacement of 2 million fossils and 390 linear meters of non-standard specimens. In 2022, phase 3 involved the relocation of 80,000 plant fossils, from macro-remains to micro preparations.

Keywords: Collections, Paleontology, relocation, MNHN, fossils, microfossils, paleobotany





Session 34 - POSTER
Open Session

Mid-Cretaceous Angiosperm Diversity in Burmese Amber

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The origin and diversity evolution of angiosperms have been a worldwide scientific issue for more than a century. There was a shortage of large fossils in the Mesozoic. Even in the middle Cretaceous, when angiosperms were more prosperous, the fossil record was still dominated by pollen microfossils, which led to serious doubts about the Cretaceous radiation of angiosperms.

The Burmese amber fossils formed in the middle Cretaceous (110 Mya to 99 Mya) provide a new perspective for the study of the origin and evolution of early angiosperms. However, at present, the paleontology reported in the Burmese amber is mainly insects and vertebrates, and the angiosperms are rarely reported, which needs to be discovered.

In the mid-Cretaceous amber fossils, we found a lot of plant fossil evidence. Some well-preserved flowers, fruits and leaves indicate that certain angiosperms may have reached great diversity at that time, and some existing branches may have originated earlier. Their appearance has affected the evolution of dinosaurs, insects, mammals and other organisms, and traces of insect activities have also been observed in fossils, which provides new insights into the common differentiation of angiosperms and related animals.

We hope to share our recent discoveries in Burmese amber, enrich the diversity of large fossils of Cretaceous angiosperms, and cooperate with paleontologists and botanists around the world to carry out preliminary classification and identification; We hope to discuss the morphological evolution, climate adaptation, and paleogeographic origin of the representative taxa; We hope to study the ecological landscape in the middle Cretaceous; We hope to confirm the radiation evolution of angiosperms in the middle Cretaceous, and provide new insights into the origin and evolution of early angiosperms' diversity.

<https://www.science.org/content/resource/125-questions-exploration-and-discovery>

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Keywords: Angiosperm, Biodiversity, Amber, Fossils, Cretaceous



Session 34 - POSTER

Open Session



First macrofossil record of *Calophyllum* (Calophyllaceae) from the Oligocene-Miocene of Li Basin northern Thailand

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Fossils from tropical Asia, which have been far from fully investigated, are important for understanding the evolution of plant diversity and associated surrounding environment. In this study, we reported well-preserved leaf fossils of *Calophyllum* (Calophyllaceae) from the lacustrine deposits of the Oligocene-Miocene Li basin, Northern Thailand. These are the first leaf fossil record of *Calophyllum* in Thailand. The fossils were identified through detailed comparison with leaves of extant species and fossil leaves. These fossil leaves were lanceolate or oblong, apex acute, base cuneate. Pinnately venation, distinct parallel lateral veins, nearly perpendicular to the midvein; secondary veins alternate, closely placed, craspedodromous, parallel, dense, and distinct on surface, forming marginal veins. Higher-level veins not observed. Detailed morphological observation indicates that these fossil leaves are provisionally assigned to *C. suraikholaensis* Awasthi & Prasad, 1990. and *Calophyllum* sp., it suggests that northern Thailand during the Oligocene-Miocene was under sub-tropical climate. We conclude that this genus probably originated in India during the Paleocene before spread from India to Indochina during the Neogene, and finally formed its modern distribution with tropical climate.

Keywords: *Calophyllum*, Miocene, Li Bansin, Thailand, palaeoecology



