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## **MTE 13** Abstracts

### 13th Symposium on Mesozoic Terrestrial Ecosystems and Biota



Bonn, Germany  
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edited by  
Thomas Martin,  
Rico Schellhorn  
& Julia A. Schultz

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**MTE13**

**13th Symposium on Mesozoic Terrestrial  
Ecosystems and Biota**

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Bonn, Germany  
2018

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## Foreword

Welcome to the 13th Symposium on Mesozoic Terrestrial Ecosystems and Biota (MTE13), hosted by the University of Bonn, Germany!

This is the second time that the MTE has been held in Germany, after MTE3 at the University of Tübingen in 1984. Germany has a long tradition of Mesozoic terrestrial research, going back to the early 19th century with the description of iconic fossils such as the pterosaur *Scaphognathus* (1831), the ichnotaxon *Chirotherium* (1835), the prosauropod *Plateosaurus* (1837), and the earliest bird *Archaeopteryx* (1861). Exciting discoveries still continue today, such as the theropod *Juravenator* (2006) from the Solnhofen limestone or the dwarf sauropod *Europasaurus* (2006) from the Harz Mountains.

MTE13 is a showcase for the most up-to-date and groundbreaking research on Mesozoic terrestrial ecosystems and organisms. Presentations cover a wide variety of Mesozoic life, from protists to mammals, and Mesozoic environments, from organism interactions to biomes. They comprise stunning 3D reconstructions based on computed x-ray investigations as well as exciting discoveries from new fossil localities in the field – just to pick a few of the many topics presented at the symposium. We hope that you find MTE13 inspiring and that you enjoy the opportunity to interact with experts in Mesozoic terrestrial research from all over the world.

We wish to express our sincere gratitude to the Deutsche Forschungsgemeinschaft (DFG) for their financial support of this symposium. We thank Karl Schilling, director of the Institute of Anatomy, who provided a venue for the congress. Finally we would like to thank the members of the scientific committee for reviewing the abstracts, Victoria McCoy for linguistic corrections, and the student helpers and volunteers from Steinmann-Institut for their valuable contributions to the success of MTE13.

Thomas Martin, Rico Schellhorn & Julia A. Schultz  
MTE13 Organizing Committee

## **Past Meetings**

- 1978** – MTE1 Paris, France
- 1981** – MTE2 Jadwisin, Poland
- 1984** – MTE3 Tübingen, Germany
- 1987** – MTE4 Drumheller, Canada
- 1991** – MTE5 Oslo, Norway
- 1995** – MTE6 Beijing, China
- 1999** – MTE7 Buenos Aires, Argentina
- 2002** – MTE8 Cape Town, South Africa
- 2006** – MTE9 Manchester, United Kingdom
- 2009** – MTE10 Teruel, Spain
- 2012** – MTE11 Gwangju, South Korea
- 2015** – MTE12 Shenyang, China



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## Earliest mordellid-like beetles from the Jurassic of Kazakhstan and China (Coleoptera: Tenebrionoidea) [oral presentation]

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Mordellidae (Coleoptera: Polyphaga) includes approximately 2400 worldwide extant species and are commonly known as tumbling flower beetles. The group contains only a few fossil records. For a long time, the fossil subfamily Praemordellinae has been regarded as the primitive group of family Mordellidae. Now it is raised to family rank and named Praemordellidae. The holotype of *Praemordella martynovi* Sczegoleva-Barovskaja, 1929, from Late Jurassic deposits at Karatau, in Kazakhstan, is re-described. The genera *Cretanaspis* Huang and Yang, 1999, *Mirimordella* Liu, Lu and Ren, 2007, *Bellimordella* Liu, Zhao and Ren, 2008 and *Wuhua* Wang and Zhang, 2011 are attributed to Praemordellidae. The newly described fossil from mid-Cretaceous Burmese amber is placed as a subfamily in Praemordellidae. Two new species are described and assigned to genus *Wuhua*, based on well-preserved specimens from the Middle Jurassic Daohugou Biota of Inner Mongolia, China. The morphological characters of Praemordellidae are given, and a key to genera of Praemordellidae is presented. Praemordellidae is closely related to extant Mordellidae, as it has the distinctive combination of a hump-backed body, strongly deflexed head, filiform antennae and pectinate tarsal claws. It, however, is different from Mordellidae in the absence of pygidium and hind femurs not well developed. It also shows similarities to Ripiphoridae: the convex body and simple tarsi, but differs from the latter in having bipectinate (in male) and unipectinate (in female) antennae. The sister relationship between Mordellidae and Ripiphoridae is supported by molecular data. Praemordellidae probably is a stem group that may include the ancestor taxa of Mordellidae and Ripiphoridae. The morphological differences of Praemordellidae, Mordellidae and Ripiphoridae may be the adoption to an ecological shift during the Jurassic to Cretaceous period due to the rise of angiosperms. The early history of this group of beetles provides new insights into the coevolution between pollinating insect and flowering plants.

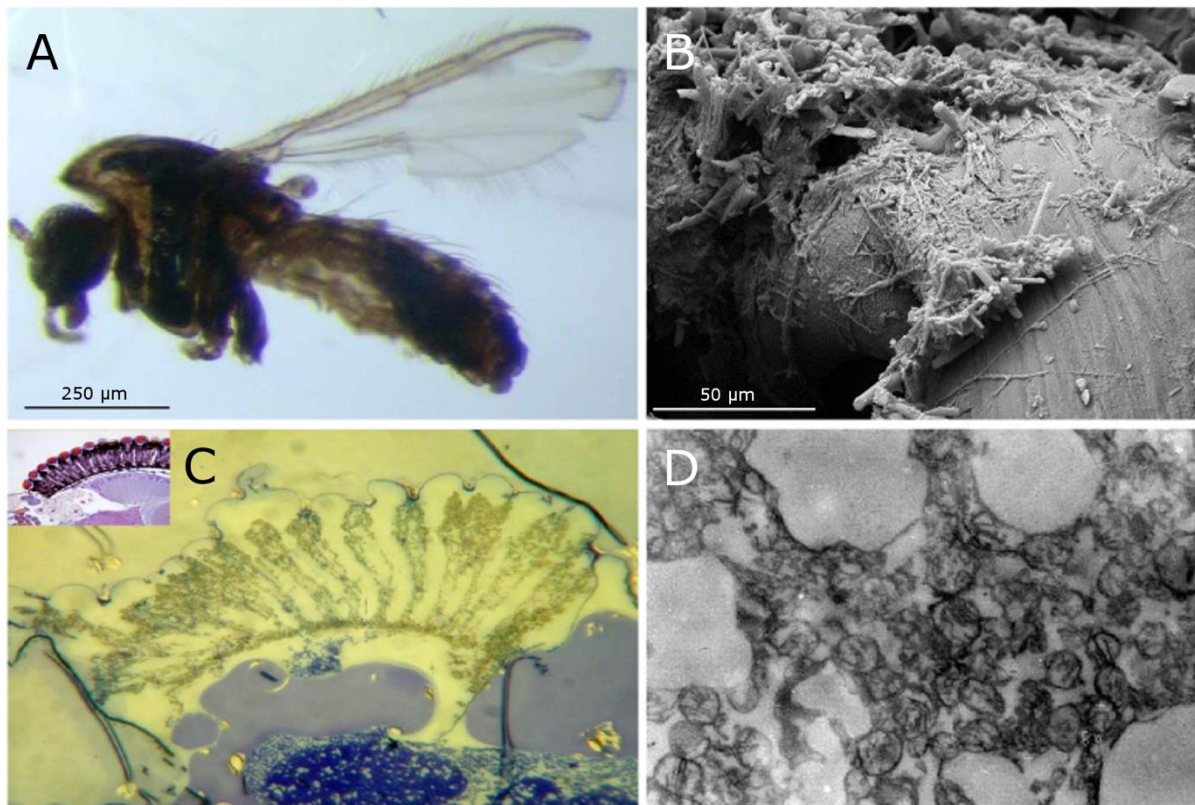
**Soft tissue preservation in amber – a comparative study on the taphonomy and limits of fossilization of resin embedded arthropods [poster presentation]**

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Amber is one of the most important sources of fossil terrestrial arthropods and gives insight into Mesozoic and Cenozoic terrestrial ecosystems. We want to present our intermediate results on a study regarding the preservation of soft tissue of different arthropod taxa from various amber and copal deposits. Many studies report an exceptional cellular and ultrastructural fidelity of fossils in amber, including non-mineralized tissue such as muscle fibers, mitochondria, and parts of the nervous system (Grimaldi et al., 1994a, Henwood, 1992a, 1992b). A known phenomenon is the preservation as an outer cast, with specimens being hollow inside. This type often occurs in Baltic amber, but for the Lebanese and Indian amber real body fossils expressing cuticle preservation are evidenced (Azar, 1997, Rust et al., 2010). These differences in preservation may refer to crucial factors such as the depositional environment, the resin compounds, or the geologic age, which indicates that the taphonomic pathway of amber fossils is not uniform. Studies regarding the taphonomy and chemical analyses of inclusions revealed the preservation of original carbon in Dominican amber (Stankiewicz et al., 1998), and the presence of reactive cellular components of a cypress twig from Baltic amber (Koller et al., 2005) but the processes leading to this exceptional conservation are still not understood. Former studies on this field have a low sample size and a protocol in terms of reproducibility is still lacking.

The characteristic of Eocene Indian amber to be completely soluble in certain solvents opens up new possibilities on the examination of amber preservation. Inclusions can be extracted from the resinous matrix and subsequently analyzed with various methods such as SEM, TEM, or Raman spectroscopy (Fig. 1). The results will be compared to inclusions extracted by dissolving or breaking amber pieces from other deposits (e.g., Eocene Baltic amber or Cretaceous amber deposits). This is the first attempt to conduct a systematic and reproducible study of the preservation of arthropod soft tissues in amber to determine the chemical characteristics of the organic remains, the fossilization processes behind it, the variability of this exceptional type of preservation with respect to different types of amber, copal deposits and their environmental conditions, different types of organic systems and tissues and a different chemical composition of the original resins. Integration of extant, and museum samples, as well as copal, will lead to the most extensive study on amber taphonomy so far.



**Fig. 1.** Extracted organisms and tissues from Eocene Indian amber (53 Ma). A: Completely preserved nematoceran fly. B: SEM image of muscle fibers and remnants of the tracheal system of a beetle. C: TEM image of a histological slice through a fossil nematoceran head in comparison to an extant one (upper left corner). Ommatidia and parts of the brain are still present (Magn. 7000). D: Close-up shot of mitochondria from the visual system of the same specimen (Magn. 12000).

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## Dental microwear texture analysis: a taphonomically robust dietary proxy for non-mammalian tetrapods? [poster presentation]

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Teeth are most resistant against diagenetic alteration and therefore often represent the only remains that enable us to infer the diet and food processing of extinct vertebrates. Since non-mammalian tetrapods generally have a homodont dentition, the shape and size of their teeth often do not provide sufficient morphological information about their feeding behavior. The stable isotope analysis of carbon and oxygen isotopes in enamel is an established approach to reconstruct the diet of extinct non-mammalian tetrapods. For a few years non-traditional stable isotope systems (e.g., Ca, Mg, Zn) are successfully applied to distinguish between faunivorous and herbivorous taxa and determine the trophic level in food webs (Hassler et al., 2018; Heuser et al., 2011; Jaouen et al., 2013, 2016; Martin et al., 2016; Skulan et al., 1997). In addition, dental microwear texture analysis (DMTA) can be used as a non-destructive dietary proxy for mechanical food properties of the last meals. It enables us to distinguish soft- from hard-object feeders among herbivores and faunivores by quantifying the microscopic wear features on the enamel surface topography (Gill et al., 2014; Purnell et al. 2007; Schulz et al., 2013).

So far, DMTA was mainly performed on extant and fossil mammalian species and has only recently been transferred to non-mammalian taxa. This is challenging because unlike mammals non-mammalian tetrapods do not chew and thus have reduced attrition (tooth-tooth contact) and abrasion (food-tooth contact) traces. Nevertheless, despite a predominant chop-and-swallow feeding strategy, abrasive wear must take place and diet related dental microwear texture (DMT) is thus expected for non-mammalian tetrapods. Here we present the first DMT data on extant and extinct non-mammalian tetrapod species. The main goal of our study is to assess the robustness of diet-related wear features on the dental surface of non-mammalian tetrapods during post mortem taphonomic alteration and fossilization. Fossil teeth encounter various taphonomic processes prior to or during burial, which may alter original diet-related DMT. Therefore, an in vitro alteration experiment simulating fluvial sediment transport was performed on teeth of two different extant reptile species, one small herbivore (*Iguana iguana*) and one large faunivorous crocodile, similar to a previous study on different mammal teeth. For this purpose the teeth were tumbled in sediment-water suspensions with siliciclastic sediments of different grain size fractions (sand: 63-125 µm, 125-250 µm, 250-500 µm) to determine if and how diet-related wear patterns on the tooth surface are mechanically altered under such conditions.

For molars of two mammalian herbivores (browser: roe deer; grazer: horse), we did not observe a significant alteration of the original diet-induced DMT on their chewing facets even after 2 weeks of tumbling in fine to middle grained sand, simulating a transport distance of around 363 km. Thus diet-related DMT can survive substantial sediment transport and it is still possible to distinguish between the two different diet categories. To test if this also applies to aprismatic and thin enamel of non-mammalian tetrapod teeth the DMT of herbivorous *Iguana* and faunivorous crocodile teeth is measured on exactly the same 160 x 160 µm enamel areas before and after tumbling for defined time intervals. These experimentally derived DMT data are compared to a DMT reference dataset of extant non-mammalian tetrapod species from different feeding categories (faunivores, herbivores, frugivores and omnivores) as well as to DMT of some fossil dinosaurs (theropods, sauropods) and

synapsids (pelycosaurs) from defined taphonomic settings. It will be discussed whether diet-related DMT are still preserved on fossil reptilian teeth and if they can potentially be used to infer the diet of extinct sauropsids and synapsids.

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## Living alone or moving in herds? Inferring social behaviour in ankylosaurs: a review [oral presentation]

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Gregarious behaviour has been inferred in a number of dinosaurian groups, including ceratopsians, ornithopods, theropods and sauropods, while this aspect of ankylosaurs, the herbivorous "tanks" of the Mesozoic, is dubious. This study reviews the taphonomical, palaeoecological, and palaeobiological context of ankylosaurian fossil record to decipher social behaviour in these armored dinosaurs.

Gregariousness in extinct vertebrates is most commonly inferred from mass death assemblages (MDAs), which include remains of animals that died in a short time due to a single agent of death suggesting a spatial concentration of multiple individuals before their death. Although the majority of ankylosaur skeletons are found isolated, in a few known cases multiple conspecific individuals are preserved within the same bonebed: 1) *Gastonia* from three sites (minimum number of individuals or MNI  $\geq 3$ , 5, and 9, respectively) of the Cedar Mountain Formation, USA; 2) *Pinacosaurus* from the formations Bayan Mandahu (MNI=12), China and Alag Teeg (MNI>30), Mongolia; and 3) nodosaurid ankylosaurs from Iharkút site (MNI=12) of Csehbánya Formation, Hungary. Taphonomy of these sites indicates that the animals died and were buried together in a single event representing true MDAs (Botfalvai et al. 2015; Kinner et al. 2016). Even though MDA provides strong support for inferring group-living, temporary aggregations of individuals irrespective of their gregarious or nongregarious social behaviour may also occur due to unpredictable and unfavourable environmental changes. MDAs of *Gastonia* and *Pinacosaurus* were deposited under semi-arid to arid climate where the seasonal drought must have represented a significant stress factor for these animals. However, these MDAs are present in multiple horizons characterized by different depositional environments and ages indicating that these ankylosaurian taxa may have indeed lived in groups (Currie et al. 2011; Kinner et al. 2016). Taphonomical history of the nodosaurid MDA in Iharkút is best described by a mass drowning event (Botfalvai et al. 2015). However, as non-gregarious animals also tend to withdraw and concentrate on higher ground refuges from a severe flood, MDA of the Iharkút ankylosaurs cannot be considered as firm evidence for gregarious behaviour, either.

A common selective force leading to herd formation in herbivores is predator-evasion by aggressive group defense and/or by blending in the group as cover. However, efficient defensive structures and formidable weapons in a large herbivore may be sufficient to deter predators even from solitary individuals. Ankylosaurs represented medium-sized herbivores of their era, and their characteristic armour extending along the entire body length and consisting of diverse osteoderm complexes, such as plates, spikes and tail clubs, is generally thought of as having primary role in defense (Scheyer and Sander, 2004; Burns and Currie, 2014). Some studies suggested different levels of efficiency of these structures in resisting and exerting forces of an attack and counterattack implying the inadequacy of some elements for passive or active defense (Hayashi et al. 2010; Arbour, 2009). Considering multiple functions, as for the crocodilian armour in axial stiffening, protection against acidosis or thermoregulation (Burns et al. 2013), may be reasonable and not mutually exclusive with mechanical protection. However, shield-like osteoderm complexes, especially in herbivores, undeniably take part in defense, be it in extant or extinct animals used in inter- and/or intraspecific interactions (e.g., Vickaryous and Sire, 2009; Zurita et al. 2010). Whether the protective

efficiency of ankylosaurian armour allowed solitary lifestyle depends on the paleoecological context at multiple levels, as evidenced by the diversity of social behaviour of extant megaherbivores with formidable weapons living in the same open habitat essentially alone (rhinoceros), in smaller groups (elephants) or in large herds (buffalo) (Owen-Smith, 1988). Thus, possessing efficient defense structures in herbivores may be a prerequisite but not necessarily a sufficient condition for a solitary lifestyle. Ankylosaurs apparently exhibited the necessary protective anatomy for being solitary, however, they could have gathered in groups depending on factors not necessarily related to predation pressure.

Ankylosaurs were wide-bodied, bulky animals with short limbs; a bauplan poorly adapted to long-distance trekking that characterizes herds of herbivores. By comparison, hadrosaurids and ceratopsians, known from monodominant bonebeds containing >100 individuals and thus referred to as gregarious, migratory quadrupeds, show more efficient limb mechanics for long-distance locomotion (Bell and Snively, 2008). Femoral shapes also indicate greater body masses for ankylosaurs than for other ornithischians with the same femoral length (Maidment et al. 2012), once again suggesting their lower capacities for long-distance foraging and/or migrating in a herd. The nodosaurid *Hungarosaurus* from Iharkút, however, is characterized by relatively gracile and elongated limb bones with a fore- to hind limb length ratio of 1:1, presence of paravertebral elements providing axial stiffening, and a hypertrophied cerebellum; a combination of features suggesting better cursorial capacities than in other ankylosaurs.

To sum up, the diverse aspects of currently available fossil evidence and extant comparisons shown in this study suggest that the majority of ankylosaurs were likely solitary, while some taxa, like *Gastonia*, *Pinacosaurus* and possibly also the Iharkút nodosaurids could have shown more tendency to form temporary and/or permanent groups of limited size and home range.

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## **Main achievements of the research program at the Las Hoyas Fossilagerstätte (Lower Cretaceous Spain) [plenary talk]**

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An important concentration of continental deposits with fossils of exceptional preservation was produced worldwide during the Kimmeridgian-Albian time interval. Such a large-scale paleontological pattern might characterize an Early Cretaceous Megabias. The Fossilagerstätte of Las Hoyas represents another paradigmatic example of such deposits. The extent to which these significant ecosystems may have channeled the evolution and preservation of the Early Mesozoic biotas is still far from accurately understood. The research on the site of Las Hoyas, carried out over 30 years, is contributing to the resolution of this challenging enigma. Once the initial phase of excavations, with the sole purpose of collecting exceptional specimens, was completed, Las Hoyas became a source of complex questions that needed to be answered by the integration of different geological, palaeobiological and taphonomic disciplines. This multidisciplinary integration has highlighted three major attributes of its fossils, associations and biota: (1) the quality of preservation due to the occurrence of microbial mats; (2) the compositional fidelity linked to the environmental dynamics; and (3) the evolutionary implications related to a wetland ecosystem.

The preservation of fossils at Las Hoyas is exceptional both in abundance and quality. Soft parts of animals alongside articulated skeletons, and even soft-bodied organisms are preserved with micro and ultrastructural biological details. Complete characean algae with their vegetative apparatus in situ, plant macroremains with epidermal and microstructural details and palynomorphs are well-preserved. Carbonaceous compressions and calcium phosphate are the prevalent preservational types. Current evidence indicates that such exceptional preservation is due to the occurrence of microbial mats, placing Las Hoyas in the "bacterial sealing" area of the taphonomic processes of Seilacher's triangle. The mechanisms involved in preservation have been experimentally tested on a microbial mat community grown in tanks under controlled conditions and using different animal carcasses. These trials have verified that mats clearly avoid skeletal disarticulation, slow down decay, promote biomineralization of organic remains, and induce the formation of moulds and delicate replicas over several years.

The Las Hoyas site has been the subject of layer-by-layer excavation since 1991. Small square areas of about 30m<sup>2</sup> are suitable for testing the homogeneity of the fossil associations throughout the layers. The Las Hoyas layers are made of laminated limestones that comprise a set of transitional microfacies: from positively graded millimetric laminae due to underflow currents and decantation of allochthonous detrital, fine carbonatic particles and vegetal debris, to stromatolite-like laminae linked to the growth of benthic microbial mats. A taphonomic analysis comparing the fossil and the facies associations indicates that the 'stromatolitic facies' contain abundant fossils but low richness, whereas the 'millimetric graded facies' have fewer fossils but a high diversity of taxa. The compositional fidelity of the fossil record from Las Hoyas is a result of the generally demic and autochthonous nature of the elements of this association: most organisms lived and died in the same area where the fossil remains were produced and eventually recorded.

Las Hoyas is interpreted as a freshwater carbonatic lentic ecosystem without any marine influence, regulated by a seasonal subtropical climate, in a lacustrine to palustrine wetland subsystem. The singular environmental conditions have recorded a highly representative biota, both in space and in time, consisting of a very high diversity of taxa; a mixture of aquatic, amphibian, and

terrestrial plants and animals. The most abundant taxa correspond to obligated aquatic organisms, so that the bias is minimal, and the diversity of some groups is amazingly close to that of any recent wetland.

The fossil associations of Las Hoyas fit perfectly into the limitations of the definition of biota: 1) a particular geographic region, 2) a specific time, and 3) a certain ecology. The biota recorded simultaneously contains relict groups from the Late Jurassic (conifers, non-teleostean neopterygians, basal mesoeucrocodylians, paramacellodid lizards) and key groups at the base of the lineages involved in the Cretaceous Terrestrial Revolution (angiosperms, modern insects, lizards and crocodiles, pterosaurs, birds, and mammals). Furthermore, the record from Las Hoyas provides the finest temporal adjustment of many groups, including the oldest record of nectar-feeding dipterans, chanid fishes, pipimorph frogs, and tapejarid pterosaurs. Some 25% of the animal taxa identified at Las Hoyas are endemic; unique restriction to a particular locality in the world is a strong indication of isolation conditions in the original wetland ecosystem. At the time, in the Barremian (Early Cretaceous, some 125 million years ago), the Iberian Peninsula was actually an oceanic island placed in the Western Tethys, just between Eurasia, North America, and Africa, thus acting as an evolutionary linkage between Laurasian and Gondwanan, Eastern and Western floras and faunas.

## The last triconodonts [oral presentation]

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Eutriconodonts are of special interest because of their phylogenetic position, as an early-diverging clade of Mammalia, and because they include early mammalian forays into carnivory. The core family, Triconodontidae, is best known from the Jurassic–earliest Cretaceous, but survived well into the Late Cretaceous (Fox 1969). An advanced subfamily, Alticonodontinae, until now known only by jaw fragments and teeth, even underwent a modest radiation in the Albian–Cenomanian of North America (Cifelli and Madsen, 1998). Herein we present preliminary findings of our study on the paleobiology of alticonodontines, based mainly on an unusually well represented taxon from the Cloverly Formation (Albian, Early Cretaceous) of Montana, USA.

The Cloverly triconodont is known by some 20 specimens (including dentulous jaws, three skulls, and a partial skeleton) collected by Farish Jenkins and colleagues in the 1970s. Ironically, although mentioned in literature spanning several decades (e.g., Jenkins and Crompton, 1979; Crompton and Luo 1993; Kielan-Jaworowska et al. 2004), the Cloverly triconodont remains unpublished. Its description is in progress. The specimens come from a monospecific site, Lewis Pocket. Although minor transport probably took place, the assemblage apparently represents a population sample because they were found in close proximity within the same horizon. Intriguingly, the co-occurrence of many specimens suggests that the species may have been characterized by some degree of sociality; by contrast, living monotremes (whose common ancestor with therians defines crown Mammalia) are mainly solitary.

Judged by molar eruption, the sample includes a wide range of developmental stages: the presumed youngest individual has one molar fully erupted and the oldest has four, with a fifth coming into use and a sixth in its crypt. A deciduous premolar may be present in one specimen, but it is clear that any tooth replacement took place before full eruption of m2 and following molars. The anterior dentition (I2, C/i1, c) is notable in having very large canines, a tricusped I2, and enlarged, procumbent i1 with sharp, mitten-shaped crown: evidently, the incisors played an important role in prey capture and manipulation.

Like basal triconodontids (Jäger et al., this volume), post-m2 lower molars of the Cloverly triconodont and other alticonodontines developed on the inside of the ascending ramus, above the tooth row, migrating forward and downward as they erupted and came into use (lower molars could not occlude until they lay anterior to the ascending ramus). Alticonodontines differ in having more molars (5+, as opposed to 3–4 in basal triconodontids). In the Cloverly triconodont, the count ranges to 6, and because unerupted molars are always present (no individual has more than 4 fully erupted), molar eruption was continuous, with effectively infinite molar count, over an individual's lifetime (in the known sample, at least). Unlike early-diverging clades of Mammaliaformes (Crompton and Luo, 1993), neither premolars nor molars were shed: the posterior part of the jaw (and corresponding part of the skull) enlarged to accommodate additional molars. Hence, the conditions of early replacement of antemolar teeth and continuous molar eruption were accompanied by a limited form of sustained or indeterminate growth.

Eutriconodonts have been uniformly considered to have been carnivorous (e.g., Simpson, 1936). The mid-Cretaceous radiation of alticonodontines in North America includes larger-bodied species than seen among Triconodontinae, suggesting increased reliance on vertebrate flesh; consumption of larger prey would also suggest increased dental wear, owing to increased processing of hard

objects (ingestion of bones, both size and number). Yet the increased molar count cannot be simply attributed to rapid molar wear, because anterior molars of the Cloverly triconodont do not show obvious senescence (although this appears to be true of some other alticonodontines, such as *Astroconodon*; Turnbull and Cifelli 1999). Intriguingly, a parallel and more impressive radiation of large-bodied triconodonts took place among the Early Cretaceous Gobiconodontidae of Eurasia. Gobiconodontids developed an independent means of adding "fresh" shearing crests to their cheek teeth via replacement of molariforms (Jenkins and Schaff 1988).

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**Age of the feathered neornithischian dinosaur from Siberia, *Kulindadromeus zabaikalicus***  
[oral presentation]

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Diverse epidermal appendages closely resembling primitive feathers in non-avian theropods are associated with skeletal elements in the primitive ornithischian dinosaur *Kulindadromeus zabaikalicus* (Fig. 1) from the Kulinda locality in the Transbaikalian region, Siberia. This discovery suggests that "feather-like" structures did not evolve exclusively in theropod dinosaurs, but were instead potentially widespread in the whole dinosaur clade. Dating of the Kulinda locality is therefore particularly important for reconstructing the evolution of "feather-like" structures in dinosaurs within a chronostratigraphic framework. Here we present the first dating of the Kulinda locality, combining U-Pb radiochronological analyses on zircons and monazites and palynological observations. Concordia ages constrain the maximum age of the Kulinda deposits to  $172.8 \pm 1.6$  Ma, corresponding to the Aalenian (Middle Jurassic). The palynological assemblage includes taxa that are correlated to Bathonian palynozones from western Siberia, thus constraining the minimum age of the deposits. The new U-Pb ages, together with the palynological data, provide evidence for a Bathonian age – between  $168.3 \pm 1.3$  Ma and  $166.1 \pm 1.2$  Ma – for *Kulindadromeus*. A Bathonian age is highly consistent with the phylogenetic position of *Kulindadromeus* at the base of the neornithischian clade. *Kulindadromeus* is consequently the oldest known dinosaur with "feather-like" structures discovered so far.



**Fig. 1.** Reconstruction of the epidermal coverage of *Kulindadromeus zabaikalicus* (by J. Dos Remedios and M. Mohamed, photo: T. Hubin).



## New squamate material from the Upper Cretaceous of Bayan Mandahu, China, and a faunal comparison with other Upper Cretaceous Gobi localities [oral presentation]

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The Upper Cretaceous localities of the Gobi Desert of Mongolia and China have yielded an exceptionally rich fossil record. One such locality in China, the Campanian age Bayan Mandahu, has yielded many vertebrate fossils including dinosaurs, crocodiles, mammals, and lizards (Jerzykiewicz et al., 1993; Gao and Hou 1995, 1996; Gao and Norell, 2000). The lizard assemblage previously recorded from Bayan Mandahu (Gao and Hou 1995, 1996; Gao and Norell, 2000) is diverse and includes iguanians (the priscagamids *Mimeosaurus*, *Priscagama*, and *Pleurodontagama*; the pleurodont iguanians *Xihaina* and *Anchaurosaurus*; and the aberrant *Isodontosaurus*); polyglyphanodonts (*Conicodontosaurus*, *Adamisaurus*); a possible lacertoid (*Globaura*); anguimorphs (*Carusia*, *Gobiderma*, *Bainguis*); and the enigmatic *Sineoamphisbaena* (Wu et al., 1996). Nonetheless, several lizard taxa recorded from contemporaneous localities in Mongolia (notably Ukhaa Tolgod, Gao and Norell, 2000) were apparently missing from Bayan Mandahu. However, recent fieldwork at Bayan Mandahu has yielded many new lizard (squamate) fossils. Analysis of these specimens, as well as re-analysis of older material, using the new technology of high resolution micro-CT scanning, has given us a more complete picture of the squamate fauna from Bayan Mandahu.

The genus *Bainguis* was erected by Borsuk-Bialynicka (1984), based on a holotype skull and several referred specimens from the Upper Cretaceous of Mongolia, and tentatively attributed to Anguimorpha. Gao and Hou (1996) attributed a specimen from Bayan Mandahu (IVPP V 10080) to this genus, cf. *Bainguis parvus*. However, our reanalysis of the specimen (Dong et al., 2018) suggests it is instead referable to *Parmeosaurus asper* Gao and Norell, 2000, based on the presence of the similar duplex ventral osteoderms, the presence of autotomy septa from the ninth caudal vertebrae, and the general similarity of the pectoral girdle and the femur. Additional new *Parmeosaurus* material from Bayan Mandahu, notably a skull, helped to confirm its affinity with the scincoids (Dong et al., 2018). Furthermore, re-examination of the original Mongolian material attributed to *Bainguis* (Borsuk-Bialynicka, 1984) suggests that the name should be restricted to the type skull only.

The new material also includes a specimen of the anguimorph *Parviderma inexacta*, previously known only from Mongolia (Borsuk-Bialynicka, 1984). This new specimen is more completely preserved than the holotype and provides important new information on this species. The extremely long marginal teeth and the narrow single frontal are characteristic of the taxon (compared with *Estesia* and *Gobiderma*). The presence of venom grooves along the anterior and posterior margins of the marginal teeth and a single lacrimal foramen enclosed by prefrontal and lacrimal, suggests a strong affinity with the Monstersauria, which agrees with the opinion of Conrad et al. (2011), but differs from the result of most phylogenetic analysis (outside the Varanoidea, see Conrad, 2008; Yi and Norell, 2013).

The new material from Bayan Mandahu also includes additional specimens of *Gobiderma*, *Carusia*, and *Adamisaurus*, and the first Chinese records of the polyglyphanodonts *Gobinatus*, and *Tchingisaurus*, and, possibly, the aberrant priscagamid *Pleurodontagama*. There are also several, as yet, unidentified taxa. Together with the identification of *Parviderma* and *Parmeosaurus*, this adds five new lizard taxa to the Bayan Mandahu assemblage, increasing its similarity to the other Upper Cretaceous localities within Gobi desert (Bayn Dzak, Ukhaa Tolgod, TugrugenShireh, Khermeen Tsav, Khulsan).

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## The history of albanerpetontid amphibians in Asia [oral presentation]

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Albanerpetontidae form an enigmatic group of extinct amphibians with a suite of unusual characters including a complex cranio-cervical joint and a peg-in-socket jaw symphysis. Most recent phylogenetic analyses have placed them either on the stem of Lissamphibia (e.g., Maddin et al., 2013), or as sister to one of the crown clades (e.g., Ruta and Coates, 2007). However, uncertainty remains, due partly to a lack of consensus on the origins and monophyly of Lissamphibia, but also to an incomplete knowledge of albanerpetontid anatomy.

Although albanerpetontids must have originated by at least the Early Triassic, the first records are currently from the Middle Jurassic of France (Seiffert, 1969), England (Evans and Milner, 1994), and Morocco (Haddoumi et al., 2016). Apart from that Jurassic Moroccan record, and another from the Early Cretaceous (Gardner et al., 2003), all albanerpetontid fossils are from Laurasia. The most complete record is European and extends, with gaps, from the Middle Jurassic to the Late Pliocene (Evans and Milner, 1994; Delfino and Sala, 2007; Gardner and Böhme, 2008). The North American record is also good but is more temporally limited (Albian-Palaeocene, Gardner and DeMar, 2014).

Given their relative abundance in Euramerica, and their inferred Laurasian ancestry, albanerpetontids should also be well-represented in Asia but, until recently, the Asian record was limited to a few elements from the Late Cretaceous (Cenomanian and Turonian) of Uzbekistan (Skutschas, 2013). The apparent absence of albanerpetontids from other well-studied Asian assemblages, including those of China and Mongolia, led to speculation that the group dispersed into Asia from either Europe or North America after the closure of the Turgai Strait or the establishment of the Bering land bridge (e.g., Gardner and Averianov, 1998).

However, two recent discoveries from the Cretaceous of Asia have prompted a reassessment. New albanerpetontid material from the Early Cretaceous (Barremian) Tetori Group of Japan (Matsumoto and Evans, 2018) shows that the group was already in Asia before their first known occurrence in North America, ruling out a west to east dispersal across the Bering land bridge. Dispersal eastwards from Europe remains a possibility. Moreover, the presence of albanerpetontids in an assemblage that is geographically and temporally close to those of the Yixian and Jiufotang Formations suggests the lack of specimens from China is probably an artefact of local taphonomic or environmental conditions. Further evidence that albanerpetontids were more widespread in Asia than previously realised has come from the mid-Cretaceous amber deposits of Myanmar (Burma), where a very small (apparently juvenile) specimen originally described as a lizard (Daza et al., 2015) has been re-identified as an albanerpetontid (Matsumoto and Evans, 2018).

The new Japanese specimens have also contributed to our understanding of albanerpetontid diversity and cranial anatomy. They have added a fifth genus to the family (*Shirerpeton*), question the monophyly of the type genus *Albanerpeton*, and reveal further differences between albanerpetontids and lissamphibians, including the presence of a discrete supraoccipital bone and the retention of epipterygoids, raising new questions as to the affinities of these unusual tetrapods.

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## The mid-Triassic Madygen Lagerstätte (Southwest Kyrgyzstan, Central Asia) [oral presentation]

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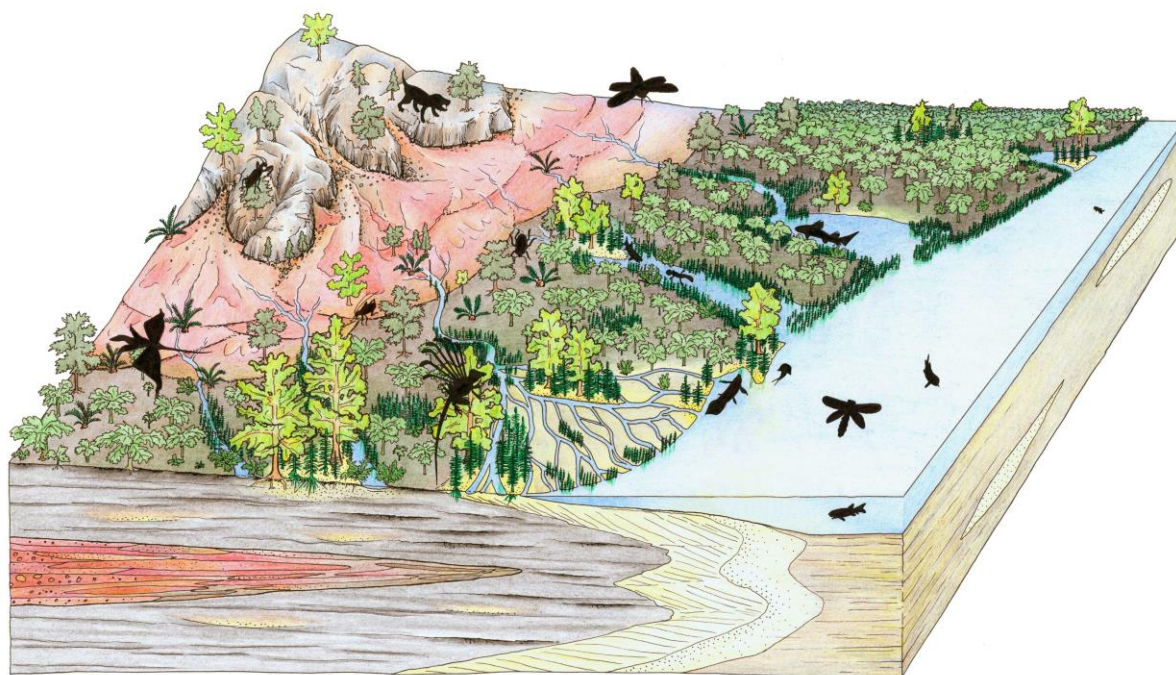
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The Madygen Formation is a 560 m-thick succession of complexly interbedded lacustrine, fluvial, and alluvial deposits outcropping near the village of Madygen in southwest Kyrgyzstan, Central Asia. Biostratigraphic and radioisotopic data point to a mid-Triassic (late Ladinian to early Carnian;  $237 \pm 2$  Ma) age of deposition (Voigt et al., 2017). Following its discovery, stratigraphic discrimination, and geological exploration in the 1930s to 1950s, the Madygen Formation became the target of several Soviet paleontological expeditions during the 1960s, unearthing numerous plant, insect, and fish fossils as well as the emblematic reptiles *Longisquama* and *Sharovipteryx* (Sharov, 1971). A more comprehensive understanding of the Madygen ecosystem and the paleoecology of its biota has arisen from the study of its sedimentological context in the course of four extensive German field campaigns to Kyrgyzstan between 2006 and 2009 (Voigt et al., 2017). Data gained from these expeditions suggest that the Madygen paleoecosystem was marked by generally favorable living conditions. Distinct sedimentary subfacies and biotic associations can be reconstructed (Fig. 1).

The most conspicuous part of the Madygen ecosystem was formed by a large perennial lake supporting a biocoenosis with at least five trophic levels of water plants, aquatic invertebrates (e.g., microconchids, molluscs, crustaceans, arthropods), bony fishes ('palaeonisciforms', a scanilepiform, *Saurichthys*, a lungfish, a coelacanth), freshwater sharks (*Lonchidion*, *xenacanth*), amphibian larvae, and a chroniosuchian reptiliomorph (*Madygenerpeton*) as apex predator. Oxygen and strontium isotope data of fish tooth enameloid indicate unequivocal freshwater conditions of the water body (Fischer et al., 2011). Common occurrence and abundance of trace fossils prove that the lake bottom was oxygenated. Surrounding the lake, a densely vegetated floodplain sustained a highly diverse entomofauna, which in turn was preyed upon by small- to middle-sized tree- and ground-dwelling tetrapods including synapsids (*Madysaurus*) and diapsids (e.g., *Kyrgyzsaurus*) (Fig. 1).

The relative abundance of shark egg capsules (*Palaeoxyris*, *Fayolia*) and juvenile bony fishes identifies the fossil Madygen lake environment as a Triassic multi-taxon spawning and nursery ground. The vegetated shorelines of the lake were a preferred area for reproduction and shelter, and were also a food resource for juveniles of various fish groups, whereas adult individuals may have lived mainly in open lacustrine waters, or even outside the Madygen lake system. Altogether, the mid-Triassic Madygen ecosystem existed in a warm-temperate climatic zone with year-round rainfall in an area of low mountains at mid-north paleolatitude, several hundred kilometers away from the nearest marine shoreline.



**Fig. 1.** Simplified model illustrating the mid-Triassic Madygen ecosystem with alluvial fan, alluvial plain, river delta and lacustrine environments (Illustration by Frederik Spindler).

Due to the abundance and the exceptional preservation of aquatic and terrestrial biota within floodplain and shallow lacustrine siltstones, the Madygen Formation has to be considered a conservation and concentration *lagerstätte* for fossil plants, invertebrates and vertebrates. The fine-grained sediments preserved coloration pattern and surface reliefs in insects as well as skin impressions in some reptile fossils. Large archosauromorph reptiles and croniosuchian (crocodilian-like) reptiliomorphs are preserved in fluvial channel deposits.

Apart from its role as the only well-known locality of continental Triassic biota in Central Asia, the high diversity and exceptional preservation of land plants (one of the most diverse Mesozoic floras of Eurasia) and insects (more than 25,000 insects of almost all contemporaneous groups were found) qualify Madygen as a crucial study site for the evolution and ecological differentiation of these groups in Mesozoic terrestrial ecosystems in the aftermath of the P/T extinction event (Voigt et al., 2017). Once situated in the transitional zone of the Euramerican, Siberian, and Cathaysian faunal and floral provinces, the mid-Triassic Madygen *lagerstätte* offers a unique taphonomic window lacking any equivalent in the Early Mesozoic fossil record.

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## The diversity of Mesozoic Tettigarctidae and palaeoecological significance (Hemiptera: Cicadoidea) [oral presentation]

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Tettigarctidae appeared in the Upper Triassic (Rhaetian) of England and is the most primitive group of Cicadoidea. This lineage currently is a relict, with only two modern species attributed to a single genus (Duffels, 1993; Moulds, 2005). Tettigarctidae differs from other cicadas in several features, such as the densely pilose tympana, absence of an abdominal resonant cavity, a pronotum that is greatly expanded and a fully developed nodal line (Nel, 1996). Unlike members of the Cicadidae, the adults of living Tettigarctidae are nocturnal, avoiding strong light during daylight hours (Wang and Zhang, 2009). Presently, fossil tettigarctids comprise 27 genera with 40 extinct species attributed into two subfamilies: Tettigarctinae Distant, 1905 and Cicadoprosobolinae Becker-Migdisova, 1947 (Zheng et al., 2016). Fossil tettigarctids range from the Late Triassic to the Eocene, and flourished especially during the Jurassic to Early Cretaceous (Whalley, 1983). Only one nymph has been reported from the Late Cretaceous and four genera with four species have been reported from the Cenozoic (Kaulfuss and Moulds, 2015). The group is distributed principally in the Northern Hemisphere, as only four genera with four species are known from the Lower Cretaceous (Aptian) in Brazil and from Tunisia, and the early Miocene of New Zealand, complementing a meagre record from Gondwana.

Two extant tettigarctids *Tettigarcta tomentosa* White, 1845 and *T. crinita* Distant, 1883 are restricted to high altitudes areas in Tasmania and southeastern Australia. Most *T. crinita* have been captured at an altitude of 1600 m in summer and *T. tomentosa* occurs at an altitude of ca 800 m in winter (Evans, 1941). Both species are medium-sized, have a pronotum that is exceedingly expanded, a tegmen dotted with reddish-brown spots or otherwise dull, and their most striking characteristic is the extreme hairiness of the body. The modern species are similar the hairy tettigarctid *Hirtaprosbole erramera* reported from the Middle to Upper Jurassic Haifanggou Formation at Daohugou, in Inner Mongolia, northeastern China. This fossil occurrence provides evidence that tettigarctids with long dense hairs had appeared by latest Middle Jurassic (Liu et al., 2016). The hairy tettigarctid from the Daohugou beds possible had a similar thermoregulatory function to that of extant tettigarctids. In this study, two new species of hairy tettigarctids are described from the Daohugou beds, one of which belongs to *Hirtaprosbole*. This species differs from the type species by a tegmen with a radius anterior (RA) vein with three branches, a radius posterior (RP) vein with two branches, and a pronotum without fissures. The new find increases the diversity of tettigarctids from the Daohugou beds, establishes the group within the Yanliao Biota and further supports a montane environment reflected in the Daohugou strata.

In addition, two new genera and two species tettigarctids from the mid-Cretaceous Myanmar (Burmese) amber adds new information regarding the Mesozoic diversity and evolutionary history of Tettigarctidae. The new find represents the first record of Tettigarctidae in Burmese amber and provides features such as apex of fore femur armed with one strong spine and vein R branching into RA and RP veins after the forking of the media posterior (MP) vein. This combination of characters previously has never been observed in the Tettigarctidae, adding valuable information to our knowledge of taxonomic diversity and morphological disparity of Mesozoic Tettigarctidae. The new



Myanmar forms exhibit body characters and wing venation patterns typical for the subfamily Tettigarctinae. One of the Myanmar amber species closely resembles *Sunotettigarcta hirsuta* from the Daohugou beds by jointly possessing wing venation patterns and a pronotum posterior area that is transversely rugose and covered by setae. These features indicate that some taxa from the Middle to Upper Jurassic Yanliao Biota persisted to Myanmar amber time, 65 million years later. This temporal persistence probably reveals a biogeographic migration route after the ecosystem collapse during the Late Jurassic of North China.

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## **Las Hoyas Early Cretaceous spinicaudatan fauna (Crustacea-Diplostraca) from Cuenca (Spain) [oral presentation]**

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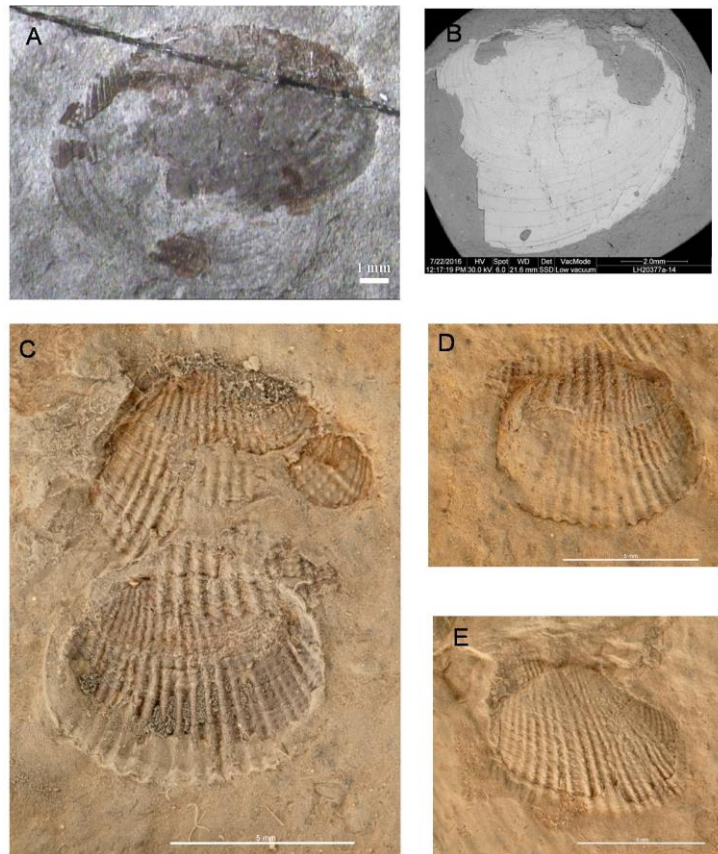
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Las Hoyas fossil site with its diverse biota including forms like bacteria to dinosaurs, is one of the best known Konservat Lagerstätte worldwide. The biodiversity of this locality is recently extended with the re-discovery at the Castilla-La Mancha Natural Sciences Museum (Cuenca, Spain) of several individuals of three spinicaudatan species found at the Las Hoyas carbonatic limestones in eight different stratigraphic levels. The spinicaudatans recorded correspond to members of the superfamilies Afrograptioidea and Eosestherioidea, and to the families Afrograptidae and Eosestheriidae and Anthronestheriidae respectively (Fig. 1).

The most relevant specimens belong to Afrograptidae probably related to the genus *Camerunograpt* or *Graptoesstheriella*. Both forms, considered as synonymous by many authors (Chen and Shen, 1985), they have different geographical ranges, now restricted to central Africa and South America (Brazil) respectively (Gallego et al., 2010). This family has a short stratigraphic range, from the Late Jurassic to the Early Cretaceous from Africa, Venezuela, Argentina and Brazil, and recently its distribution has extended to the Early Cretaceous of England and Spain (Liao et al., 2017). The distribution of the genera confirms the revision of the species dispersions along the Gondwana break up and Laurasia. The new material allows us to analyze and discuss the taxonomy and diagnostic characters of these genera adding other members of the family Afrograptidae as *Afrograpt*, *Congestheriella* and *Surreyestheria*. The main diagnostic characters of this group consist of the presence of multiple continuous or interrupted stout radial ribs perpendicular to growth lines, which rise in the umbonal region and reach the ventral margin, in addition to the presence of radial striated ornamentation in the growth bands and beaded growth lines (Novojilov, 1957; Astrop and Hegna, 2015). Future studies will be carry out for the cladistics and morphometric analysis in order to clarify the fundamental diagnostic characters and the phylogenetic relationships of this branchiopod superfamily. The other taxa are important components of the Jurassic-Cretaceous biota from China and Asia and they have a high palaeoenvironmental and palaeocological significance according their local stratigraphic distribution.

Energy Dispersive Spectroscopy (EDS) were applied at the Universidad Autónoma de Madrid and Museo Nacional de Ciencias Naturales (Madrid). These investigations provided additional information on the chemical components of carapaces and the taphonomy of these fauna. The EDS analysis of Eosestheriidae - Anthronestheriidae - Afrograptidae and the surrounding rock matrix showed high-intensity peaks of P and Ca in the carapaces indicating a predominantly calcium phosphate composition. In contrast, the rock-matrix-EDS spectra exhibited Ca and C peaks, indicating the presence of the major components of carbonate compounds (CaCO<sub>3</sub>). Moreover, minor elements (i.e., Mg, K, and Al) have also been recorded in the carapace and rock samples.

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**Fig. 1.** Spinicaudatans from Las Hoyas (Lower Cretaceous, Spain). **A.** ?Anthronestheriidae LH 30784. **B.** ?Eosestheriidae LH 20377a. **C-D.** Afrograptidae LH 18044b, a, LH 23230a. Scale bars: A= 1 mm. B= 2 mm. C-D= 5 mm. A, C-D. Stereomicroscopical images. B. SEM image.

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**Terrestrial habitats in the heart of the Late Jurassic Morrison Formation, and implications for ecosystems dominated by herbivorous dinosaurs [oral presentation]**Carole T. GEE<sup>1</sup><sup>1</sup> Rheinische Friedrich-Wilhelms-Universität Bonn, Germany; [cgee@uni-bonn.de](mailto:cgee@uni-bonn.de)

The Late Jurassic Morrison Formation is globally renown for its spectacular and biologically diverse dinosaur fauna, but less famous for the plant communities that must have dominated the 150 million year old landscape of the Western Interior of North America. However, since plants are the basic building blocks of habitats, understanding the fossil flora is pivotal to accurately deciphering the ecology and climate of the Morrison Formation. Here I show that an increasing number of paleobotanical lines of evidence in the form of fossil cones, wood, leaves, and pollen and spores in Utah, Wyoming, and Colorado—the heart of the Morrison Formation—point to habitats comprised of mixed coniferous forests or woodlands. These evergreen conifer forests were dominated by araucarians, but included pinaceous and cheirolepidiaceae trees and ginkgophytes. Lower-growing plants such as ferns, tree ferns, and *Equisetum* may have colonized moister sites such as the understory of closed forests, along bodies of water, or in wetlands. When compared to their nearest living relatives, nearly all fossil plants described so far from the Morrison Formation require mesic conditions that offer a moderate amount of moisture, if not even wetter conditions. A new occurrence of Morrison logs from near Dinosaur National Monument in NE Utah yields fossil wood with steady growth and no annual rings, indicating a lack of climatic seasonality, even subtropical monsoonal–dry cycles, and a lack of water stress. Reconstruction of minimum tree height suggests that the araucariaceous trees grew to at least 25 m tall, which suggests a forested landscape of good-sized, robust trees. Habitats of extensive conifer forests would have provided a constant food supply for the herbivorous dinosaur fauna, which surely consisted in large part of bulk feeders. Evergreen conifers with abundant foliage would have reduced the foraging pressure of the herbivores on individual trees, allowing for the regeneration of foliage and the long-term sustainability of the ecosystem. Based on emerging data, it is likely that widespread conifer forests with a variety of species made up the major habitats in the heart of the Late Jurassic Morrison Formation and were thus the major primary producers of this important Mesozoic ecosystem.

## Australia's polar Cretaceous mammals: longer lifespans may be indicative of hibernation [oral presentation]

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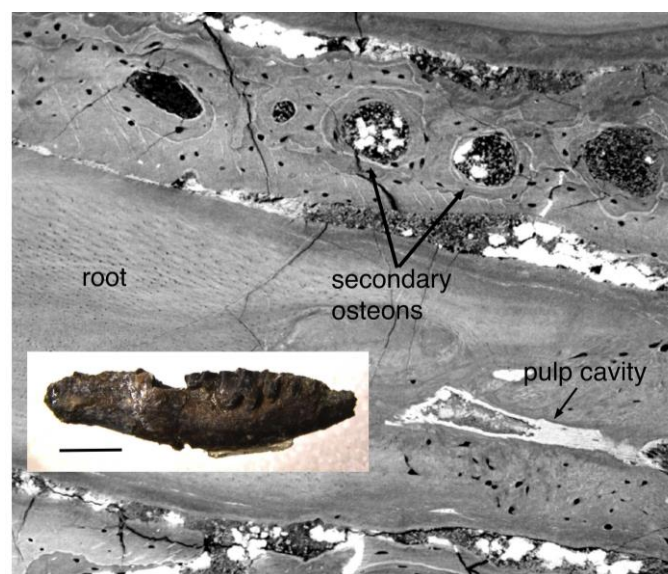
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Excavations at the Flat Rocks site in Victoria, Australia have produced rare Early Cretaceous (Aptian) mammals, from fluvial sandstones and mudstones. *Teinolophos trusleri* with "pseudo-triangulate" molars is within the Monotremata and *Ausktribosphenos nyktos* and *Bishops whitmorei*, with a tribosphenic dentition, are in Ausktribosphenidae (Pascual and Goin 2002, Rich and Vickers-Rich, 2004). Earlier scans of *Teinolophos* (Rich et al., 2016) suggested that, although the jaws have suffered some cracking, the internal preservation was promising. Nine specimens (four *Teinolophos*, two *Ausktribosphenos* and three *Bishops*) were provided from Museums Victoria and imaged at sub-micron resolution at the European Synchrotron Radiation Facility (ESRF) and Swiss Light Source (SLS). In fact, the internal histological detail of the dentary bone and tooth tissues proved to be beyond expectation, and some initial results are presented here.

Clear images of osteons were seen in the dentary bone, and, importantly, some specimens, e.g. *Bishops* (Fig. 1), had well developed secondary osteons and reversal lines. Secondary osteons are produced by remodelling of bone, due to micro damage, and are rare in small animals, which are unlikely to experience high loading demands (e.g., small rodents). However, they are more prevalent in mammals with longer lifespans, so allowing time to create significant damage (Currey, 2002). This is, therefore, of particular interest in these tiny Early Cretaceous mammals and is suggestive of a longer lifespan than would be expected from their estimated body masses when compared to extant mammals of similar size.

To investigate this further, we are examining SRCT data of the tooth root cementum, and the degree of tooth wear in individual specimens. Tooth root cementum is a continuously growing dental



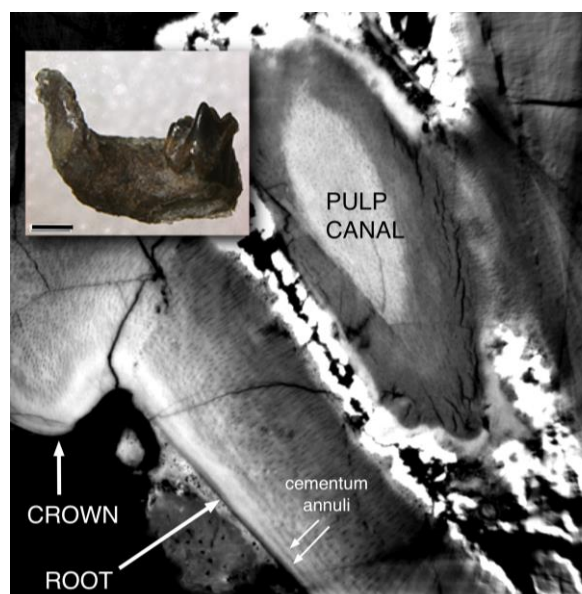
**Fig. 1.** NMV P209975. *Bishops whitmorei*, showing remodelling and development of secondary osteons. Inset shows the specimen in buccal view; scale bar 2mm.

tissue which has incremental annuli, from which an individual's age at death can be assessed. Examining multiple individuals gives a minimum estimate for the maximum lifespan of a particular species. A strong correlation between body mass, lifespan, and basal metabolic rate (BMR) has been reported (De Magalhães et al., 2007), so, by estimating lifespan and body mass, we are also able to provide an estimation of metabolic rate for our Early Cretaceous mammal fossils. We have previously scanned population sized samples of Mesozoic mammals, from both the Early- and Middle-Jurassic, for cementum count analysis and metabolic rate estimation, and although this Flat Rocks sample is limited in comparison, we hope to shed some light on two questions:

- A. Are there differences in estimated lifespan and BMR between the three Early Cretaceous Flat Rocks mammal taxa, and in comparison to extant therian mammals of similar body mass?
- B. In the Aptian, south-eastern Australia lay within the Antarctic Circle, at about 70 degrees of latitude, so are there life history clues as to how the small Flat Rocks mammals were adapted to living through the polar winter, with months of twilight and relatively low mean annual temperatures?

Analysis for cementum annuli, so far, has produced two clear examples: an *Ausktribosphenos* with three annuli and a *Bishops* with 2.5 (Fig. 2), which is a longer lifespan than would be expected for a mammal of such small size (~8g for *Bishops*). These two individuals with countable annuli have very few secondary osteons, but another *Bishops* specimen has notably more remodelling and development of secondary osteons, and far more advanced tooth wear (Fig. 1). While relative degree of tooth wear cannot be an absolute indicator of age at death, due to individual dietary variation, it is suggestive of a lifespan beyond three years. Hopefully, further analysis of the cementum increment data will produce definitive ages for such older individuals of all three taxa, including *Teinolophos*.

The longest living extant mammals of similar small body size are all heterotherms, with the ability to enter short periods of torpor or longer periods of hibernation in which body temperature and metabolic rate are both considerably decreased. We suggest that, as our data provisionally shows the ausktribosphenidans, at least, to have had extended lifespans, they likely had low metabolic rates and/or entered a state of torpor or hibernation as a strategy to survive the polar winter. Interestingly, Turbill et al. (2011) conclude that hibernation is a physiological mechanism permitting small mammals to remain dormant and increase survival when conditions are not optimal for reproduction, which appears to have coevolved with a relatively slow life history.



**Fig. 2.** NMV P208484. *Bishops whitmorei*, showing the cementum annuli. This specimen gives a count of 2.5 years. Scanning at TOMCAT beamline, SLS. Inset shows the specimen in buccal view; scale bar 1mm.

Regarding larger members of the fauna, analysis of bone microstructure in Cretaceous dinosaurs from Victoria, provides no evidence to support seasonal hibernation (Chinsamy et al., 1998; Woodward et al., 2018). Although encouraging caution with small sample sizes, as is also the case here for the mammals, Woodward et al. (2018) suggest that important life history insights at the individual level are still obtainable and critical for foundational knowledge. Our use of non-destructive Synchrotron Radiation Computed Tomography (SRCT) gives access to the life histories of the small mammals inhabiting the Cretaceous southern polar ecosystem that would otherwise be unavailable.

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**Jurassic flora from Cianowice (Southern Poland) [poster presentation]**

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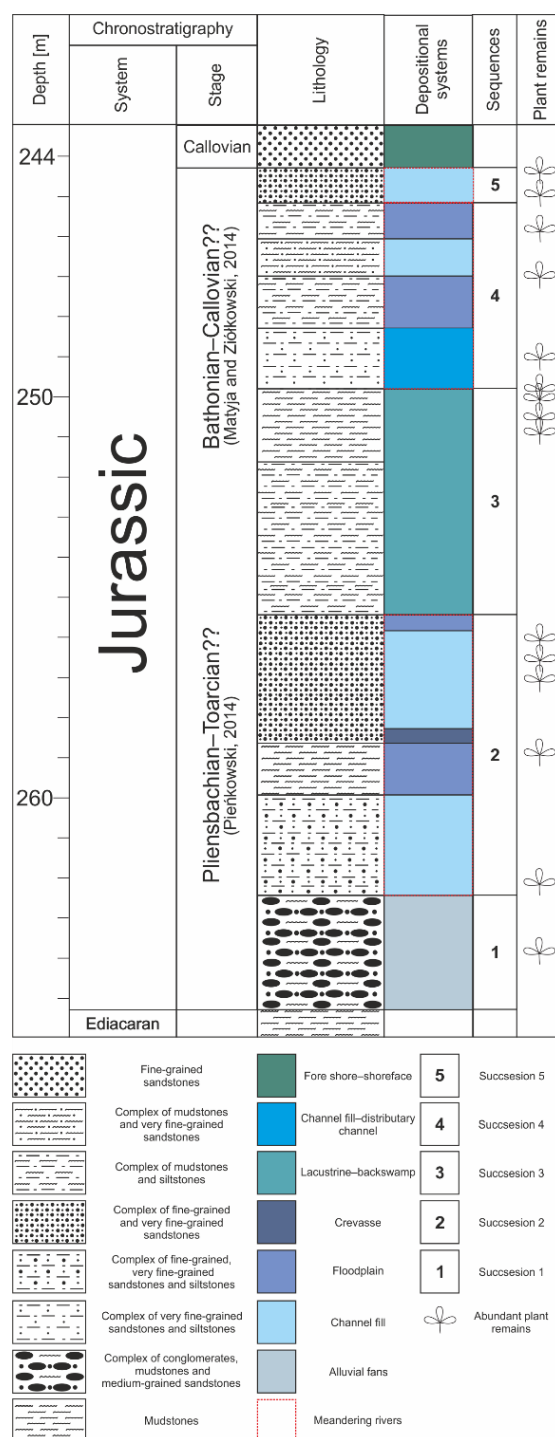
<sup>3</sup>Hungarian Natural History Museum, Hungary

The Cianowice borehole is located in southern Poland within the Małopolska block, near the Kraków-Lubliniec Fault Zone (Fig. 1). This zone separates the Małopolska Block from the Upper Silesian Block. Such a position affected by the complex structure of the tectonic region causes problems with determining the age of sediments. Sedimentological analyses of this site were carried out by Pieńkowski (2014). Examined sediments, with a thickness of 21.8 m, are composed of grey, brown and green-grey terrigenous deposits accumulated in 5 depositional successions (Fig. 2). The whole siliciclastic complex is divided into five successions representing mainly fluvial plain and lacustrine habitats. The stratigraphical position of the Cianowice sediments is still under discussion. Pieńkowski (2014) suggest that an Early Jurassic age is most probable, but Matyja and Ziółkowski (2014) proposed a Middle Jurassic (Bathonian-Callovian) age. Further biostratigraphical or chemostratigraphical investigations are needed to confirm the age of these strata. Description of fossil plant macroremains, which was the main aim of this study, can provide useful data to more precisely determine the age of the Cianowice complex.

Numerous plant fossils described from 265.5-244.5m profile depth were preserved mainly as single leaf segments fragments without apices and bases, compound leaf fragments, parts of the shoots and a few *Cycadolepis* scales. Nearly 100 specimens preserved as compressions with organic matter were examined and described (Fig 3). The flora is dominated by Bennettitales (73%), represented by 6 genera: *Otozamites*, *Ptilophyllum*, *Pterophyllum*, *Nilssoniopteris*, *Anomozamites* and *Cycadolepis*. Cycads (13%) were present as only two genera *Ctenis* and *Pseudoctenis*. Other groups were sporadically represented: seed ferns 5% (*Pachypteris*, *Ctenozamites*), horsetails 4% (*Neocalamites*), Ginkgoales 3% (*Pseudotorellia*) and ferns 1% (*Coniopteris*).

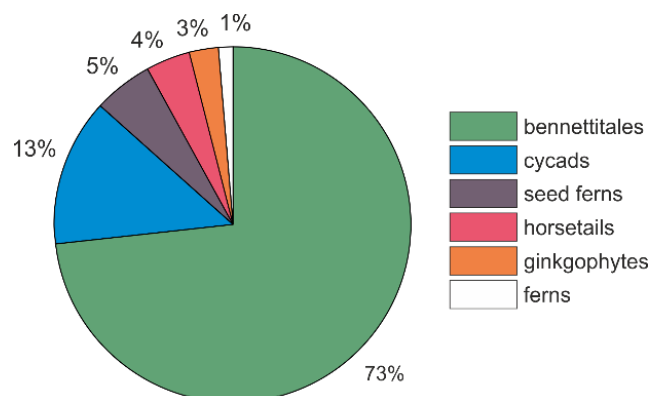


**Fig. 1.** Location of the Cianowice 2 borehole (after Pieńkowski 2014, modified).



**Fig. 2.** Shortened lithological profile of Cianowice 2 borehole, (after Pieńkowski 2014, modified).

Floras with Bennettitales as the main component are known from two sites in Europe: Sardinia, Italy (i.e., Krasser, 1912, 1913, 1920; Scanu et al., 2012, 2015) and Mamers, France (Philippe et al., 1998), and both are dated as Middle Jurassic and assigned to coastal environments (Barbacka et al., 2014). The only European flora with a significant representation of Bennettitales from a delta/fluvial depositional environment is known from Yorkshire (Harris, 1969; Van Konijnenburg-van Cittert and Morgans, 1999). Although this flora is also dated as Middle Jurassic, there are other groups such as conifers and ferns which are very diverse, unlike at the Cianowice site. If the stratigraphical position of Cianowice is confirmed as Early Jurassic, the described benettitalean dominated flora will be unique among others known from this period in Europe.



**Fig. 3.** Participation of major taxonomical plant groups in analysed material.

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## Early evolution and palaeobiology of pygmy grasshoppers (Orthoptera: Tetrigidae) with the description of a new genus and species [oral presentation]

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Tetrigidae are a highly diverse group of Caelifera with more than 1,900 described species belonging to 280 genera (Cigliano et al. 2017). However, regarding their evolution, biology and ecology, they still receive only limited attention. Concerning the fossil record just as well as Recent Tetrigidae, little more has been done other than describing new species and thus, concerning their phylogenetic position within the Orthoptera, they still are a problematic group with uncertainties regarding species descriptions and the interpretation of morphological characters.

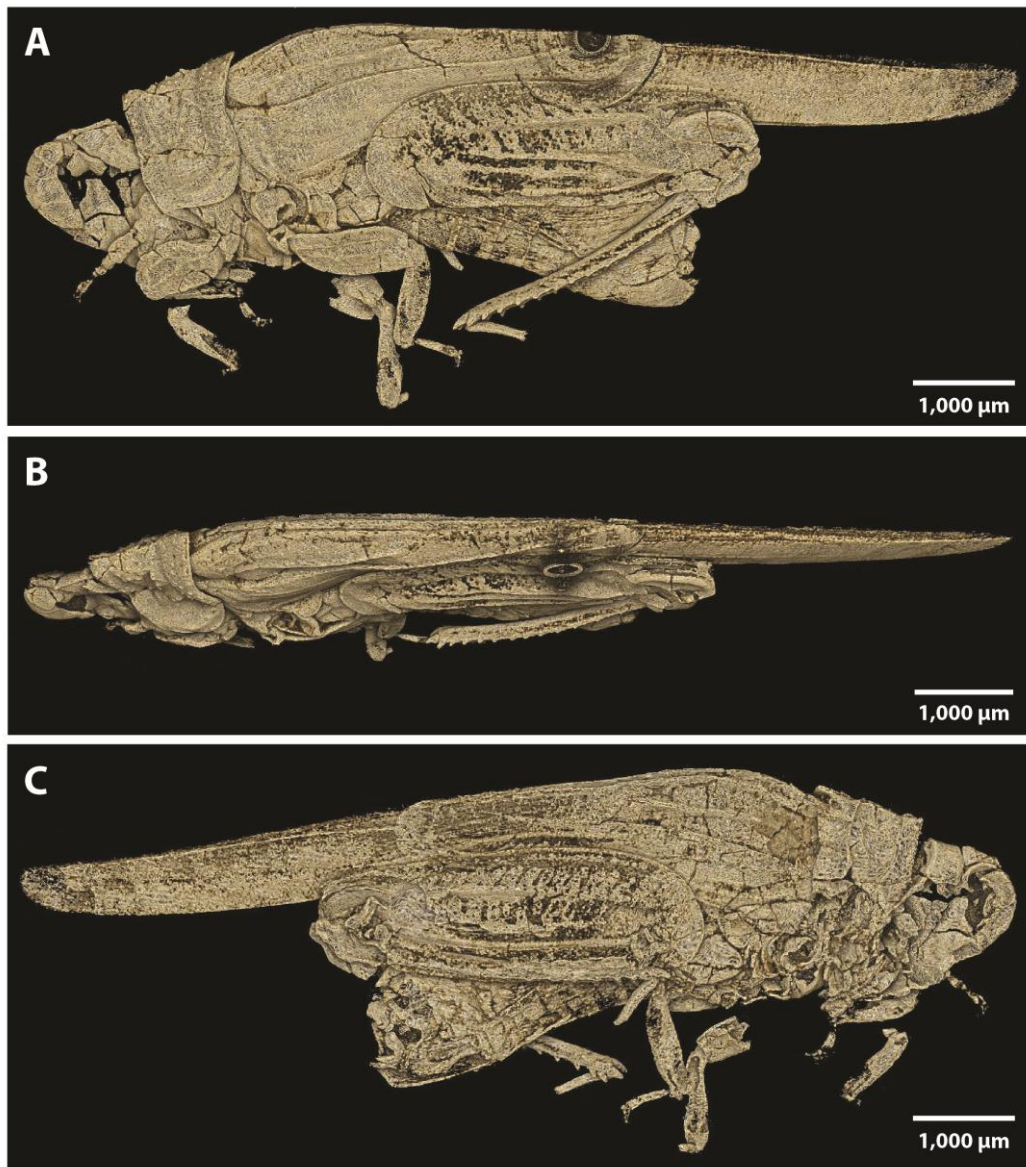
Phylogenetically occurring among the most basal Caelifera, Tetrigidae show a very scarce fossil record starting in the Early Eocene, so very little is known about early tetrigid evolution (Heads et al. 2014). The formerly oldest species *Archaeotetrix locustopseiformis* Sharov (1968) and *Prototetrix reductus* Sharov (1968) from the Early Cretaceous of the Turga Formation in Russia cannot be reliably assigned to the Tetrigidae and consequently are excluded from this group.

The Early Cretaceous is highly important for insect evolution due to the radiation of the angiosperms. The Crato Formation, is the only Gondwanan, non-marine conservation deposit of Aptian to Albian age, and provides unusual insights into early insect evolution and diversification, as illustrated by outstanding fossil preservation (Martill et al. 2007).

A new genus and species of Tetrigidae is described from a well-preserved, complete male specimen with a body length of 6.5 mm (total with wings: 9.3 mm; Fig. 1). The holotype is characterised by a rather short pronotum, relatively long fore wings and very long hind wings exceeding well beyond the abdomen. Auditory organs are absent. The hind legs are saltatorial with no incision between the antegenicular teeth and the knee of the hind femur that would be typical for adult Tetrigidae. The abdomen resembles that of modern Tetrigidae and the integument is largely granulose. Even though there was some degree of compression, synchrotron data indicate an originally rather slim habitus other than, for example, Tridactylidae also recovered from the Crato Formation.

Regarding all characters as well as the incompleteness of the specimen leaving important characters unrecognized, it has to be concluded that one specimen does not provide sufficient data for a safe assignment to an existing group within the Caelifera.

We propose the specimen to be placed as a basal stem-line representative of the Tetrigoidea. With several characters indicating a relationship to the Tetrigidae, others however are clearly contradictory to such an assignment. This specimen may represent an early evolutionary state before the divergence of Tridactylidea and Acrididea in the late Palaeozoic.



**Fig. 1.** 3D reconstruction from SR $\mu$ CT scans of specimen SMNS-160 in (A) lateral view of complete specimen. Side-view of un-exposed part. Important aspects as the short pronotum with granulate integument, the quite long fore wings and very long hind wings are visible. Hind legs are saltatorial with broad femur and spines on the tibia. Subgenital plate strong; (B) laterodorsal view of complete specimen illustrating the three-dimensionality of the specimen; and (C) lateral view of exposed side, more poorly preserved. Internal structures can be recognised at the distal part of the abdomen.

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## Epidermal structure of *Sinozamites* (Cycadales) deciphered from the Middle Triassic Linjia flora in Northeast China [oral presentation]

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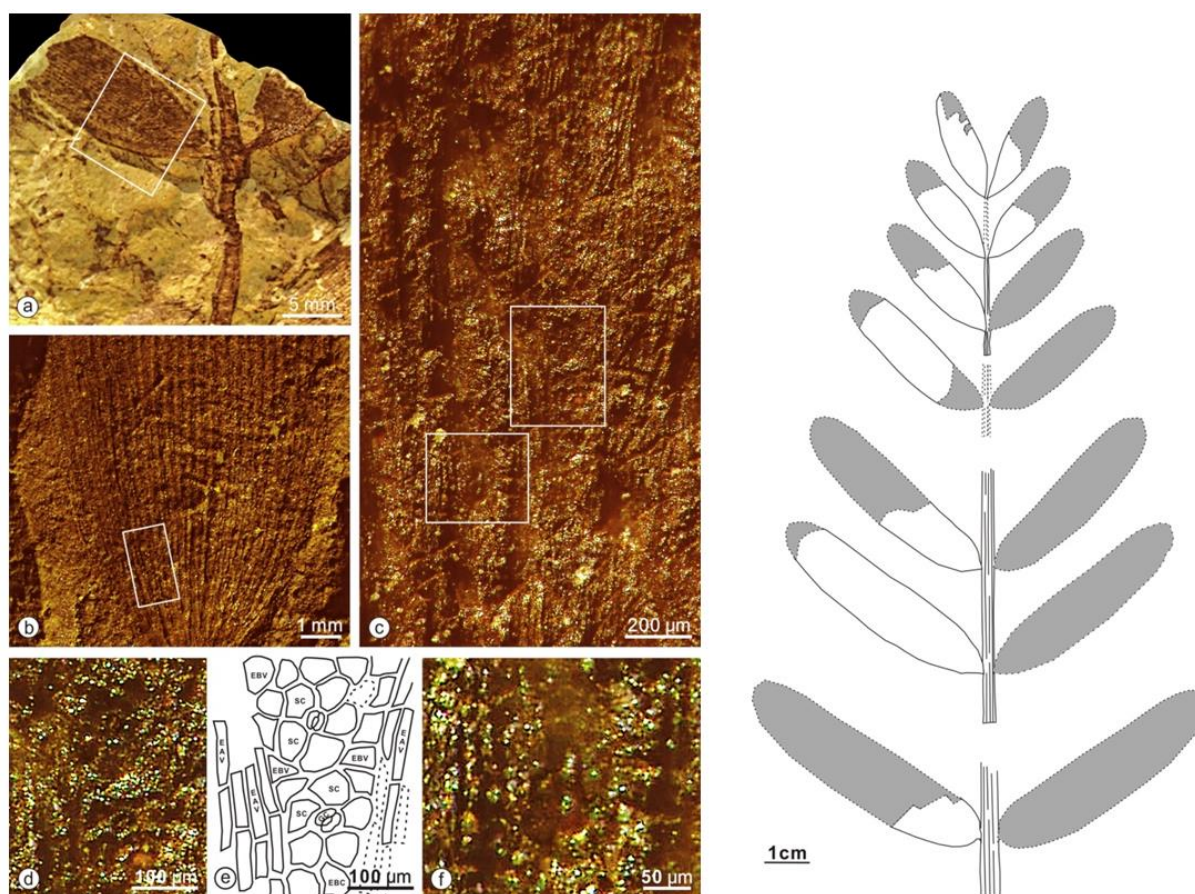
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*Sinozamites* Sze 1956 is one of the representative genera of Cycadophyta in the Middle and Late Triassic of North China. Cycadophyta is composed of Cycadales and Bennettitales. Since the genus was erected, its epidermal structure has been unclear, resulting in its uncertain systematic position for a long time (Sun et al., 2016).

Based on our recent work (Han et al., 2018), the epidermal structure of *Sinozamites myrioneurus* (Fig. 1, left) from the Middle Triassic Linjia Formation in Benxi of Liaoning, Northeast Liaoning (Zhang et al., 1983), is deciphered by the large depth-of-field technique, suggested by Tan et al. in 2013.

In this study, both hydrochloric and nitric acid are used in removal of surface impurities to gain clear images. On the basis of the haplocheilic stomatal apparatuses, the genus is assigned to Cycadales. The authors also reconstruct part of the *Sinozamites myrioneurus* leaf (Fig. 1, right) on the



**Fig. 1.** The leaf, veins and stomatal apparatuses (Left, a-f, based on the specimen with the Registration No.: PMOL-B01319A) of *Sinozamites myrioneurus* and the reconstruction of the leaf (Right). a: Part of the leaf; b: enlargement of the frame in a, showing veins of the leaf segment; c: enlargement of the frame in b, showing cells along veins and cells between veins; d: stomatal apparatuses and ordinary epidermal cells, enlargement of the upper frame in c; e: stomatal apparatuses and ordinary epidermal cells referenced to d, EAV: ordinary epidermal cells along veins, EBV: ordinary epidermal cells between veins, SC: subsidiary cells, GC: guard cells; f: stomatal apparatuses and ordinary epidermal cells, enlargement of the lower frame in c.

basis of the relationships between the upper and lower sterile organs, including leaf segments and rachises. Fossil and extant cycadophytes with similar names and morphologies to the genus *Sinozamites* are compared. Here the classification of *Sinozamites* is arranged and part of the leaf is reconstructed, but also the large depth-of-field technique is developed. It is able to be predicated that more epidermal structures of fossil plants and their systematic positions will be deciphered with the help of this method.

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**A re-evaluation of the taxonomy and diversity of the Late Jurassic sphenodontian *Opisthias rarus* Gilmore 1909 (Lepidosauria: Rhynchocephalia) [oral presentation]**

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The Rhynchocephalia are a group of reptiles that originated in the Middle Triassic, around the same time as the first dinosaurs. Today this group is represented by a single species, the famous Tuatara (*Sphenodon punctatus*) from New Zealand, but the clade was much more diverse in the Mesozoic (Jones et al. 2013). Over the years, it has been argued that the Tuatara, and the Rhynchocephalia as a whole group, was unchanged through time. However, recent discoveries show a different history. Fossils from the Mesozoic, especially from the Jurassic period, show that rhynchocephalians were diverse and morphologically well-adapted to different environments and ecological roles (Herrera-Flores et al. 2017).

The Late Jurassic rhynchocephalian *Opisthias rarus* was described by Gilmore (1909) from the Morrison Formation of the United States. After its initial description, several new specimens of *Opisthias* have been recovered from different localities of the Morrison Formation, USA as well as some occurrences in Dorset, England and Pombal, Portugal (Evans and Fraser, 1992; Ortega et al. 2009; Maldonado, 2013). *Opisthias* is frequently cited as part of the Late Jurassic terrestrial faunas, however, its taxonomy and actual diversity are poorly understood, as well as its possible paleoecological interactions with other Mesozoic lepidosaurs, such as lizards. For decades *Opisthias* has been recognized as a monospecific genus, but recent works suggest that specimens of *O. rarus* may represent more than one species and must be re-evaluated (Maldonado, 2013).

Systematic paleontology

Lepidosauria Haeckel, 1866

Rhynchocephalia Günther, 1867

Sphenodontia Williston, 1925

Eusphenodontia Herrera-Flores et al. 2018

Neosphenodontia Herrera-Flores et al. 2018

Opisthodontia Apesteguía and Novas, 2003

*Opisthias rarus* Gilmore 1909

Material (Fig. 1): USNM 2860 (holotype), USNM 2858 (Smithsonian Institution, National Museum of Natural History), two dentaries from the Late Jurassic of Morrison Formation, USA. DORCM 610831 (Dorset County Museum), a dentary from the Late Jurassic-Early Cretaceous of Purbeck Formation, England.

USNM 2860 (holotype) is an almost complete mandible. The coronoid process is broken, however it is possible to elucidate that this element was narrow and high with a semi-triangular shape. The dentary includes approximately 17 teeth, including a caniniform tooth. Additional teeth of dentary present heavy signs of wear and some of them are incomplete or broken. The hatchling teeth are heavily worn and the caniniform tooth is broken. This specimen likely represents an adult individual and has a total length of 35 mm.

USNM 2858 (paratype) is a fragment of a mandible from a juvenile individual that lacks the angular, surangular and articular bones. The coronoid process is broken but preserves the semi-triangular shape also seen in the holotype. Additional teeth include 12 elements that are almost

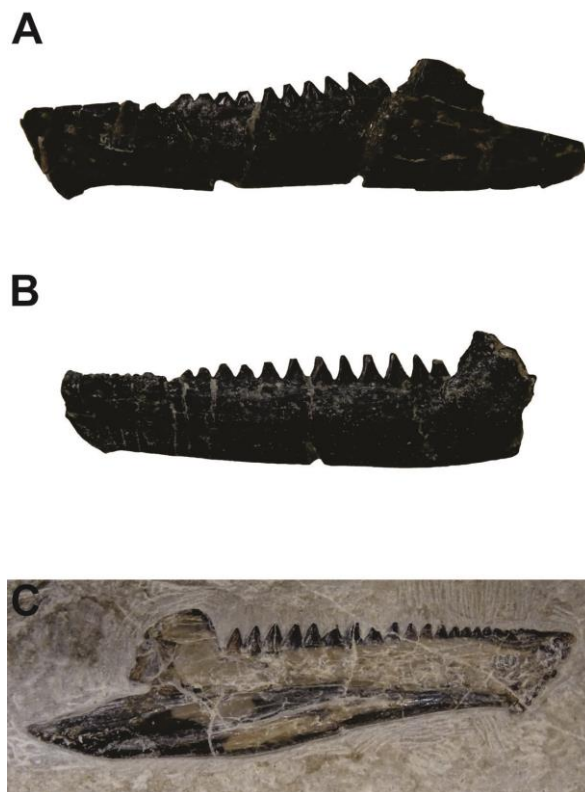


complete with slight signs of wear. Hatchling teeth include about 8 elements which are very small and heavily worn. A caniniform tooth is preserved but it is damaged. Length as preserved is 22.3 mm.

DORCM 610831 is an almost complete lower jaw of an adult individual preserved in lingual view. The coronoid process is complete with a round squared shape. This element includes approximately 20 teeth. Additional teeth include about 16 elements while hatchling teeth is a short row of about 5-6 very small teeth. Remains of a caniniform tooth are not observable in this specimen. Length as preserved: 49 mm.

Discussion: The morphology of the type specimens of *O. rarus* (USNM 2860, 2858) clearly differs from the specimen from Dorset, England (DORCM 610831). The shape of the coronoid process is distinct. In the type specimens, as well as in other undescribed specimens from Morrison Formation reviewed by the authors, the coronoid shape is triangular, while in the specimen from England, it is more square-shaped. Also, the number of additional and hatchling teeth is different in the English specimen, compared with those of Morrison Formation. It is important to note that we also observed that specimens of *Opisthias* from the Morrison Formation include grooves in the additional teeth of dentary, these are not present in DORCM 61083. These morphological differences suggest that DORCM 61083 might represent a different species. This confirms that the diversity of *Opisthias* has been underestimated and this genus is not monospecific. The study of more specimens from other localities of the Morrison Formation seems necessary because it may help to elucidate if *O. rarus* represents a species complex rather than a single species. Maldonado (2013) recently suggested that there is at least one additional species of *Opisthias*. This study shows that the reexamination of the microvertebrate fauna of some important Late Jurassic localities is necessary because most studies have only focused on the study of larger taxa, such as dinosaurs.

Acknowledgements: We thank the Smithsonian Institution and Dorset County Museum for the access provided to the specimens used for this study. This work was supported by the Arthur J. Boucot Award from the Paleontological Society and Bob Savage Memorial Fund to J. Herrera-Flores.



**Fig. 1.** A) USNM 2860, left dentary in labial view; B) USNM 2858 left dentary in labial view; C) DORCM 61083, left dentary in lingual view.

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## Late Cretaceous climate change recorded in the Songliao lacustrine deposits, China [oral presentation]

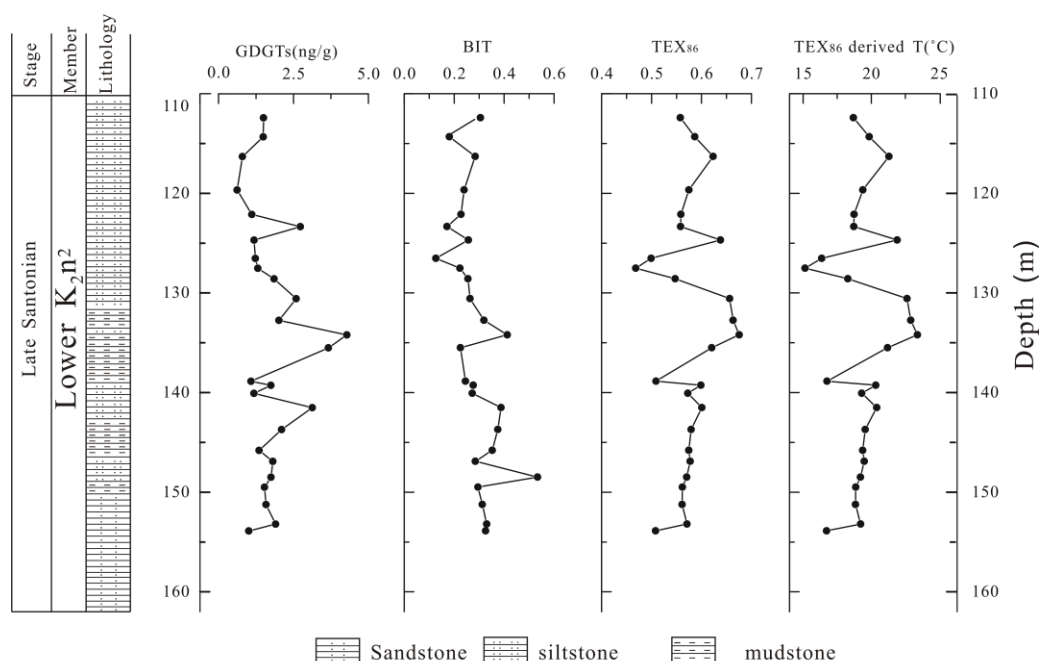
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The Late Cretaceous is often characterized as having a variable greenhouse climate (Forster et al., 2007), however, the relatively few continental sites preserving geologic records from this time exist limiting information on terrestrial climate and environments. Worldwide, the Songliao Basin located in the northeastern China is one of the largest Cretaceous-age continental rift basins. Thus, this well-preserved lacustrine deposit provides a unique record of terrestrial paleoenvironmental conditions during the Cretaceous. Here, we applied the palaeotemperature proxy, TEX<sub>86</sub> (tetraether index of 86 carbon atoms, based on the membrane lipids of aquatic Thaumarchaeota) derived from Late Cretaceous-age lacustrine deposits (lower Nenjiang Formation) from the Songliao Basin to reconstruct the palaeotemperature.

The membrane lipids of Archaea consist of isoprenoid glycerol dialkyl glycerol diethers and glycerol dibiphytanyl glycerol tetraethers (GDGTs) (DeRosa and Gambacorta, 1988). Crenarchaeota biosynthesize a specific GDGT, named crenarchaeol, which contains four cyclopentane ring and one cyclohexane ring, in addition to some more generally occurring GDGTs. Both archaea-derived isoprenoid and bacteria-derived branched GDGTs, produced by yet unknown bacteria, are identified in the Core LD6-7 sediments taken from the northwestern side of the Songliao Basin. The isoprenoid GDGT distribution are dominated by GDGT 0 and Crenarchaeol, which accounts for 22–43% and 46–66 % of the total isoprenoid GDGTs, respectively. The ratios of the GDGT-0/Crenarchaeol < 2, and the BIT (Branched versus Isoprenoid Tetraether, Hopmans et al., 2004) index are between 0.2–0.53, suggesting that the TEX<sub>86</sub> proxy could be used for the palaeotemperature reconstruction of the lake.



**Fig. 1.** The vertical variation of GDGTs, BIT, TEX<sub>86</sub> and reconstructed temperature (T) for Core LD6-7.

The reconstructed temperature is at 15.1–23.4 °C (Fig. 1) during the early Late Santonian (corresponding lower Nenjiang Formation). This finding agrees with the lake water temperature estimates based on the reservoir temperature calculations in the same lake (Shen et al., 2008). The TEX<sub>86</sub> proxy indicates that the Songliao Basin was located in the subtropical climate zone during the Late Santonian, which is in agreement with the temperature estimates for the Late Cretaceous of the northwestern circum-Pacific (Zakharov et al., 1999).

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## The Middle–Late Jurassic Yanliao Biota and the Yanshan Movement [oral presentation]

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The Yanliao biota is the most important terrestrial Lagerstätten in the Jurassic of China. It has yielded a very rich fossil assemblage, including insects, myriapods, spiders, harvestmen, conchostracans, anostracans, ostracods, bivalves, gastropods, fishes, salamanders, lizards, pterosaurs, dinosaurs, mammals, plants and fungi. It has received extensive attention, since it contributes significantly to understanding multiple major scientific questions, such as the origin and early evolution of mammals, the earliest feathered dinosaurs, the origin of birds and angiosperms, the origin and early diversification of parasitic insects and so forth. The Yanliao biota may be divided into an early assemblage represented by the Daohugou biota (ca. 165–161 Ma) from the Middle–Upper Jurassic Haifanggou Formation (168–161 Ma) and its correlated strata, and a late assemblage represented by the Linglongta biota (ca. 161–155 Ma) from the Upper Jurassic Tiaojishan Formation (161–153 Ma) and its correlated strata. The associated flora is named the *Coniopteris* - *Phoenicopsis* assemblage, which originated in the middle Early Jurassic of North China and went extinct in the Late Jurassic (ca. 155 Ma).

The superposition of westward subduction of the Pacific Plate and the closure of the Okhotsk ocean (superposition of southward subduction of the Siberia Plate) resulted in the Yanshan Movement. The North China craton went through dramatic tectonic deformations during the Middle and Late Jurassic, resulting in the formation of a series of faulted basins, and the development of the well-known exceptional terrestrial Yanliao biota associated with the deposition of coal. The early assemblage of the Yanliao biota developed after the start of the Yanshan Movement (ca. 168 Ma, Stage A1) on a set of molasses formation and made a major transformation after the tectonic (ca. 161 Ma, Stage A2) and large-scale volcanic eruptions of the early Tiaojishan Stage.

The unconformity of Stage A2 displays a particular significance for comparison of the three Middle-Late Jurassic exceptional biotas of East and Central Asia, namely the Yanliao biota, Shar Teg biota, and Karatau biota. Thus, the Daohugou assemblage correlates with the Shar Teg biota and the Tiaojishan assemblage correlates with the Karatau biota. The age of the volcanic ash layer (157.51±0.94 Ma) 0.5 meter above the black shale of the rich insect-bearing layer would be enough to limit the age of Karatau biota. This would also provide strong evidence to indicate that the Jurassic Yanshan Movement was strongly related to the superposition of southward subduction of the Siberia Plate.

The Stage B of the Yanshan Movement occurred between the Tuchengzi or Zhangjiakou/Yixian formations, which formed the famous Jehol Biota. The transition between Yanliao and Jehol biotas should occur within the Tuchengzi Formation or even earlier.

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## Dental function, tooth morphology and occlusion in basal Triconodontidae [oral presentation]

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Eutriconodonta are a monophyletic taxon of basal crown Mammalia, which are characterized by their plesiomorphic triconodont molar pattern. Within the Eutriconodonta, the family Triconodontidae exhibits a modified version of this molar arrangement. Their molars are characterized by equal cusp height of all three main cusps, with more advanced forms adding a fourth (distal) cusp. Further, the molar morphology of different genera of the Triconodontidae is highly similar, to a degree that complicates their identification solely based on molar morphology (Kielan-Jaworowska et al. 2004). Although new taxa within the Triconodontidae have been described in recent decades, major hypotheses on their dental function and occlusion date back to the 20<sup>th</sup> century and have not been put to test since. We reexamined the basal Triconodontidae *Triconodon mordax* and *Priacodon fruitaensis* with micro-computed tomography ( $\mu$ CT), in order to examine tooth eruption, morphology and occlusion.

Simpson (1928) noted an unusual eruption pattern of the m4 of *Triconodon*. The last molar is formed in a crypt on the medial side of the coronoid process, well above the functioning tooth row. Our reexamination of multiple specimens suggest that this is a unique eruption pattern, unknown (and likely absent) outside of the Triconodontidae. A possible explanation for the unusual placement of the last molar could be a terminal addition to the molar row. Simpson (1928) further hypothesized (without providing direct evidence) that the replacement of the premolars might have been sequential in *Triconodon*. We can confirm this pattern by  $\mu$ CT data. This is consistent with the phylogenetic position of the Eutriconodonta at the base of the crown group Mammalia (Luo et al. 2004; Martin et al. 2015). Intriguingly, the series of *Triconodon* fossils displays a previously unrecognized high degree of variability in dental and jaw morphology.

The occlusion of *Priacodon fruitaensis* was examined with the Occlusal Fingerprint Analyser (OFA). Our analyses show that *Priacodon* had an embrasure occlusion with the primary cusp a occluding between upper molars. This differs from the previous assumption that the occlusion in Triconodontidae resembles that of *Morganucodon*, with cusp a occluding in between B and A of the antagonist upper molar (Mills 1971). Furthermore, we conclude that the embrasure occlusion was a common feature of all Eutriconodonta.

Crompton and Luo (1993) reconstructed a noticeable roll during occlusion for members of the Triconodontidae. However, upper molars of *Priacodon fruitaensis* were inclined within the maxilla, thereby reducing the extent of the required roll. The roll during occlusion, as simulated with the OFA, falls within the range of extant mammals.

The molars of *Priacodon* have cusps of equal height and therefore lack a single prominent structure which guides the chewing stroke after the initial contact with their antagonists. As cusps along the molar row come in contact in a rapid succession, the system required a high degree of precision for the molar row to be well aligned at the beginning of the chewing path, and even before the first dental contact. The uniform cusp pattern along molar row in the Triconodontidae has been compared to that of pinking shears. This comparison still holds up. We further note the trenchant cusps of the lower molars can sharpen themselves in-between their upper antagonists, over the functional use of the teeth.

Our results highlight the usefulness of the OFA methods in testing existing hypotheses on occlusion and dental function of extinct taxa. The Triconodontidae exhibit previously unrecognized occlusal patterns, which are potentially linked to a shift to a more carnivorous diet.

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### 3D reconstruction of an archosauromorph leg from the Triassic of Central Asia based on microCT data [poster presentation]

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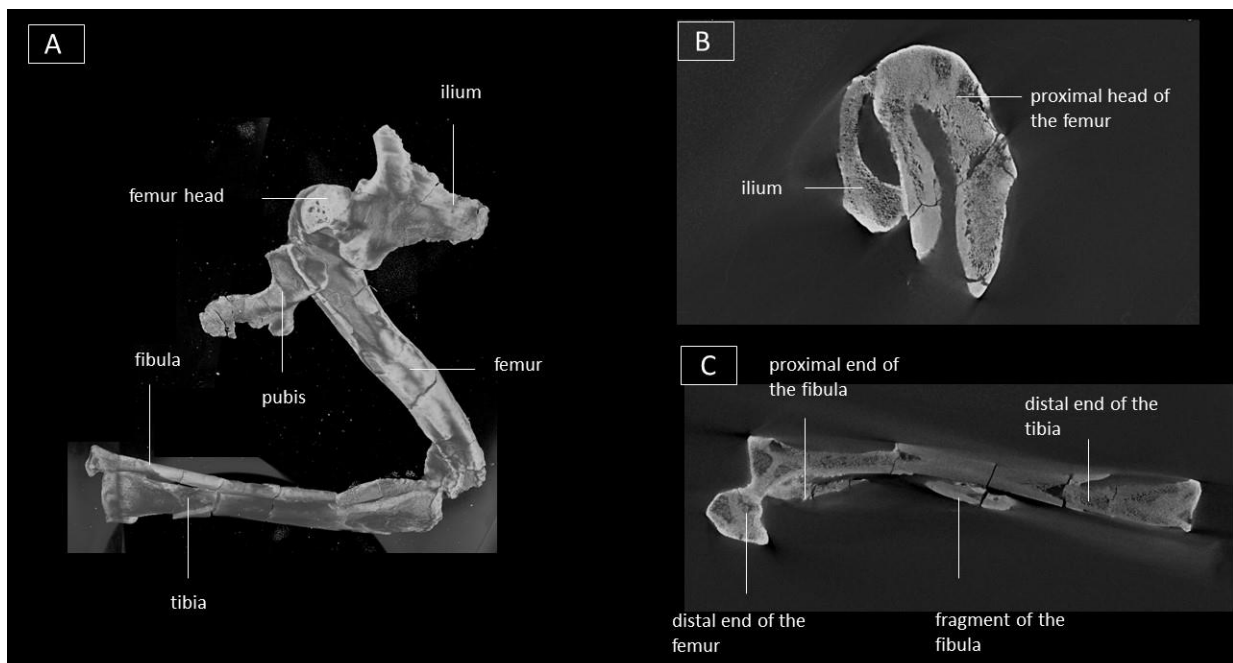
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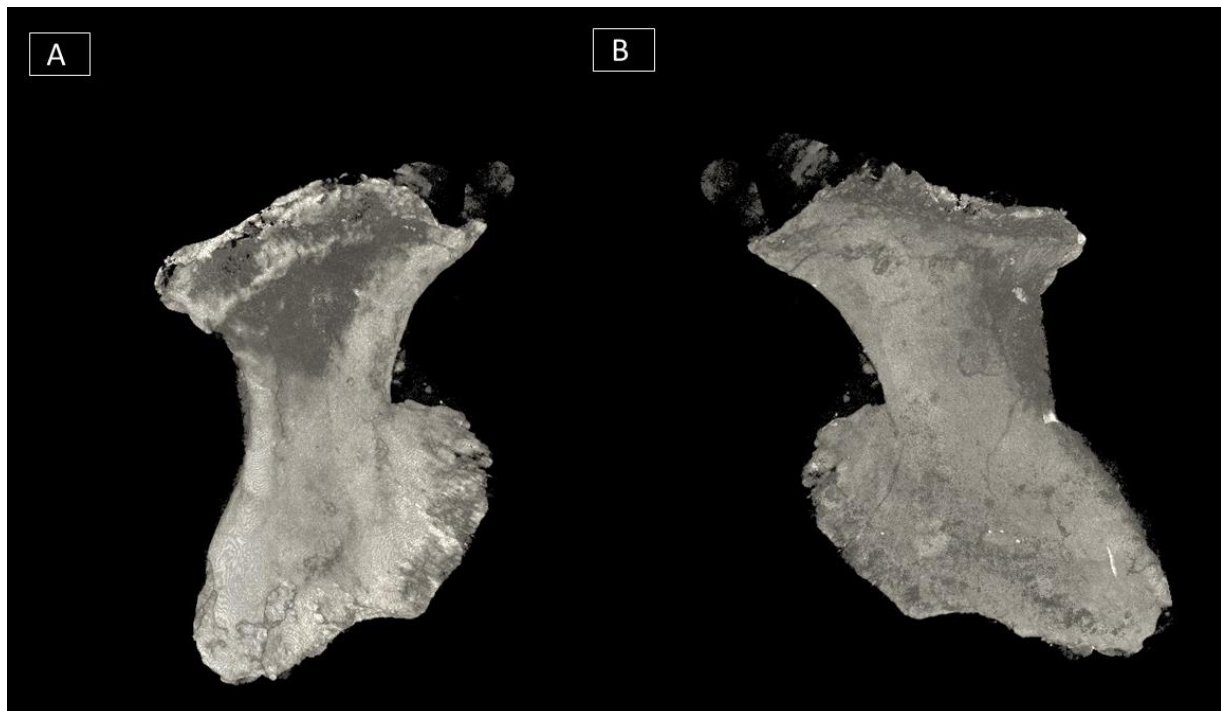
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During the 2007 field campaign of the Freiberg Palaeontology Working Group an only slightly deformed articulated pelvis and hindlimb of a small reptile has been excavated in fluvial deposits of the late Middle to early Late Triassic Madygen Formation of Kyrgyzstan, Central Asia (Voigt et al. 2017). This specimen combines several features indicative for its belonging to non-archosauriform archosauromorphs - the short and plate-like pubis and ischium that together define a thyroid fenestra, a perforating foramen between astragalus and calcaneus, a large medial centrale that does not contact the tibia and at least three distal tarsals - with certain hindlimb characteristics reminiscent of derived archosaurs and a crurotarsan-like ankle. Among others, the articulation between astragalus and calcaneum is convex-concave (concavity on astragalus) and the calcaneum possesses a long, posteriorly-deflected calcaneal tuber and a ball-shaped fibular facet. A phylogenetic analysis found this reptile nested within Archosauromorpha as the member of a clade that includes rhynchosaurs, *Trilophosaurus*, *Prolacerta* and archosauriforms, but not protorosaurs. The convergently acquired archosaur-like features of the Madygen specimen seem to be functionally related with a semi-erect to erect posture, suggesting that it was a ground-dweller.



**Fig. 1.** A: articulated and associated elements of the pelvic girdle, femur, tibia and fibula. Femur length is 84 mm, tibia length is 78 mm. B: contact between the right ilium and the left femur as 2D section of the CT scan (not to scale). Note the extended spongiosa of the femur head. C: contact between the femur and the tibia, fibula. Lateral section through the tibia in 2D (not to scale).

Because certain bones are covered with limonitic cements, making the interpretation of anatomical details difficult, and to gain a digital mount of the pelvis and hindlimb with joints in a natural position, the specimen was scanned as several scans using x-ray computed tomography (x-ray Nanotom s) at 110 kV and 200  $\mu$ A. The long bones and articulated pelvic elements were scanned as 3-part multiscan using a 2-detector with an effective voxel size of 0.02478 mm and 1800 images per 360° with a timing of 750ms resulting in a magnification ratio of 2.017 (Fig. 1 A, B, C). The isolated ischium was scanned as a single detector scan with an effective voxel size of 0.0262 mm and 2000 images per 360° with a timing of 1000 ms resulting in a magnification ratio of 1.908 (Fig. 2 A, B). The associated pes was scanned as a 2-detector scan with an effective voxel size of 0.0148 mm and 1800 images per 360° with a timing of 750 ms resulting in a magnification ratio of 3.377. Finally, the isolated calcaneum was scanned as single detector scan with an effective voxel size of 0.0180 mm and 2000 images per 360° with a timing of 750 ms resulting in a magnification ratio of 3.377. Cone beam reconstruction of all scans was performed using datos x-ray (GE Sensing & Inspection Technologies GmbH Phoenix). The scans were visualized and segmented using VG Studio Max 3.1 for the 3D reconstruction of the hind limb. Among others, we were able to recover the sediment-covered lateral surface of the ischium (Fig. 2 A, B). Apart from a clarified bone surface morphology the scans reveal the structure of the spongiosa in the limb and girdle elements in detail.



**Fig. 2.** A: exposed side of the left ischium, B: previously hidden side of the left ischium. The ischium measures 29 mm at its longest distance. Figures not to scale.

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## Invertebrate trace fossils associated with cycad leaves from the Middle Jurassic Grojec clays of Southern Poland [poster presentation]

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A rich and diverse fossil flora exists in the Grojec area located in the vicinity of Kraków, Poland (Fig. 1). This locality is dated as Middle Jurassic, probably of middle Bathonian age. During this time, the region was a very important basin for the accumulation of kaolinite and illite clay minerals (Kozłowski, 1957). Fragments of plants are preserved in these fine-grained light and dark clays, or rarely, in fine-grained sandstone with a significant admixture of clay, and occur as impressions, casts and moulds that contain rare organic matter.

The Jurassic flora from Grojec is dominated by numerous ferns (ca. 80%), but also contains horsetails, cycads, seed ferns and bennettitaleans. These floral elements were described by Raciborski (1894) and Reymanówna (1963); and later revised by Jarzynka and Pacyna (2015) and Jarzynka (2016).

During an examination of one of the frequently occurring species of *Ctenis potockii*, a few elongate structures were observed on leaf impressions. Leaves of *Ctenis potockii* are once-pinnate. The leaflets are quite large, up to 6.0 cm wide, oblong, smooth and separated from each other; only at the apex of the leaf are the leaflets fused. The veins are prominent, usually parallel and forked near the base, and rarely anastomosing. Some features that leave impressions on the leaf surface indicate that the leaf lamina of *C. potockii* was relatively thin. These enigmatic surface structures are impressions that are often straight or sometimes curved or sinusoidal grooves 0.5 to 0.75 mm wide (Fig. 2). They occur irregularly and can be present under the entire surface of a leaflet. We interpret these structures as feeding and resting traces produced by an unknown small invertebrate, occurring immediately below the fallen *Ctenis potockii* leaf. Such a type of trace was first recognized by Uchman et al. (2004) from the Oligocene of Switzerland and described as "leaf underminings". This term has been used by other authors to describe similar structures which have been noted mostly

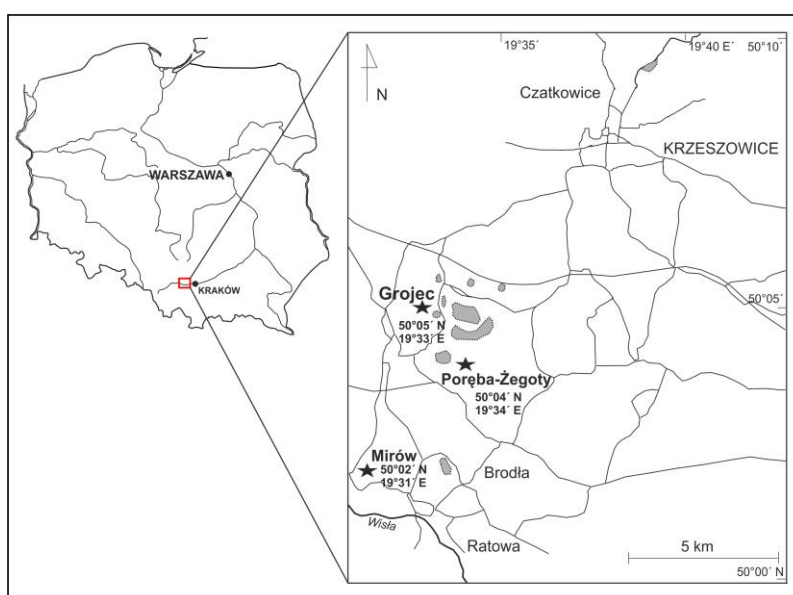
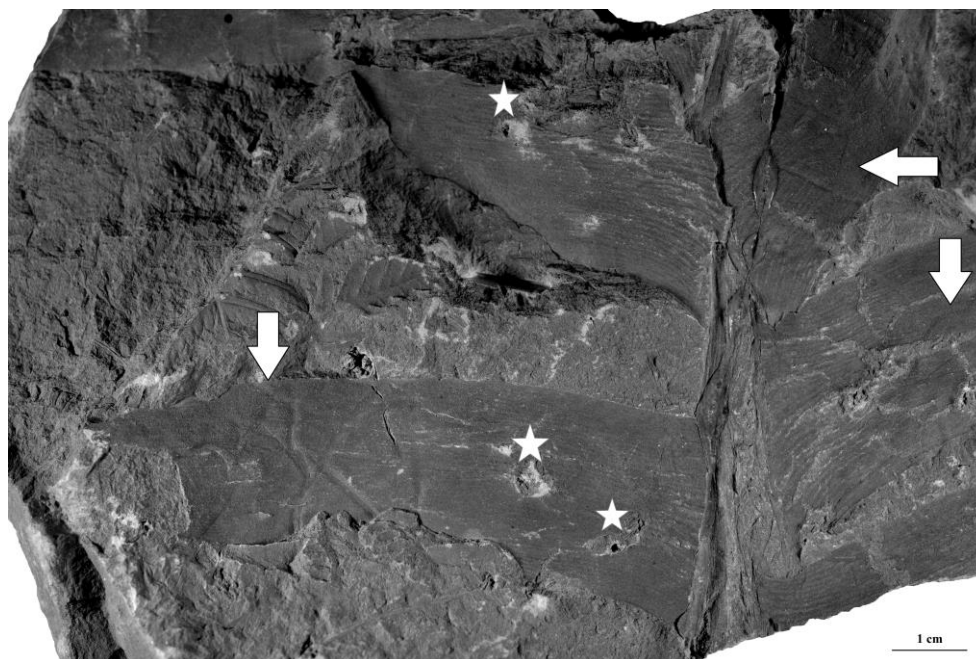


Fig. 1. Location map of the Grojec area (after Kozłowski, 1957; Jarzynka and Pacyna, 2015).

from younger Cretaceous, Eocene, Oligocene and Miocene strata, and are associated principally with dicotyledonous angiosperms bearing thin leaf blades, such as *Cinnamomum* (cinnamon) and *Rhamnus* (buckthorn) (Uchman et al., 2004; Worobiec et al., 2015). The deposited leaves likely assumed a protective role and provided nutrients to the unknown invertebrate (Uchman et al., 2004; Naurstad, 2014; Worobiec et al., 2015). Epidermal leaf mines from the Grojec area also have been observed associated with vertical root traces penetrating the ground and puncturing the leaf blade.

As far as we are aware, the described structures are the sole occurrence of this trace in the Jurassic, and the only one associated with cycads in the literature.

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**Fig. 2.** Underminings (arrows) on the impression of a *Ctenis potockii* leaf, with vertical root traces (stars).

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**Food choice in Tritylodontidae (Cynodontia)** [oral presentation]

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We present the first study on tooth wear patterns in Tritylodontidae, a diverse group of mammalian cynodonts. Stratigraphically, the studied sample comprises a total of ten species from the Upper Triassic to the Lower Cretaceous, and body sizes ranging from small/medium to large animals. Based on details of their tooth morphology, which is similar to that of some mammals such as multituberculates and muroid rodents, tritylodontids traditionally were considered as herbivores. To test their hypothesized adaptation to herbivory and the influence of differing body sizes on diet, we chose a novel approach by applying stereoscopic microwear and 3D surface texture analysis to similar target areas of comparable size on the cheek teeth.

The tooth wear signals from both methods suggest that all analyzed tritylodontids were generalist feeders and none was a dietary specialist adapted to herbivory. There was no correspondence between body size and food choice. Stereomicroscopic microwear analysis revealed that wear features were predominantly fine with numerous small pits and less abundant fine scratches as principal components. However, almost all analyzed facets show coarser microwear features such as coarse scratches, large pits, puncture pits and gouges pointing to feeding on harder food items or exogenous effects (contamination of food with grit and/or dust), or both. 3D surface texture analysis indicates predominantly fine but rounded surface texture features with large void volume, low peak densities, and various stages of roundness of the peaks.

We interpret this as indicators for consumption of food items with low to moderate intrinsic abrasiveness and can exclude regular rooting behaviour. Possible food items include plant vegetative parts, animal matter (i.e., insects), and plant reproductive structures (fruits, seeds).

In summary, although the tritylodont tooth morphology and perfect occlusion suggest plants as the primary food resource, our tooth-wear analysis suggests a wider dietary range including animal matter. The application of two independent methods of tooth wear analysis strengthens the results—being naturally different with respect to magnification, variables quantified and illumination. Combined, these complementary methods facilitate a more detailed dietary reconstruction and functional interpretation for Tritylodontidae.

**What can bone histology reveal about life style and life history in stem-turtle *Pappochelys rosinae* (Middle Triassic) from Southern Germany [oral presentation]**

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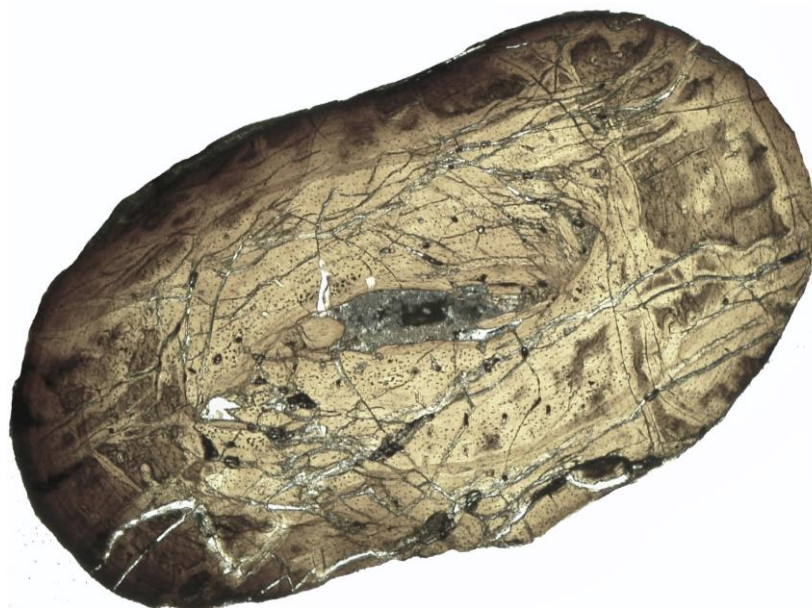
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The origin and phylogenetic relationships of turtles are controversially discussed as is the environment in which they evolved. The anapsid skull, as well as the shoulder girdle with its position within the rib cage, and the bony shell make turtles unique. The evolutionary history of turtles had long been obscured due to the lack of transitional forms.

For nearly 100 years the oldest known turtle relatives were *Proterochersis* and *Proganochelys* from the Norian (middle Late Triassic) of central Europe and Thailand. These fully shelled stem-turtles had an anapsid skull and a complete carapace and plastron. Based on different methods (limb element ratios, bone histology), Joyce and Gauthier (2004) and Scheyer and Sander (2007) found that both taxa essentially had had a terrestrial life style. With the discovery of the 'half-shelled' stem-turtle *Odontochelys* from marine sediments of Carnian age (early Late Triassic) of Guizhou Province in China (Li et al. 2008) an aquatic origin of turtles was again considered. *Odontochelys* is in numerous morphological features more plesiomorphic than *Proterochersis* and *Proganochelys*, having a rudimentary carapace but a fully developed plastron. Whether *Odontochelys* was a marine inhabitant or simply was washed in remains to be settled.

In 2015 the still more plesiomorphic stem-turtle *Pappochelys rosinae* was reported from lake-deposits from the Ladinian (Middle Triassic) of Southern Germany. Phylogenetic analysis found *Pappochelys* to nest on the turtle-stem below *Odontochelys* and *Proganochelys* (Schoch and Sues 2015, 2017). *Pappochelys* lacks carapacial or plastral turtle shell elements but shares various skeletal features with other stem-turtles (Schoch and Sues 2017). It has a diapsid skull and ornamented dorsal ribs that are short, T-shaped in cross-section, and aligned laterally without strong ventral curvature. It also has a short trunk, straight vertical scapula and robust paired gastralia, some of which bifurcate distally.



**Fig. 1.** Cross-section of femur of *Pappochelys rosinae*.

Here we present histological data of *Pappochelys* bones such as ribs, vertebrae, and gastralia as well as humeri and femora (Fig. 1). Microanatomy reveals insights into the preferred life style of *Pappochelys* (terrestrial vs. aquatic). Histological analysis provides data on life history (i.e., age, growth pattern and growth rate). The histology and microanatomy of skeletal elements of *Pappochelys* are further compared to similar-sized diapsids from the same locality as well as to other terrestrial and aquatic taxa.

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## The non-marine record of the Triassic predatory fish *Saurichthys* (Actinopterygii, Saurichthyidae) [poster presentation]

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Recent analyses (Scheyer et al., 2014; Tintori et al., 2014a; Romano et al., 2016) show that actinopterygian fishes seemingly benefited from the major biotic crisis at the Permian-Triassic boundary, with increases in taxonomic diversity, morphological disparity and utilization of trophic niches. In the Early Triassic, actinopterygians represented important apex predators in marine and freshwater ecosystems, a guild earlier composed mainly of chondrichthyans and later predominantly of aquatic tetrapods.

The 'palaeopterygian' *Saurichthys* is an emblematic Triassic fish taxon, with nearly 50 species occurring in the majority of marine and freshwater fossil assemblages of this period. Their streamlined body, long pointed jaws, and symmetrical posteriorly-located unpaired fins – as well as several other specializations – made *Saurichthys* a successful 'pike-like' predator. However, although the marine record of *Saurichthys* is well-researched, the freshwater occurrences have received relatively little scientific attention. This is likely due to the scarcity and fragmentary preservation of the freshwater material, as opposed to the abundant complete skeletons found in the marine deposits.

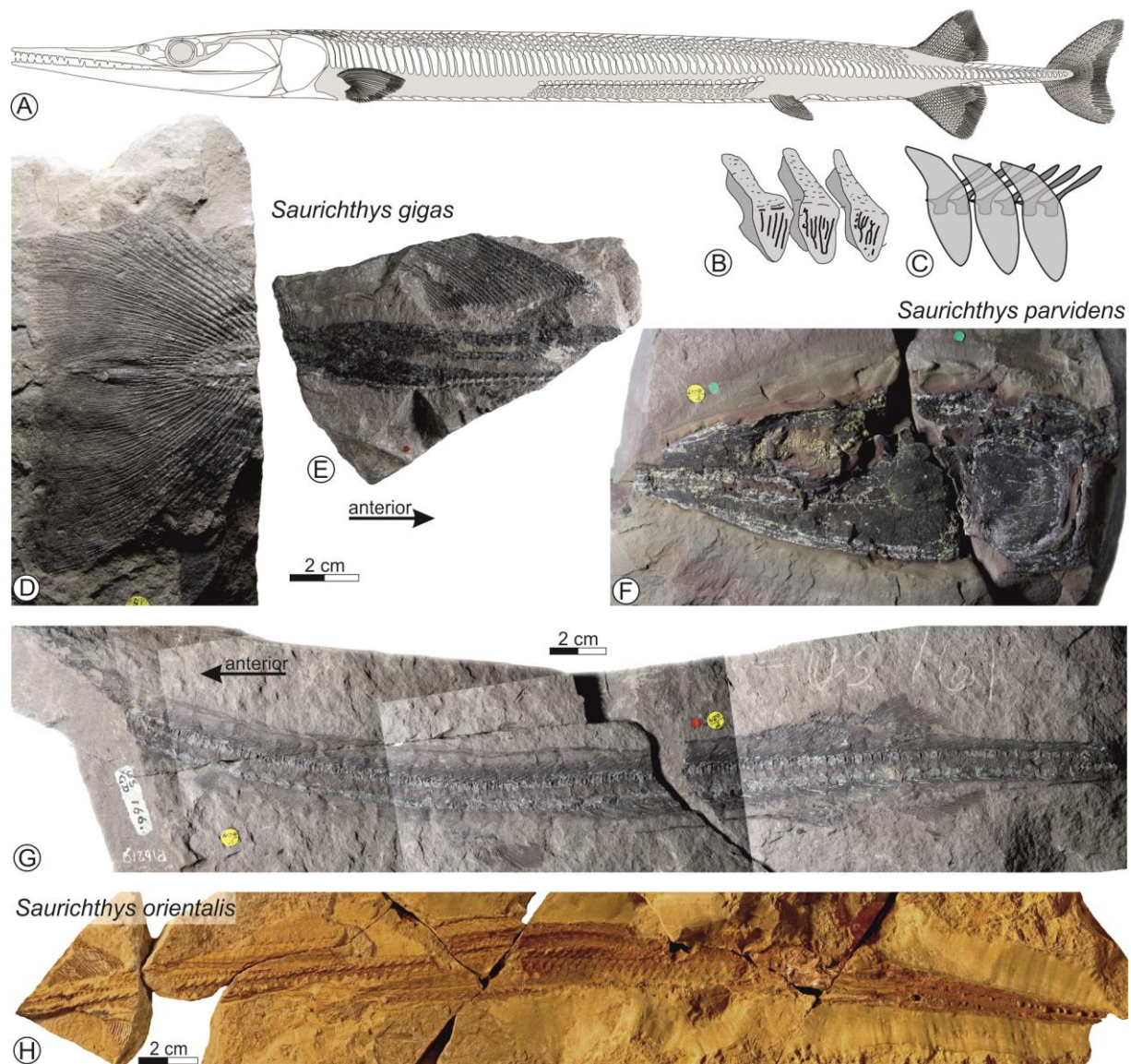
To date, Early Triassic saurichthyid remains have been reported from freshwater localities in Australia (skull fragments from the Knocklofty Formation, Tasmania; the Arcadia Formation, Queensland; and the Blina Shale, Western Australia); the Karroo Basin in South Africa (jaw fragments and teeth); and several localities in European Russia (skulls and skull fragments). All this material remains specifically unidentified.

Middle Triassic freshwater saurichthyids occur in a several localities in Australia, India, South Africa, European Russia and Kyrgyzstan (Central Asia). Six nominal species in total were described from these sites, four of which were based on reasonably complete specimens (Fig. 1).

Late Triassic non-marine occurrences are restricted to a questionable skull fragment from Greenland and a posterior body portion from the Ordos Basin in North China (*S. huanshenensis*), where doubts persist concerning both the dating and the sedimentary environment (F.-X. Wu, pers. comm.). Several cranial fragments from the German Keuper may also come from freshwater deposits. Most recently, diagnostic remains of *Saurichthys* have been recovered from the Norian Chinle Formation (Arizona, Western North America; Kligman et al., 2017).

The Early Triassic saurichthyids are morphologically similar to the Australian *S. gigas* and *S. gracilis* (Anisian), the Central Asian *S. orientalis* (Ladinian/Carnian) and the Chinese *S. huanshenensis* (Rhaetian?); leading Kogan and Romano (2016) to hypothesize that the freshwater realm offered refugia for representatives of the early saurichthyid morphotype, defined i.a. by the possession of large, thick, ornamented body scales, fins with segmented lepidotrichia and two dorsal vertebral elements per lateral scale (Fig. 1 A-C). In the marine realm these features had already had been replaced by more derived forms in the Spathian (upper Olenekian; Tintori et al., 2014b). However, a current restudy of the type series of *Saurichthys parvidens* from the Anisian Hawkesbury Sandstone of Brookvale, New South Wales (Fig. 1 G; Kogan in prep.) demonstrates that freshwater saurichthyids do not necessarily share the early morphotype. The well-preserved but hitherto poorly described material is only slightly younger than the Gosford fauna containing *S. gigas* and *S. gracilis*, and exhibits several derived characters in fin morphology, vertebral morphology and squamation. The





**Fig. 1.** Early saurichthyid morphotype and *Saurichthys* from freshwater deposits. A, *Saurichthys madagascariensis*, the best-known early saurichthyid to date, with B, shape and ornamentation pattern of mid-lateral scales and C, the 1:2 ratio of mid-lateral scales and dorsal arcualia; D, E, *Saurichthys gigas*, Terrigal Formation, Gosford, New South Wales, Anisian; F, G, *Saurichthys parvidens*, Hawkesbury Sandstone, Brookvale, New South Wales, Anisian; H, *Saurichthys orientalis*, Madygen Formation, Madygen, Kyrgyzstan; Ladinian/Carnian.

non-marine depositional setting of the Brookvale locality is supported by sedimentological data, the co-occurrence of terrestrial fossils and the absence of marine organisms. This potentially has implications for understanding the palaeobiology of saurichthyids; by indicating repeated immigration in terrestrial basins, these data suggest a preadaptation to low salinities.

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**The Early Cretaceous Crato flora (Araripe Basin, Brazil): floristic, ecological and environmental aspects of an equatorial Gondwanan ecosystem [oral presentation]**

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The late Early Cretaceous Crato Fossil Lagerstaette (CFL) opens a unique window to the equatorial zone of the Gondwana paleo-continent. CFL is part of the Mesozoic Araripe Basin located in SW Ceará (NE Brazil) and represents a key geoheritage site of the GGN-UNESCO Geopark Araripe. A  $\pm 10$ m thick section of putatively exclusively lacustrine or partly lagoon-like laminated limestones yields numerous fossils of terrestrial and aquatic biota (Fig. 1), partly in anatomical preservation, and thus documents excellently biodiversity of an ancient ecosystem. Known for more than 100 years, numerous fossil taxa have been reported so far from CFL, but the inventory of the fossil biota is far from being completely described and analyzed regarding community and trophic structures. Moreover, although geological, geochemical, and sedimentological data have been published they still await integration with the fossils in a model of the Crato "world".

As well as faunal elements including arthropods, molluscs, and vertebrates (amphibians, reptiles, fishes), the paleoflora constitutes a major component of the overall biota and carries with in important palaeoenvironmental information. From the evolutionary point of view Crato plants exhibit both decline and radiation among gymnospermous groups but, most importantly, the diversity of angiosperms early in their radiation. The latter are present with the ANITA clade, monocots and early dicots (Mohr, 2007). Among gymnosperms Gnetales and allied taxa were at their maximum diversity in Earth history.

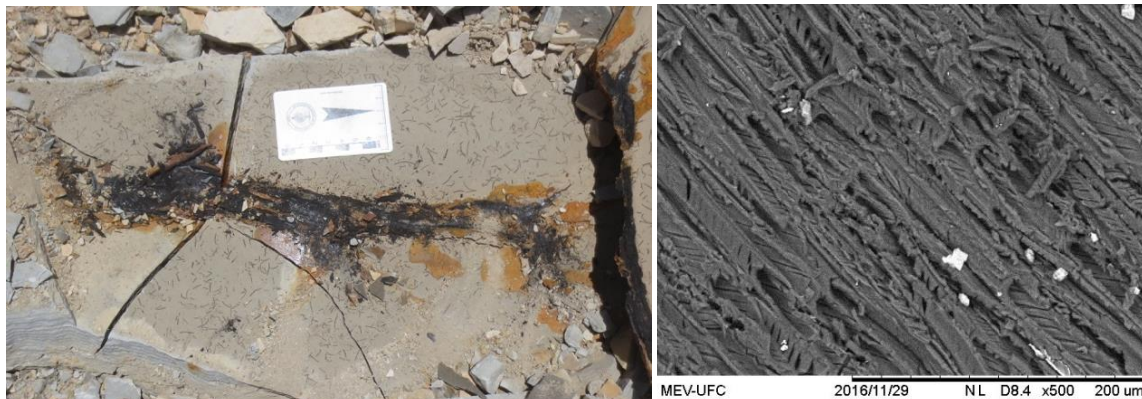
Fossil plants, and plant-derived material such as charcoal (Fig. 2) and amber, are excellent proxies for the reconstruction of the regional environment. Autecological aspects of particular fossil-species such as reproductive strategies also offer important implications for habitat conditions and local



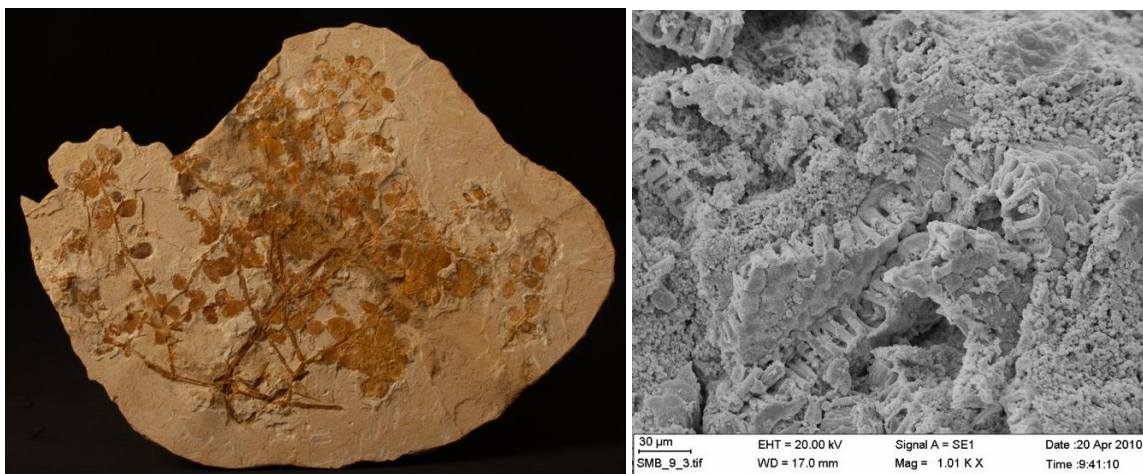
**Fig. 1.** Relative abundance of fossil remains in the outcrops in the Crato limestone quarries near Nova Olinda, Ceará, random arrangement of specimens collected by students during one day's field work (November 2016).



climate. For instance, the gnetalean-like shrubby plant *Cariria orbiculoconiformis* (Kunzmann et al., 2011) is a R-strategist well-adapted to live under a semiarid climate. The preservation of plant fossils is unique in several circumstances. Herbaceous and shrub-like plants are in some cases preserved as complete individuals. Plant parts are only moderately diagenetically flattened and often show preservation of internal and external cell structures (Fig. 3). The plant fossils are found both as coalifications, as charcoalifications and as FeO petrifications. This conference contribution presents a review of published data of the Crato flora as well as new information (de Assis Oliveira Westerkamp, 2018) evaluating both environmental and ecological interpretations.



**Fig. 2.** Charcoalified branch of the cheirolepidaceous conifer *Duartenia araripensis*, left: specimen in the field, right: xylotomical cell structure under SEM (de Assis Oliveira Westerkamp, 2018).



**Fig. 3.** The whole-plant aspect: *Cariria orbiculoconiformis* L. Kunzmann et al. 2011, gnetalean-like plant, left: holotype, FeO preservation of plant tissue, right: cell structures of pollen-producing organs under SEM.

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## **The global transition from a Mesozoic-aspect to a post-Mesozoic-aspect world: major patterns of ecological and evolutionary change in plant–insect interactions [plenary talk]**

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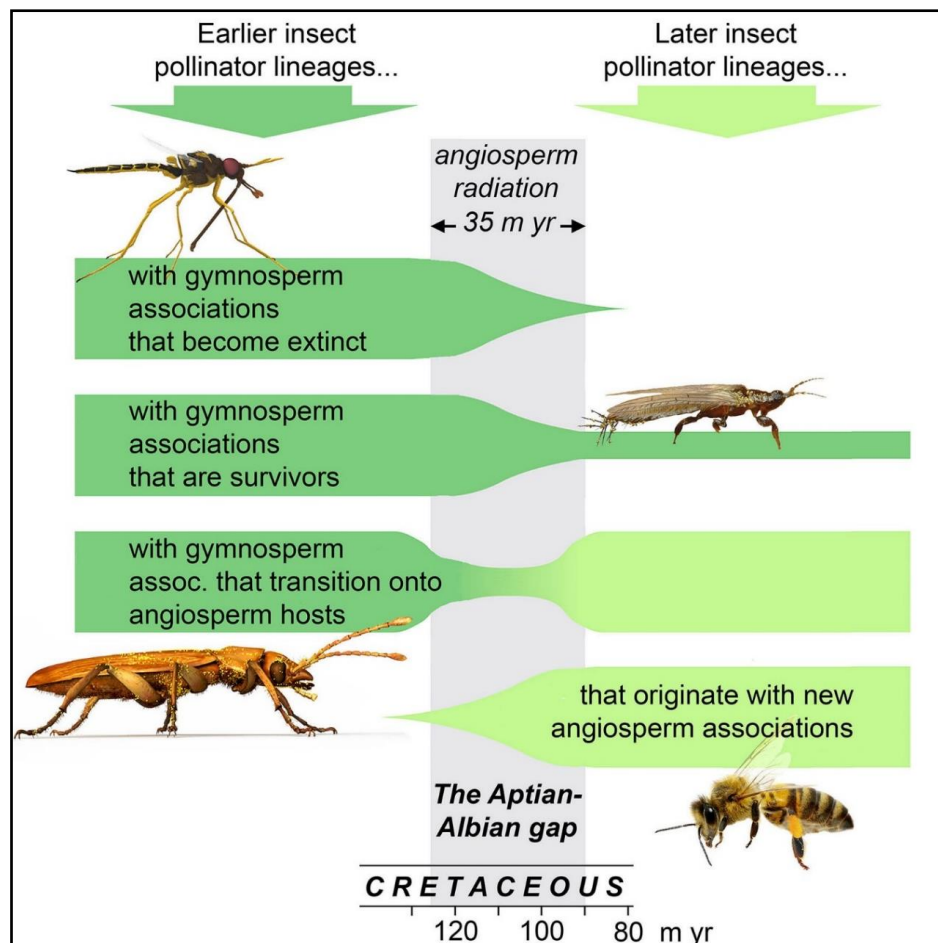
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A major transformational event during the later Mesozoic was the global shift from a gymnosperm-dominated to an angiosperm-dominated flora. This transition occurred during a 35 million-year-long interval from the Aptian through Turonian stages. It was characterized by significant extinction and origination of plant and their insect associated lineages, resulting in considerable lineage turnover. This spike in lineage turnover had minimal change in total family-level insect diversity before versus after the event (Peris et al., 2017) – a pattern mirrored when a long-term family-level diversity dataset of only plant associated families was compared before and after the event (95 versus 110 families). Closer inspection of the ecological dynamics of these pollinator and herbivore lineages revealed that the associational patterns during this interval were conditioned by the shift from a gymnosperm to angiosperm world.

For pollinators, the associations with their host plants was established often by the direct evidence of identifiable pollen found among mouthparts and other body structures of insects entombed in amber or from well-preserved compression deposits (Peris et al., 2017). Four distinct patterns are known from this transition (Fig. 1). The first pattern was the extinction of gymnosperm pollinating lineages that became extinct with the appearance of angiosperms. This pattern is seen in many species with long-proboscid mouthparts, such as mesopsychid scorpionflies, zhangsolvid flies and kalligrammatid lacewings. A second pattern involved gymnosperm pollinating lineages unable to pollinate angiosperms but continued in pollination of a limited number of gymnosperm hosts after suffering significantly decreased levels of diversity. Examples include merothripid thrips and probably cycad weevils. A third pattern consists of pollinator lineages that initially were hosted by gymnosperms but later transitioned successfully to angiosperm hosts. Instances of this include false blister beetles and tanglevein flies. The fourth pattern are those pollinator lineages that lacked gymnosperm associations in their history, and originated during the angiosperm radiation.

Like the pollinators, there are parallels for insect herbivores that involved patterns of gymnosperm versus angiosperm hostplant use during this time interval. However, the herbivore data are more indirect than that of pollinators. For leaf-mining herbivores, the associations with host plants was determined by categorization of particular, well defined, leaf-mine interaction morphotypes, known as damage types, or DTs (Labandeira et al., 2007). The first pattern consists of the distinctive leaf mines, DT71, DT139 and DT177, which only occur on Triassic and Jurassic gymnosperms such as voltzialean and ginkgoalean foliage, and likely were made by polyphagan beetles. The second pattern, the most tentative of the four, consists of DT36 blotch leaf mines, currently found on a variety of Late Cretaceous and Cenozoic woody dicot angiosperms, but attributable to leaf-mining sawfly lineages extending deep into the preangiospermous Mesozoic. A third pattern are those leaf-mining lineages from early-derived moth and beetle groups that made the switch from ferns (DT352), conifers (DT280) and ginkgophytes (DT341) to angiosperms that have the same mine morphologies (e.g., Ding et al., 2015). Lastly, there are leaf-mining lineages, such as leafmining moths (DT327), leafcutter moths (DT38, DT225) and leafmining flies (DT104, DT152) found only in association with angiosperm floras (Doorenweerd et al. 2015).

The evidence indicates that there were four patterns resulting from insect pollinators and leaf miners that confronted the challenge of the angiosperm radiation. They were (i) extinction of some gymnosperm hosted lineages; (ii) continuation of other lineages on the same gymnosperm hosts but at markedly decreased diversities; (iii) lineage continuation, but with a host-plant shift from gymnosperms to angiosperms; and (iv) independent origination on angiosperms. These data are incomplete, and need to be supplemented with examples from other host-specialized feeding guilds such as galls, and also require greater reliance on direct rather than indirect data.



**Fig. 1.** The four basic ecological-evolutionary cohorts of insect pollinators across the global shift from a gymnosperm-dominated to angiosperm-dominated flora during the Early Cretaceous. Examples of each cohort, with unique mouthparts and feeding styles, from top to bottom, are: (i) long-proboscid zhangsolvid flies; (ii) mouthcone bearing merothripid thrips; (iii) mandibulate oedemerid beetles; and (iv) glossa-bearing bees.

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**The diversity of continental Mesozoic invertebrates from Argentina** [poster presentation]

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In Argentina, invertebrates represent an important component of the continental Mesozoic faunas, and are represented mainly by arthropods (spinicaudatans='conchostracans', insects and ostracods) and mollusks (bivalves and gastropods). Despite their importance, there are few studies on the diversity and ecology of the invertebrate groups from the non-marine geological units. In the last few years, new field collections and studies by our research team have provided a more complete picture of the invertebrate diversity in South America during the Mesozoic Era (mainly Triassic–Jurassic). Our initial studies were primarily descriptions of several new taxa; however, more recently, we have focused on other objectives such as biostratigraphy, palaeoecology, taphonomy and geochemistry. The significant palaeo-invertebrate potential of the Argentinean Mesozoic sequences derives mainly from two extensive geological areas: Central-Western and Patagonia. The Central-Western Argentina region has two main Triassic basins: 1) Ischigualasto-Villa Unión Basin (=Bermejo Basin), La Rioja-San Juan provinces; and 2) Cuyana Basin (also named 'Cuyo Basin'), Mendoza-San Juan provinces. The Patagonia region includes: 1) Extra-Andean Chubut in the homonymous province, Cañadón Asfalto Basin (Jurassic–Cretaceous) and 2) Deseado Massif, Santa Cruz Province (Jurassic–Cretaceous).

The studied fossil specimens (insects, spinicaudatans, and ostracods) are housed in the collection at the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA-CCT-CONICET), Mendoza City, under IANIGLA-PI acronym; Museo Egidio Feruglio, Chubut, under MEF-PI, Paleoinvertebrate collection, Museo Regional Provincial "Padre Manuel Jesús Molina", under MPM-PI, Río Gallegos, Santa Cruz Province and temporarily in the Paleontological Collection "Dr. Rafael Herbst", Paleozoology Section (CTES-PZ) at the Universidad Nacional del Nordeste (UNNE), Corrientes City, Argentina.

In the Triassic sequences, the most common and best studied fossil invertebrates are spinicaudatans and insects; however several undescribed notostracan crustaceans and ostracods (darwinuloids) as well as bivalved mollusks have also been recorded. The Triassic spinicaudatans include thousand specimens and around 30 described species that belong to the families Lioestheriidae (2 spp.), Palaeolimnadiopseidae (1), Pemphilimnadiopseidae (1), Ulugkemiidae (3), Euestheriidae (12), Loxomegaglyptidae (6), Eosestheriidae (1), Polygraptidae (2), Fushunograptidae (1) and Estheriteoidea (1). The Triassic insect fauna includes more than 510 specimens of insects classified into 12 orders, 25 families and 87 described species. The insect records comprise both fragmentary and (occasionally) articulated specimens with various preservation modes including impressions/molds of wings, part of bodies and complete bodies attributable mainly to hemipterans, blattids, beetles and, less commonly, orthopterans, mecopterans, grylloblattids, plecopterans, miomopterans, dipterans, hymenopterans, odonatans and glosselytrodeans (e.g., Lara, 2016). Until now, the studied fossil insects have provided valuable information about the ecological organization of the Triassic communities, the evolution of Mesozoic insects, and have been valuable tools for local stratigraphic correlations and preliminary phylogenetic analyses. Additionally, they have provided taphonomical and palaeobiological information about the relationships of plant-insects-habitat and the reconstruction of ecosystems in response to palaeoenvironmental and climatic conditions.

The Jurassic units contain fossil invertebrate remains of bivalved mollusks (Unionids, 3 spp.) and gastropods (2 spp.), as well as spinicaudatans, ostracods and insects. Fourteen spinicaudatan species from the families Euestheriidae (2 spp.), Anthronestheriidae (2), Eosestheriidae (3), ?Triglyptidae (1), Fushunograptidae (4), Afrograptidae (1), and Palaeolimnadiopseidae (1) have been recorded, many of them representing the first fossil records of these species. These species are separated into distinct, stratigraphically-disjunct assemblages that allow us to tentatively define informal biozones and that may be useful for stratigraphic correlation and relative dating of the various stratigraphic units. Additionally, twelve species of ostracod, including darwinuloids (7 spp.) and cytheroids (5), four described species of fossil insects (hemipterans, mecopterans, beetles, trichopterans, and dipterans), and four ichnospecies of trichopteran larval cases, have been recorded in the Jurassic strata from Argentina (Monferran et al., 2016).

The Cretaceous invertebrates are poorly represented, primarily due to limited field collecting. At present, four spinicaudatan species have been described (Polygraptidae (1), Anthronestheriidae (2) and Euestheriidae (1)) and there are two undescribed species, one belonging to Anthronestheriidae. Different authors have also recorded seventy ostracod species (cytheroids Limnocytheridae (18 spp.), cypridoids Ilyocyprididae (32), Cyprididae (6), Candonidae (9), Pontocyprididae (2), and Paracyprididae (1) and darwinuloids (2)). The Cretaceous insect fauna is known from only five species described from eight specimens (blattids, odonatans, hemipterans, beetles, orthopterans, trichopterans).

These results allow us to observe the structure of arthropods communities, particularly their palaeodiversity and palaeogeographical distribution, over different periods. For example, the Triassic spinicaudatan fauna includes the oldest record of some families (e.g., Eosestheriidae), the first appearances of other groups (e.g., Lioestheriidae, Pemphilimnadiopseidae) and provides information about the local stratigraphic distribution of some taxa and the predominance of Euestheriidae and Loxomegaglyptidae in the Triassic sequences. Furthermore, the spinicaudatan studies provide information about different associations that inhabited perennial lakes (large Euestheriidae and Eosestheriidae) and shallow ephemeral lakes (small Afrograptidae, Fushunograptidae and Anthronestheriidae) during Jurassic times. Finally, these results are also relevant on a broader geographic scale, providing the first records for a number of taxa in any Triassic deposits worldwide (e.g., Xyelinae-Hymenoptera), in Triassic deposits in South America (e.g., Diptera, Hymenoptera, Sternorrhyncha-Hemiptera, Eoscarterellidae-Hemiptera, Geinitziidae-Grylloblattida) and in Triassic deposits in Gondwana (e.g., Hennigmattidae-Diptera). These also provide new evidence of the close faunal connections between Laurasia and Gondwana during the Mesozoic. Further studies on the palaeoecology and palaeogeography of invertebrates from Argentina will offer an excellent opportunity to expand the regional palaeocommunity reconstructions of the Mesozoic Era in South America.

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**New data on the microvertebrate fauna from the Jurassic-Cretaceous site of Ksar Metlili (Anoual Syncline, Eastern Morocco): significance for African and Gondwanan vertebrate evolution [oral presentation]**

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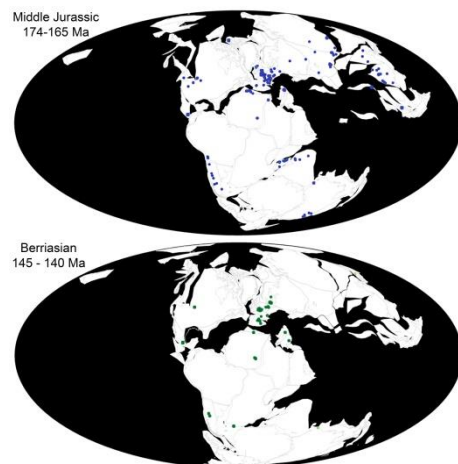
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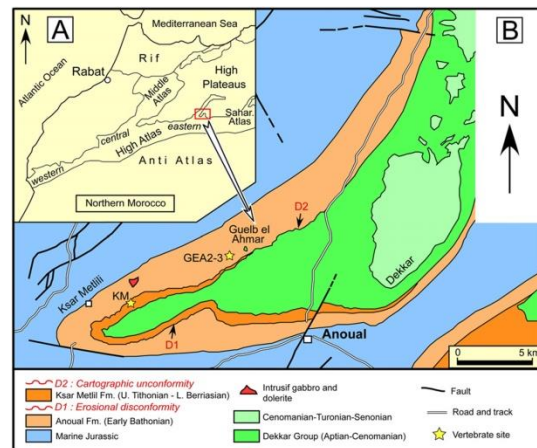
The Jurassic-Cretaceous transition is a critical period for continental vertebrate evolution. Some major modern terrestrial vertebrate groups (e.g., lissamphibians, squamates, mammals and birds) and angiosperms emerged at this time, in the key palaeogeographic context of Pangea fragmentation (Fig. 1) and early evolution of Gondwanan and Laurasian faunas, which was accompanied by an abrupt cooling and a global drop in sea level (Gheerbrant and Rage, 2006; Zouhri et al., 2017).

This work aims at improving our very poor knowledge of Gondwanan and especially African faunal palaeobiodiversity and evolution at this time (Sigogneau-Russell et al., 1998; Fig. 1), based on study of the two successive Moroccan microvertebrate faunas of Ksar Metlili (?Berriasian, Early Cretaceous, Ksar Metlili Formation; Sigogneau-Russell et al., 1988) and Guelb el Ahmar (Bathonian, Middle Jurassic, Anoual Formation; Haddoumi et al., 2016) from the Anoual Syncline (Fig. 2). These faunas are among the richest known for the Mesozoic of Gondwana as a whole, and Morocco is a key region because of its geographical position on the African shore of the Tethys, well placed to record faunal interchanges between Laurasia and Gondwana (Sigogneau-Russell et al., 1998; Gheerbrant and Rage, 2006; Zouhri et al., 2017). Furthermore, the diverse faunal associations preserved in the Anoual microvertebrate sites provide key insight into African and Gondwanan palaeoecosystems, including some uncommon species rarely found at large bone beds.

Here we focus on the Ksar Metlili site, previously known as the Anoual site, which produced more than 24,500 microvertebrate remains representing 28 species of eight main groups, ranging from selachians to mammals, that were identified and studied using comparative anatomy, taxonomic and statistical approaches. It includes noteworthy taxa (Fig. 3): the oldest therian mammals from Gondwana (and one of the richest Mesozoic mammal assemblages), some of the last known non-mammalian cynodonts, a basal ornithomorph, a possibly freshwater teleosaurid crocodylomorph, and some of the scarce choristoderan reptiles and albanerpetontid amphibians known from Gondwana. A large scale faunal comparative study of Ksar Metlili with some closely aged sites, such as Guimarota (Kimmeridgian, Late Jurassic, Portugal), reveals noticeable shared taxa with Laurasia, resulting from either trans-Tethyan dispersals and/or a vicariant Pangean descent, but few Gondwanan affinities. It suggests peculiar palaeobiogeographical relations of North Africa within Gondwana at the Jurassic-Cretaceous transition. Finally, the faunal similarities between Guelb el Ahmar and Ksar Metlili call into question an Early Cretaceous age for the latter, and instead suggest a more likely Jurassic (at least Late Jurassic) age.



**Fig. 1.** Continental vertebrate sites known from the Middle Jurassic (top) and the Early Cretaceous (bottom). Each point represents a site. Modified from paleobiodb.org.



**Fig. 2.** Location (A) and simplified geological map (B) of the Anoual Syncline. Modified from Haddoumi et al. (2008).



**Fig. 3.** Some remarkable taxa from the Ksar Metlili fauna. From left to right and from top to bottom: albanerpetontid, choristodere, *Theriosuchus*, teleosaurid, ornithopod, non-mammalian cynodonts and therian mammals. Drawings and SEM photographs by M. Lasseron, others by L. Cazes. Life reconstructions by M. Witton, C. C. Tat, M. Witton, and N. Tamura.

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**What's the role of cockroaches in Late Mesozoic ecosystems?** [oral presentation]Xin-Ran LI<sup>1,2</sup> & Diying HUANG<sup>1,3</sup>

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Some cockroaches today are well-known household pests, a fact that is highly associated with their diet. Most Recent cockroaches are omnivores that serve either as scavengers or detritivores, or both. This dietary propensity allows cockroaches to easily infest human habitation, and can sometimes become herbivores or predators (Roth and Willis, 1960). Cockroaches are generally believed to have originated during the Mesozoic. Specifically, crown cockroaches that have concealed ovipositors and produce oothecae for protecting eggs, likely have a Jurassic origin, while the age of origin for stem cockroaches that have exposed ovipositors is far from certain.

What did Mesozoic cockroaches consume, and what role did they play in the nutrient and energy cycle? In terms of morphology, cockroaches are conservative compared to other insects, from the Jurassic to Recent. Accordingly, the life history of modern cockroaches is likely similar to or even the same as that of their ancestors. However, fossil records are rare that can provide a persuasive account. Current work on Mesozoic dictyopteran insects, with an emphasis on Cretaceous Myanmar (Burmese) amber allows easier access to understand the evolutionary history of these insects. Cockroaches occurring in Myanmar amber roughly are categorized into three morphological types: flat-bodied journeymen, long-legged acrobats, and armoured fliers. Exhibiting the flat habitus typical of some modern cockroaches, some of our fossil material are stem cockroaches, while many others are assigned to extant families, the majority of which are Corydiidae. A minority of the fossil cockroaches are tentatively classified as Ectobiidae or Blattidae. These lineages are typical scavengers or detritivores. Vršanský et al. (2013) speculated that such cockroach groups may have fed on dinosaurs' feces, and feces is one food source of Recent cockroaches (Bell et al., 2003). Consequently, it is not surprising that Mesozoic cockroaches may have had a similar diet. However, whether or not these cockroaches did feed on dinosaurs' feces and how much feces they consumed remain unclear. Some extant cockroaches are wood-feeding, represented by *Cryptocercus* and *Panesthiinae*. These forms are scavengers and not herbivores because they feed on dead, even rotting wood. Unfortunately, wood-feeding cockroaches are hardly recorded as fossils, because they spend most of their life time hiding in the galleries. Besides, they may not be recognized owing to their less specialized morphology. Some hypothetical predatory cockroaches also have been recorded, such as the families Eadiidae, Libriblattinidae, Manipulatoridae and Raphidiomimidae (Vršanský, 2009; Liang et al., 2012; Vršanský and Bechly, 2015). Their inferred predatory behavior was judged from their fossil morphology—agile body, elongate appendages, and/or prognathous mouthparts. This long-legged body type also occurs in Myanmar amber, but these taxa are not particularly specialized for predation in comparison to general Recent forms, some of which are occasionally generalist predators (Bell et al., 2003). There are three alternative scenarios for these long-legged body types. First, the long legs made these insects highly maneuverable as carnivorous kleptoparasites, which provided the ability to wander about a spider web or escape from the web owner. Second, the long legs were used to stride over the gaps or barriers on plant surfaces, for example acanthae and calyx tubes, to feed on live plant material, including pollen. The third type found in Myanmar amber is represented by Ponopterixidae only. The protective elytra of

Ponopterixidae are found also in the living genera *Diploptera* and *Prosoplecta*, which are excellent fliers. The niche of Ponopterixidae, however, remains enigmatic.

In summary, there is no robust evidence supporting the occurrence of specialized herbivorous or predatory cockroaches during the Mesozoic. It is more likely that, in Mesozoic terrestrial ecosystems cockroaches play a significant role similar to their modern descendants, being scavengers or detritivores, and obviously, the prey of many animals.

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**Convergent evolution of a mobile bony tongue in flighted dinosaurs and pterosaurs [oral presentation]**

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The tongue, with fleshy, muscular, and bony components, is an innovation of the earliest land-dwelling vertebrates with key functions in both feeding and respiration. Here, we bring together evidence from preserved hyoid elements from dinosaurs and outgroup archosaurs, including pterosaurs, with enhanced contrast x-ray computed tomography data from extant taxa. Midline ossification is a key component of the origin of an avian hyoid. The elaboration of the avian tongue includes the evolution of multiple novel midline hyoid bones and a new position for a larynx suspended caudal to these midline elements. While variable in dentition and skull shape, most bird-line archosaurs show a simple hyoid structure. Bony, or well-mineralized, hyoid structures in dinosaurs show limited modification in response to dietary shifts and across significant changes in body-size. In Dinosauria, at least one such narrow, midline element is variably mineralized in some basal paravian theropods. Only in derived ornithischians, pterosaurs and birds is further significant hyoid elaboration recorded. Furthermore, only in the latter two taxa does the bony tongue structure include elongation of paired hyobranchial elements that have been associated in functional studies with hyolingual mobility. Pterosaurs and enantiornithine birds achieve similar elongation and inferred mobility via elongation of ceratobranchial elements while within ornithurine birds, including living Aves, ossified and separate paired epibranchial elements (caudal to the ceratobranchials) confer an increase in hyobranchial length. The mobile tongues seen in living birds may be present in other flighted archosaurs showing a similar elongation. Shifts from hypercarnivory to more diverse feeding ecologies and diets, with the evolution of novel locomotor strategies like flight, may explain the evolution of more complex tongue function.

## Origins of mammals and evolution of Mesozoic mammaliaform biotas [plenary talk]

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Mammaliaforms is a clade consisting of crown mammals and their near relatives. It originated in the Late Triassic and its major groups diversified through the Jurassic and the Cretaceous (Kielan-Jaworowska et al. 2004). Mesozoic mammaliaforms provide direct osteological correlates to the biological adaptations of extant mammals, which enable us to map the transformation of the mammalian characters through evolution (Crompton and Jenkins 1979; Luo 2007; Rowe et al. 2011; Zhou et al. 2013). Mammaliaform clades also developed significant morphological disparity (anatomical uniqueness) in teeth and in postcrania, respectively for diverse feeding functions and for different locomotor modes. New fossils from the last 20 years have revealed an increasingly more informative picture of the anatomical transformations that occurred during the origination of mammals:

- 1) Mammal-like patterns of cranial growth can now be inferred from tooth replacement, as accompanied by ontogenetic increase in skull size of some mammaliaforms;
- 2) The main steps of transformation of the petrosal, the inner ear and its cochlear canals have been established for stem mammaliaforms (reviewed by Luo et al. 2016);
- 3) Mandibular ears in mammaliaforms are more primitive than previously supposed (Luo et al. 2017; Schultz et al. 2018), and derived features of the definitive mammalian middle ear evolved convergently among crown mammals;
- 4) Brain endocasts of stem mammaliaforms have already increased in size, to be within the size range of crown mammal groups, and show some modern mammal-like features;
- 5) The shoulder girdle of stem mammaliaforms is similar to that of juveniles of the monotreme *Ornithorhynchus*, and different from those of other crown mammals;
- 6) The tarsals and cruro-tarsal joint of stem mammaliaforms, with the exception of docodonts, show mostly the plesiomorphic features of pre-mammalian cynodonts.

Studies of the newly discovered skeletal fossils revealed a wide (and previously unknown) disparity among the Jurassic and Cretaceous mammaliaforms in limb bones and in the manual and pedal elements. This provides new insights into the ecomorphological diversity of Mesozoic mammaliaforms.

The disparate limb structure and autopod (manual and pedal) phalangeal characters can be correlated, morphometrically, with different locomotor modes and substrate preferences in extant mammals that are known for their ecological specializations. By combined analyses of limb and phalangeal proportions of both extant mammals and Mesozoic mammaliaforms, it becomes feasible to infer the ecomorphological adaptations of Mesozoic mammaliaforms (Bi et al. 2014; Chen and Wilson 2015; Meng et al. 2017; Grossnickle et al. 2017). Furthermore, the new discoveries have included haramiyidans (*Maiopatagium*, *Vilevolodon* and *Arboroharamiya*) with skin membranes for gliding (Meng et al. 2017; Han et al. 2017), the docodont *Castorocauda* with a broad tail for swimming, and the docodont *Docofossor* with short and broadened claws for fossorial life (Ji et al. 2006; Luo et al. 2015; Meng et al. 2015). In general, Jurassic mammaliaforms had developed a wide range of locomotor modes associated with fossorial, semiaquatic, terrestrial, arboreal, and volant adaptations. The stem mammaliaforms of the Jurassic were functionally versatile and ecologically diverse, to the same extent as extant marsupials.

Jurassic mammaliaform communities, as exemplified by the Middle-Late Jurassic Yanliao Biota of China, are dominated by such mammaliaforms such as haramiyidans and docodonts. Crown mammal taxa are only a minority. This is in sharp contrast to the Early Cretaceous mammal communities that are dominated by the crown mammal clades of multituberculates, eutriconodonts and spalacotherioids, as seen in the Jehol Biotas of China. The Jurassic and Cretaceous mammal communities were re-assembled by separate clades in different geological times, as morphological disparity and ecological diversity evolved iteratively in successive diversification of mammaliaforms. This suggests that the mammalian paleoecological communities in the terrestrial ecosystem have been re-assembled through the Jurassic–Cretaceous transition. The significant ecomorphological diversification in the mammal community of the Jurassic was driven by stem mammaliaforms in more basal phylogenetic positions, independent of the Cretaceous ecological diversification driven by more derived clades of crown mammals, and also completely independently of the therian radiation in the Cenozoic.

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## **Titanosaurian osteoderms and manus and pes shape revealed from ichnological and skeletal records of South Asia (Indo-Pak peninsula) [oral presentation]**

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**Titanosaurian osteoderms from Pakistan:** Several types of titanosaurian osteoderms (Fig. 1) were collected from the Latest Cretaceous Vitakri Formation. The first type is represented by simple thin plates (5-7cm in diameter, compact) referred to *Sulaimanisaurus*; the second type comprises cancellous mosaic plates referred to *Marisaurus*. Osteoderms with cancellous structure and denticle-like symphyses are referred to *Pakisaurus* and cancellous fibrous bone plates with ventral glenoidal surface are referred to *Nicksaurus*. Apparently, titanosaurs possessed osteoderms of differing shapes. Malkani (2003) reported large oval rugose plates as osteoderms of titanosaurs, but later (Malkani 2018) considered these plates as pedal unguals of the titanosaurs *Pakisaurus* and *Balochisaurus*.

**Titanosaurian manus and pes shape revealed from Mesozoic ichnological and skeletal records of South Asia (Indo-Pak peninsula):** A small sized subcircular pedal footprint (22.5cm x 16.5cm) with rounded heel from the Late Cretaceous of India (Mohabey 1986) (Fig. 1) shows three large oval toes on digit II, III and IV, and was referred to a titanosaur by Malkani (2018).

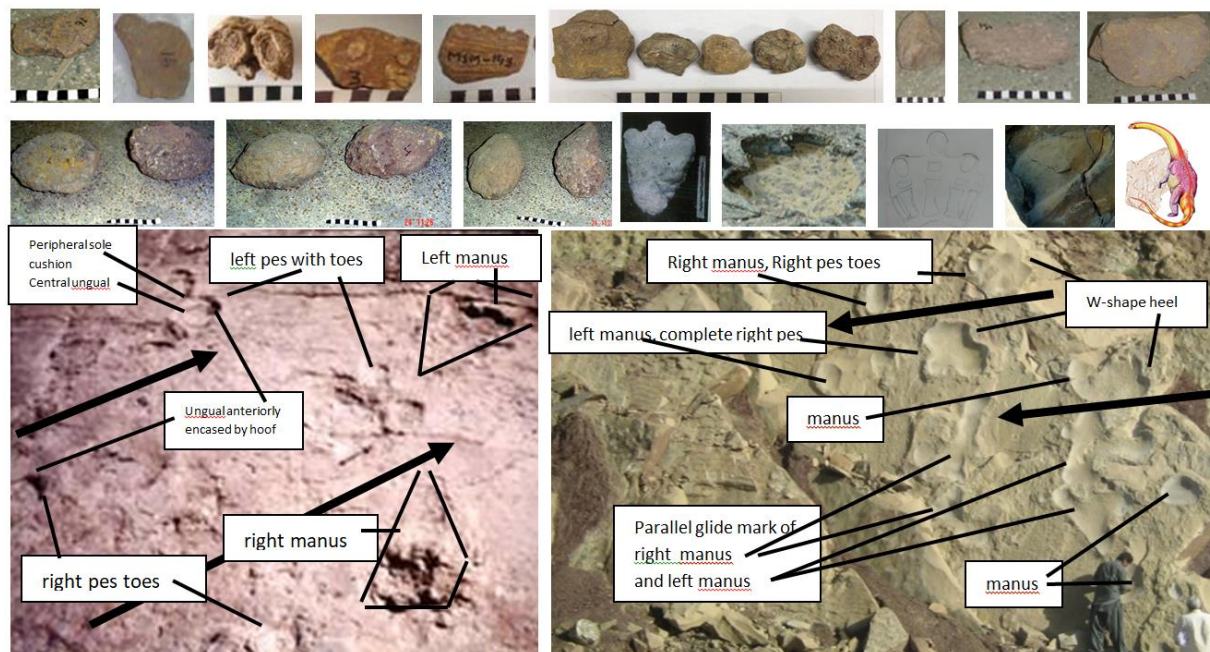
Trackways of the basal titanosaur *Malakhelisaurus mianwali* (Fig. 1) were reported by Malkani (2007, 2008) from the Middle Jurassic Samanasuk limestone of the upper Indus region. The trackway pattern shows three parallel trackways (Fig. 1) indicating a herd. The trackways have a relatively wide gauge (internal trackway width of 0.4 m), asymmetric D shaped manus (about 50 cm x 70 cm) without unguals, a large circular symmetric pes with five digits (about 1.3 m x 1.3 m), with large oval anteriorly directed toes on digits II, III, IV and reduced outer digits I and V, and feeble W-shaped heel. The central digit is pointing anteriorly. The distinctive toe impressions clearly indicate three portions with a central oval-shaped ungual which is enveloped by a sole cushion of about 5 cm width or thickness, anteriorly encased by a broad reversed U-shaped hoof (Fig. 1). The heteropody ratio is 1:4.5. Based on the gauge of the trackway, the hip height is estimated at 4-5 m.

Footprints of the titanosaur *Pashtosaurus zhobi* (Fig. 1) were reported by Malkani (2014) from the Latest Cretaceous Vitakri sandstone bed of the middle Indus. The first trackway shows left and right pes and manus, and the second trackway shows left and right manus (glided) and right pes (Fig. 1). The ichnite indicates a herd movement, a relatively narrower gauge (0.20-0.25 cm internal trackway width), D-shaped manus (50-55 cm x 70-75 cm) without claws, and a giant circular symmetric pes with five digits (1.27 m long and 1.28 m wide), with distinctive large oval anteriorly directed toes (all along the front edge) on digits II, III and IV, and reduced outer digits I and V. The central oval ungual is enveloped by a fleshy sole cushion which is anteriorly encased by a U-shaped hoof. The central digit III is inserted in a forward position which creates a W-shaped heel like in extant camels. One manual imprint shows marks of D-shaped metacarpals I, II, III, IV and V. The heteropody ratio is about 1:4.5.

The tracks are referred to titanosaurs rather than to stegosaurs. Titanosaurs have a symmetric five digits pes with toes on central digits II, III, IV and reduced outer digits I and V without toes, while stegosaurs have a symmetric pes with only three digits. The pes of titanosaurs is very large while stegosaurs have a triangular pes of moderate size. Unguals are oval in titanosaurs, and half oval and posteriorly blunted in stegosaurs. Titanosaurs have a five digits manus without claws while stegosaurs have a five digits manus with two unguals (Peter Galton, pers. comm.). Similar oval



unguals (previously considered as osteoderms) were reported from Malawi (Gomani 2005), Argentina (Powell 2003), and India (Huene and Matley 1933, Demic and Wilson 2009). The probable phalangeal formula is 1-2-2-2-0, with a toe formula of 0-1-1-1-0. Based on the relatively narrower gauge and stocky nature, the hip joint height of the track-maker is estimated at 3-5 m (Fig. 1). From Indo-Pakistan many metacarpals, metatarsals and unguals have been reported. Large oval unguals are assigned to *Balochisaurus* and *Pakisaurus* (Fig. 1). The giant circular pes with large oval unguals is an adaptation of titanosaurs for balancing the heavy body. The footprints are diagnosed as belonging to titanosaurs (instead of ornithischians) on the basis of their wide gauge, the giant circular pes (instead of triangular and moderately sized pes), large oval unguals (instead of half oval and posteriorly blunted unguals of moderate size), and D-shaped manus without unguals. The Middle Jurassic and Latest Cretaceous ichnites reveal the evolution of basal titanosaurs to most advanced titanosaurs.



**Fig. 1.** Row 1, photos 1-5: types of osteoderms; photo 6: coprolites or osteoderms; photos 7-9: types of osteoderms or unguals. Row 2, photos 1-3: large oval unguals; photo 4: pes print from India; photo 5: pes print from UK; photo 6: line drawing of pes, photo 7: manus print level 2; photo 8: models of Zhob ichnite and trackmaker *Pashtosaurus zhobi* (ichnite model by Dr. Nicholas Allen and trackmaker model by Dr. Dmitry Bogdanov). Row 3, photo 1: Middle Jurassic ichnite; photo 2: Latest Cretaceous ichnite. Arrows show trackways. Scale: each black unit is 1 cm.

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## Mesozoic vertebrates from Pakistan and their paleobiogeographic affinities [poster presentation]

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The Late Jurassic Sembar Formation yielded the basal titanosaur *Brohisaurus* which is based on postcranial elements. The latest Cretaceous (Latest Maastrichtian 68-66Ma) Vitakri Formation yielded titanosaurs, theropods, mesoeucrocodyles and pterosaurs.

Pakisauroids are large and slender-bodied titanosaurs that are characterized by a mid-caudal ratio of about 1 and include *Pakisaurus*, *Sulaimanisaurus* and *Khetranisaurus*. *Pakisaurus* is distinguished by tall and slender caudals and extremely slender tibiae (Fig. 1) and is based on the type series of presacral and tall caudal vertebrae, sternals, scapulae, humeri, radius, ulnae, ilia, femora, tibia, fibula, foot bones and osteoderms from South Kinwa and remains from West Bor, North Alam, Top Kinwa, Shalghara and Zubrapeak. *Sulaimanisaurus* is based on squarish mid-caudals from South Kinwa and other remains from Sangiali, Shalghara and Mari Bohri. *Khetranisaurus* is characterized by a mid-caudal ratio slightly above 1 and is represented by caudal vertebrae from Mid Kinwa and exemplars from Bor, Mari Bohri and Grut (Malkani 2017a, b, e).

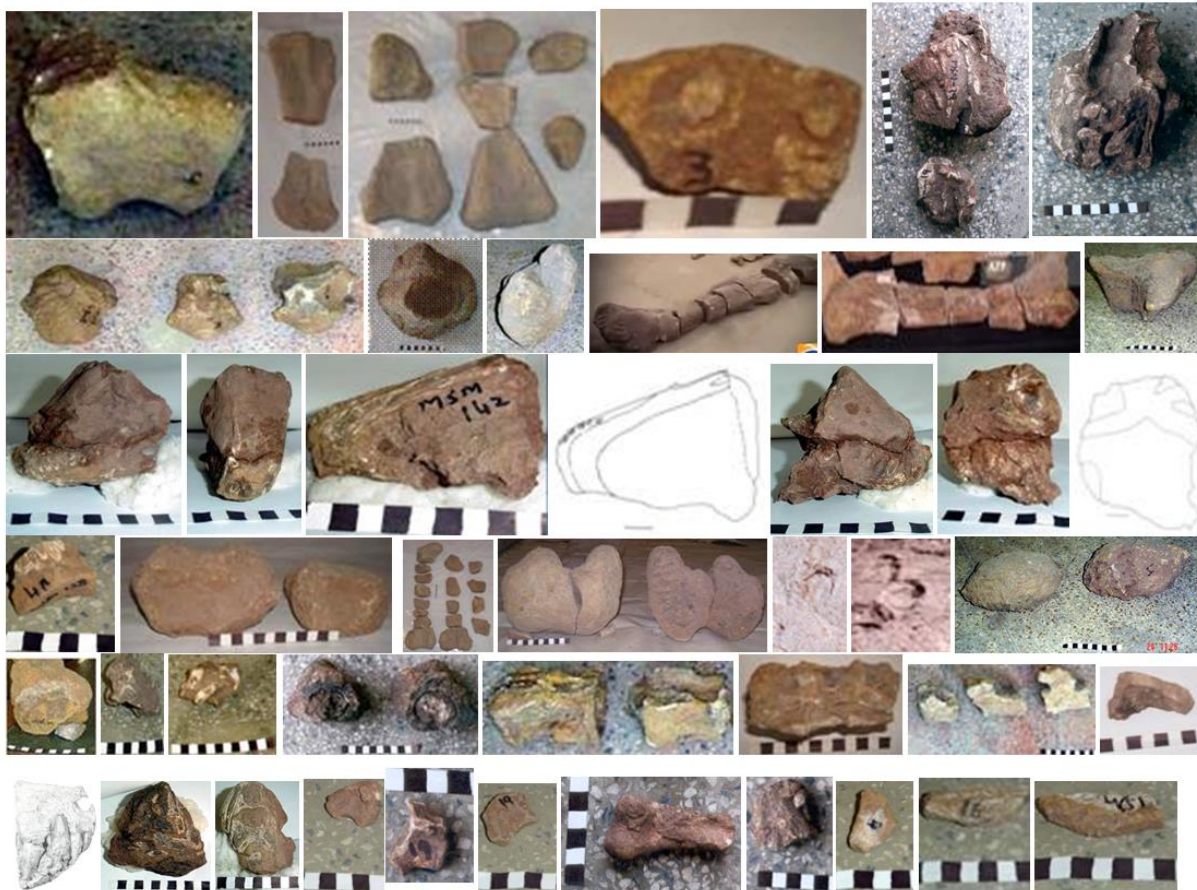
Marisaurs are medium sized and stocky-bodied titanosaurs (mid-caudal ratio is about 1.5) and include *Marisaurus*, *Gspisaurus* and *Maojandino*. *Marisaurus* is based on caudal vertebrae (including the first biconvex vertebra), scapula, pubis, distal ischium/pubis and femur from Mari Bohri and exemplars from South Bor and eastern Top Kinwa. *Gspisaurus* is based on adult skulls (Fig. 1) from Alam. *Maojandino* is based on axial and limb elements from Alam (Malkani 2017a, c, e; 2014a; 2015a, b).

Balochisaurs are small and stocky-bodied titanosaurs characterized by a mid-caudal ratio of about 2 and include *Balochisaurus*, *Saraikimasoom* and *Nicksaurus*. *Balochisaurus* is distinguished by a stocky tibia, a biconvex first caudal, and a mid-caudal ratio of about 2 and is based on the type series of presacral and broad caudal vertebrae (including the first biconvex caudal). It is represented by sternals, humerus, manus, ilia, femur, stocky tibia, fibula, ribs and neural spines from Mari Bohri and exemplars from Kinwa, Zubra, and Grut. *Nicksaurus* is based on cranial remains, very broad vertebrae and stocky limb bones from north Kinwa. *Saraikimasoom* is based on a very small complete skull (Fig. 1) from South Kinwa (Malkani 2017a, c, e; 2014a; 2015a, b).

*Vitakridrinda* is a large bodied theropod based on femora, centra, braincase, more than nine teeth (D-oval shape with distinct great hollow and thin peripheral bone) and cranial remains from Alam, and referred vertebrae and limb bones from Sangiali, Shalghara, Mari Bohri, South and Top Kinwa. *Vitakrisaurus* is another large bodied theropod based on hand/manus, vertebrae and leg bones from South Bor.

*Pabwehshi* Wilson et al. 2001 is a mesoeucrocodyle based on a rostrum from Top Kinwa. *Induszalim* is a mesoeucrocodyle based on a rostrum, vertebrae and humerus/femur from Alam and referred vertebra from Mari Bohri (Fig. 1). *Sulaimanisuchus* is a mesoeucrocodyle based on dentaries and tibia from South Kinwa. *Khuzdarocroco* is a mesoeucrocodyle based on ribs/phalanges from Khuzdar. The pterosaur *Saraikisaurus* is based on a dentary from Top Kinwa and a referred dentary from South Kinwa. Tracks have been recorded for the basal titanosaur *Malakhelisaurus*, the large theropod *Samanadrinda*, and the small theropod *Himalayadrinda* (Malkani 2015d), as well as for the most advanced titanosaur *Pashtosaurus*, the pterosaur *Anmolpakhi alleni* and small vertebrates such as possibly birds, frogs, lizards, snakes, and others.

The majority of these fossils show a close relationship to Gondwana, but some endemic faunal elements like a very small skull of the titanosaur *Saraikimasoom*, a rostrum of the mesoeucrocodyle *Induszalim*, and a dentary with teeth of the pterosaur *Saraikisaurus* may be explained by a fragmentation of Gondwana that lead to a certain endemism among the Mesozoic Indo-Pakistan terrestrial vertebrates.



**Fig. 1.** Row 1, photo 1-4: *Pakisaurus*; photo 5-6: *Gspisaurus*. Row 2, photo 1-6: *Balochisaurus*. Row 3, photo 1-7: *Saraikimasoom*. Row 4, photo 1-4: *Nicksaurus*, photo 5: hoof print, photo 6: three parts of toe, photo 7: unguals. Row 5 photo 1-5: *Vitakridrinda*; photo 6-8: *Vitakrisaurus*. Row 5, photo 1: *Pabwehshi*; photo 2-7: *Induszalim*; photo 8-9: *Sulaimanisuchus*; photo 10-11: *Saraikisaurus minhui*. Scale each black unit is 1 cm.

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## Diversity of euharamiyidans in the Jurassic Yanliao Biota as reflected in dental morphology [oral presentation]

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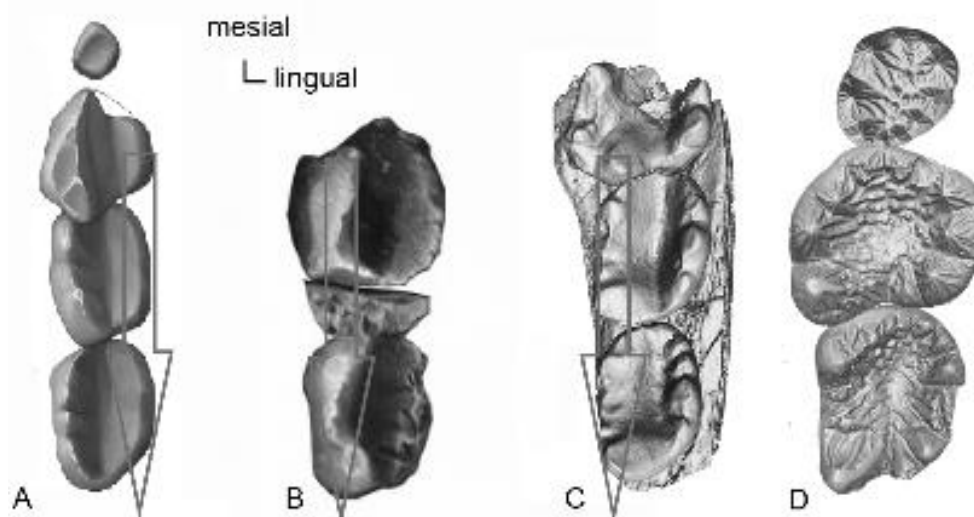
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"Haramiyidans" are enigmatic animals that have commonly been considered relatives of multituberculates (Butler and Hooker, 2005; Hahn and Hahn, 2006) and possibly also gondwanatherians (Krause et al., 2014). These groups are generally thought to form the clade Allotheria, within Mammalia, although alternative views exist (Luo et al., 2015). Members of this group, such as *Thomasia*, represent some of the oldest known mammals, with most species occurring in the Jurassic. For many decades, haramiyidans were known only from isolated teeth. More recently, however, skeletal material was reported for eight haramiyidan species, representing six genera, from the early Late Jurassic Linglongta phase of the Yanliao Biota, China. These include *Arboroharamiya*, *Shenshou*, *Xianshou*, *Maiopatagium*, *Vilevolodon*, and possibly *Megaconus* (Zheng et al., 2013; Zhou et al., 2013; Bi et al., 2014; Meng et al., 2017; Luo et al., 2017; Han et al., 2017). Although these new discoveries have provided significant morphological information about haramiyidans, some critical features, such as the dentition, were only briefly described for most of the taxa.

We have now obtained the detailed morphology of upper and lower teeth from specimens assigned to *Shenshou*, *Xianshou*, and *Arboroharamiya* through more extensive specimen preparation, X-ray micro-computerized tomography (CT) and X-ray micro computed laminography (CL). The new morphological data allow a thorough comparison between the Triassic "haramiyidans", such as *Haramiyavia*, *Thomasia*, and *Theroteinus*, and those of the Yanliao Biota and other Jurassic localities,



**Fig. 1.** Comparison of some euharamiyidan upper teeth in occlusal view. A, *Maiopatagium*; B, *Shenshou lui*; C, *Shenshou* sp.; D, *Arboroharamiya jenkinsi*. The empty arrows in A-C indicate the primary functional cusp row and contrast the occlusal modes between *Maiopatagium* and *Shenshou*. Some images have been photographically flipped for convenient comparison. Photographs are not on the same scale. Sources of figures are from Meng et al. (2017) for A and Bi et al. (2014) for B.

revealing that the Triassic forms are dentally more primitive. Of the Yanliao forms, *Shenshou* exhibits the primitive dental morphology with relatively small cusps A1/a1 on the upper and lower cheek teeth, respectively. In addition, there is significant variation in the dental structures of several specimens which may represent additional species diversity (Fig. 1). Our newly prepared specimens of *Shenshou* sp also show that the tooth morphology of *Shenshou* is similar to that of *Maiopatagium*, confirming a conclusion that was previously based only on the morphology of the upper cheek teeth. However, the unequivocal dental morphology and wear pattern of *Shenshou* also show that its occlusal pattern differs considerably from that of *Maiopatagium*; the former has a multituberculate M2/m2 occlusal mode, whereas the latter has a multituberculate M1/m1 occlusal mode (Fig. 1). Therefore *Maiopatagium* has the most primitive occlusal mode of all the Yanliao euharamiyidans, similar to that suggested for *Haramiyavia* (Jenkins et al., 1997; Luo et al., 2015). This difference in occlusion mode suggests a greater phylogenetic distance between these two genera than between other Yanliao euharamiyidans. Among the Yanliao euharamiyidan species, *Arboroharamiya jenkinsi* (Fig. 1) represents the most derived form in dental morphology and body size, whereas *Xianshou* (possibly including *Vilevolodon*) is morphologically intermediate between *Shenshou* and *Arboroharamiya*. In terms of dental morphology, the general evolutionary pattern of the Yanliao euharamiyidans is characterized by many features, including an increase in the size of P4/p4, P4 becoming basined (compare Fig. 1A and C to D), inflation of cusps A1/a1 on cheek teeth, increase of the number and complexity of enamel fluttings, and modification of occlusal modes; the latter, however, is not fully understood at this point.

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**Choristoderan evolution and distribution** [oral presentation]

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Choristodera is an extinct group of freshwater aquatic reptiles, known from the Middle Jurassic to the Miocene. The group is primarily distributed in Laurasia, although inconclusive jaw fragments were recently reported from the Middle Jurassic of Morocco, North Africa (Haddoumi et al., 2016). Although the chronological range of the group is relatively long, the fossil record is limited and, to date, only eleven genera have been assigned to the group. Three morphotypes are recognized within Choristodera: short-necked longirostrine (neochoristoderes); short-necked brevirostrine and long-necked brevirostrine (non-neochoristoderes). The group shares a unique combination of characters, including a dorsoventrally depressed, cordiform skull and conical subthecodont teeth, and all phylogenetic analyses have supported the monophyly of the clade. Choristodera typically occurred as part of a mesic vertebrate assemblage (including fish, frogs, salamanders, turtles and crocodiles), in relatively warm temperate climates, but they were occasionally distributed in sub-tropical areas and rarely in dry climates (Matsumoto and Evans, 2010).

The position of Choristodera within Diapsida remains uncertain with various hypotheses: on the stem of Archosauromorpha + Lepidosauromorpha (e.g., Evans, 1988, Dilkes, 1998; Gao and Fox, 1998); as stem archosauromorphs (e.g., Evans, 1988, Gauthier et al., 1988; De Braga and Rieppel, 1997); or as sauropterygian relatives (Müller, 2004). This uncertainty is partially caused by a lack of early choristodere fossils. The attribution of the enigmatic Late Triassic *Pachystropheus* (Storrs and Gower, 1993) to Choristodera remains problematic, as the known material shares no unique characters with choristoderes. Thus the first authentic record of a choristodere is *Cteniogenys* from the Middle Jurassic of Europe. The fossil record shows a peak in diversity in the Early Cretaceous of eastern Asia (seven genera, 12 species), especially in the Jehol Biota of China, and also Japan, Mongolia and eastern Siberia. However, understanding the history of this diversification has been limited by a paucity of Jurassic fossils from Asia, namely a few disarticulated postcranial elements from the Middle Jurassic of Siberia and Trans-Baikalian Russia (Averianov et al., 2006) and a possible jaw fragment from the Late Jurassic of Xinjiang, China (Richter et al., 2010). Recently, however, a fully articulated choristodere skeleton was discovered from the Tiaojishan Formation of China, Late Jurassic (Oxfordian) age. This is the first complete Jurassic choristodere recovered worldwide. The newly discovered specimen not only provides important information on the pre-Cretaceous history of the group in eastern Asia, but also on the early evolution of Choristodera.

Determining the interrelationship of choristoderes has been complicated by a lack of consensus as to whether the Jurassic *Cteniogenys* or the Paleocene-Miocene *Lazarussuchus* was the most stemward taxon. However, the inclusion of the new complete Asian Jurassic choristodere in phylogenetic analysis contributes to a stabilisation of ingroup relationships. The results support the position of *Cteniogenys* as the sister taxon of all other choristoderes. Moreover, the new Asian Jurassic choristodere is placed on the stem of an Asian-European small choristoderan clade (all non-neochoristoderes except *Cteniogenys*). This result may contribute to an understanding of the current hiatus in the European record. The oldest (Jurassic) and youngest (Miocene) records of choristoderes are both from Europe, but there is currently no Cretaceous record (Matsumoto et al., 2013). If, as the new analysis suggests, the European Palaeocene-Miocene *Lazarussuchus* is the sister taxon of small Asian choristoderes (monjurisuchids, hyphalosaurids), choristoderes may have re-invaded Europe

from Asia after primitive Jurassic genera like *Cteniogenys* became extinct. This needs, of course, to be tested by the recovery of further European and Asian choristoderes. Nonetheless, the new Jurassic choristodere from Asia has improved our understanding of choristoderan diversity, morphology, evolution and distribution.

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**Original compounds in copal and amber from the Cretaceous to the Recent: preliminary data for investigating the preservation of defensive chemicals in fossil plants [oral presentation]**

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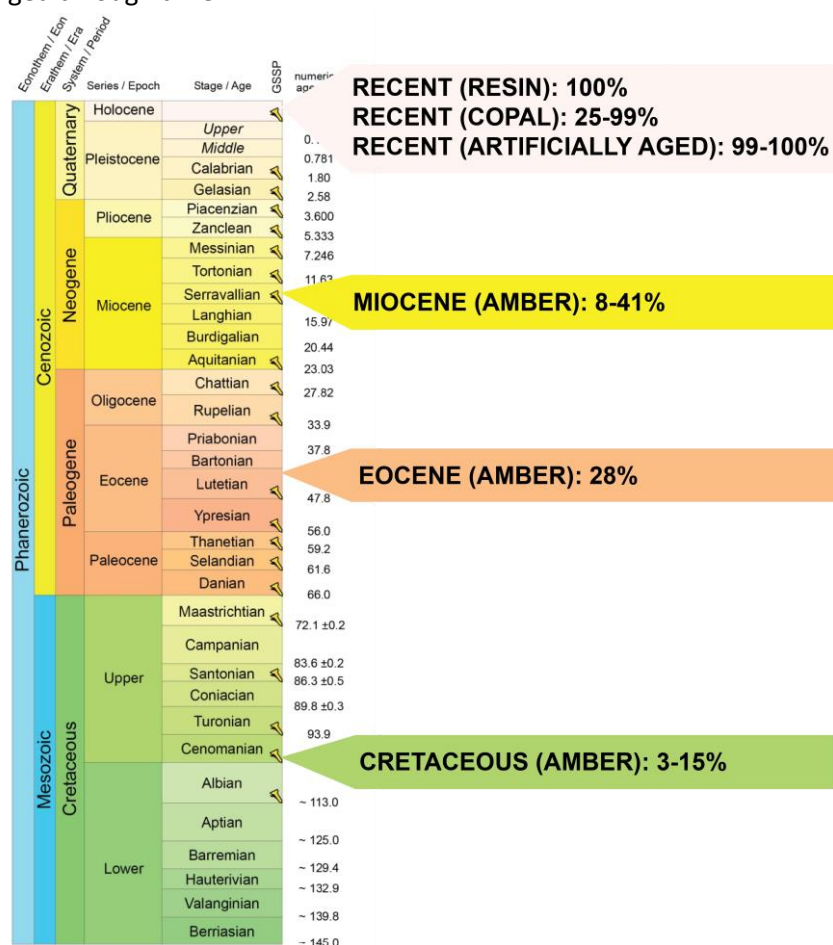
Plant-herbivore interactions are a major component of modern and fossil ecosystems (War et al., 2012). In the fossil record, there is extensive evidence for herbivore attacks on plants but currently only a very limited record of plant defenses against herbivores. The fossil plant defenses are particularly dominated by physical structures such as trichomes, spines, thick cuticle and plant architecture (Labandeira and Currano, 2013). Modern plants also employ a diverse range of complex chemical defenses against herbivores; although fossil plants certainly had chemical defense systems, they have only been studied on the basis of morphological features associated with their use (e.g., Pott et al., 2012). Direct evidence of defensive chemicals in fossil plants would significantly expand our understanding of plant-herbivore interactions in fossil ecosystems.

Here we investigate the preservation and degradation of plant defensive chemicals in amber (fossilized tree resin). Resin is a complex mixture of chemicals, typically dominated by terpenoids and phenols, which is produced by trees as a physical and chemical defense against herbivores, pathogens, and other damage. By understanding how these defensive chemicals preserve and degrade in amber, we can begin to constrain the limits of preservation and degradation of chemical defenses in other types of plant fossils, such as leaves, which could be directly tied to patterns of insect attack.

We obtained samples of resin, copal (subfossil resin), and amber (fossil resin) from the Cretaceous to the Recent and chemically analyzed them using solid phase microextraction gas chromatography mass spectrometry (SPME GC-MS) following standard methods for amber and resin (van der Werf et al., 2014). We identified a total of 128 chemical compounds, and determined which represented original chemical compounds (those found in resin) and which represented diagenetic compounds (those found only in copal or amber). For each sample, we calculated the percent of the sample that was composed of original chemical compounds. We also used principal component analysis (PCA) to compare the overall chemical composition, both original compounds and degraded compounds, of all samples.

As resin fossilizes, becoming copal and then amber, most of the original chemical compounds degrade into more stable diagenetic compounds (e.g., pinene degrades to p-cymene). However, there are some original compounds (such as caryophyllene) that are relatively stable and preserve even in the oldest samples we analyzed. Therefore, although there is a decrease in original chemical compounds through time (Fig. 1), all samples retained remnants of their original chemical composition. Moreover, original chemicals are not lost completely, but rather they are changed into more stable forms which retain some information about the original composition. The PCA indicated which modern resins were most similar to the original resin composition of each copal and amber sample.

These results suggest that it should be possible to find stable remnants of the original chemical defense systems of fossil plants throughout geologic time. For the oldest plant fossils (e.g., Devonian liverworts from the Catskill Delta deposits that are said to preserve oil-body cells, which contain chemical defenses in extant liverworts), the presence of stable diagenetic compounds could be used to determine what structures once contained defensive chemicals. For younger plant fossils (e.g., leaves from the Urticale family with preserved glandular trichomes from the Cretaceous Hell Creek formation, or leaves from the Eocene Messel deposits exhibiting wound reaction tissue due to insect attacks which, in modern leaves, often contains chemical defenses produced in response to the attack), the most stable original compounds are likely to still be preserved to provide some direct evidence about the composition of the chemical defense systems. Finally, PCA analysis of modern and fossil representatives of a specific taxon could indicate whether or not its chemical defense system has changed through time.



**Fig. 1.** Summary of the preservation of original chemical compounds in resin, artificially aged resin, copal and amber from the Cretaceous to the Recent.

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## New fossils from the Yanliao-Jehol biotas and existing problems related to evolution of the mammalian middle ear [oral presentation]

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Discoveries of Mesozoic mammals from the Jurassic Yanliao and Early Cretaceous Jehol biotas, China, have revealed many important features related to evolution of the mammalian middle ear. These include the ossified Meckel's cartilage (Wang et al., 2001; Meng et al., 2003), a key structure from Jehol fossil mammals, that revealed the transitional stage from the mandibular middle ear to definitive mammalian middle ear. The discovery was accompanied by several findings that provided additional details on the transitional mammalian middle ear (Luo et al., 2007; Ji et al., 2009; Meng et al., 2011). More recently, fossils from the Yanliao Biota presented two distinct configurations of auditory apparatus in euharamiyidans: one with the auditory bones attached to the dentary (*Vilevolodon*) (Luo et al., 2017), and the other with the auditory bones fully detached from the dentary (*Arboroharamiya*) (Han et al., 2017), even though these animals are similar in dental and osteological features. Interestingly, among the auditory bones in *Arboroharamiya*, the surangular was interpreted to be present as one of the auditory bones. These new discoveries have raised various issues on development and evolution of the auditory bones in mammaliaforms. These structures have also generated inconsistent character sets that were used to reconstruct competing higher-level phylogenetic relationships for mammaliaforms that, in turn, predict different origin time and evolutionary modes of mammals.

The existing problems related to the auditory region are several, but the outstanding ones are: 1) presence or absence of the postdentary trough and bones in euharamiyidans; 2) different morphologies of the auditory bones in euharamiyidans and their evolutionary and developmental interpretations; 3) the nature of the surangular in *Arboroharamiya*, and its evolutionary and developmental interpretations; 4) other elements, such as hyoids, in the basicranial region of some euharamiyidans whose identities remain unclear but may affect interpretation of the middle ear structures; and 5) the function of a mandibular middle ear in association with the jaw-joint that is capable of palinal move.

With new specimens and further preparation of specimens that have been briefly reported, in association with X-ray micro-computerized tomography (CT) and micro computed laminography (CL), new evidence emerges and helps to answer some questions related to the issues enumerated above. We confirm lack of the postdentary trough in the dentary of euharamiyidans, which is supported by lack of the anterior limb of the ectotympanic. We confirm the interpretation of the stapes of *Arboroharamiya jenkinsi* (Meng et al., 2016), which is consistent with the unequivocal stapes of *A. allinhopsoni* but contrary to an alternative interpretation (Schultz et al., 2017). We recognize the fundamental differences in morphology and orientation of all auditory bones between *Vilevolodon* (Luo et al., 2017) and *Arboroharamiya* (Han et al., 2017). Some auditory elements of arboroharamiyids and *Shenshou* show comparable morphology, but all differ from those of *Vilevolodon*. A pair of structures similar to the surangular of *A. allinhopsoni* is present in the holotype of *A. jenkinsi* (Zheng et al., 2013), although displaced. An element identified as the hyoid in the holotype of *Xianshou linglong* (Bi et al., 2014) is common in other taxa and co-exists with the

auditory bones in *A. allinohopsoni* (Han et al., 2017) and *A. jenkinsi* (Zheng et al., 2013). The nature of this element is uncertain but it is most probably a hyoid, not an auditory element. Function of the mandibular middle ear in *Vilevolodon* remains an open question. When the powerful lower jaw moves palinally in chewing, the most challenging mechanic issue has to do with the manner in which the relationship between the delicate elements attached to the dentary and those associated with the inner ear is maintained.

Given the current interpretations on the auditory bones and other structures, such as the dentition, euharamiyidans present an extraordinary example for diverse and mosaic evolution of mammals and kin. Further investigation to clarify many uncertain characters would be critical to resolve, if possible at all, the higher-level phylogeny of mammals while allotherians are included.

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## **2D extruded FEA: a novel biomechanical technique on the study of early mammals [oral presentation]**

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The Cenozoic has long been considered the "Age of Mammals"; however, the origins of this incredibly successful group date back to the Late Triassic, meaning that almost 70% of their evolutionary history took place in the Mesozoic (Kielan-Jaworowska et al., 2004). Based on the fragmentary nature of their fossil record, early mammals were long considered generalised insectivores that did not diversify ecologically until after the demise of non-avian dinosaurs. However, recent discoveries of exceptionally preserved fossils, like *Agilodocodon*, *Arboroharamiya* and *Maiopatagium* (Zheng et al., 2013; Meng et al., 2015; Meng et al. 2017), have completely changed our understanding of Mesozoic mammals and suggested that they were more ecologically diverse than previously thought.

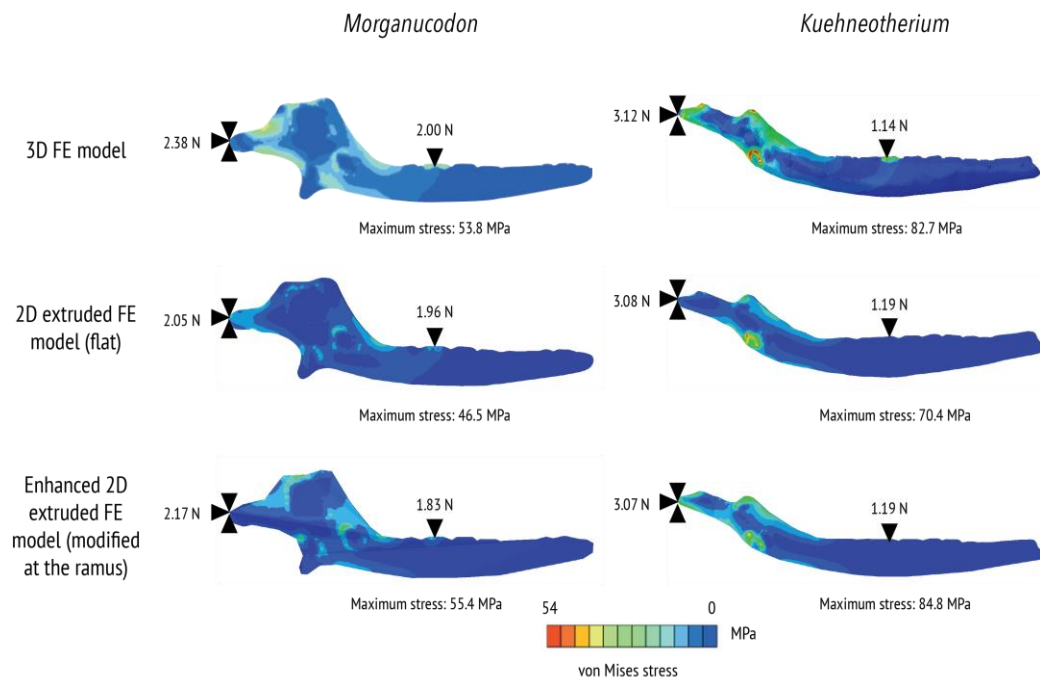
On that basis, Gill et al. (2014) reconstructed the jaws of the Early Jurassic mammals *Morganucodon* and *Kuehneotherium* and analysed them using a suite of techniques, including Finite Element Analysis (FEA) and microwear. As a result, they uncovered previously unknown diversities of feeding functions and dietary ecology among these stem mammals, and concluded that they were not generalised insectivores.

FEA is an engineering technique that has been commonly used in vertebrate paleontology to assess the performance of the skull and/or jaw in response to a feeding load (Rayfield, 2007). This method uses digital models built from computed-tomography (CT) scan data; however, these data can be expensive and are not always easily accessible. Therefore, we have developed and tested a new approach to FEA which we call 2D extruded FEA. In this technique, the models which are analysed are not made from CT scan data, but rather are built digitally from a simple 2D outline of a jaw which is then medially extruded to an average width. We have also developed enhanced 2D extruded models that are digitally manipulated to more accurately represent the 3D geometry of the jaw, particularly at the ramus.

We have validated these models using the Gill et al. (2014) models of the early mammals *Morganucodon* and *Kuehneotherium*. In terms of stress magnitude, both taxa performed well when using the simple 2D extruded FE models, but performed better when using the enhanced 2D extruded models (Fig. 1, Table 1). In terms of strain magnitude and reaction forces at the bite point and the jaw joint (condyle), both models performed well, but with no clear advantage of one over the other (Table 1).

2D extruded FE models for mammalian jaws constitute a reliable, inexpensive and accessible alternative to 3D FE models built from CT scan data. These models are efficient when replicating stress and strain patterns in relatively flat bones, such as mammalian jaws. The use of 2D extruded FEA opens up the possibility of performing large scale studies in a more efficient and economic manner and understanding how the morphology of the mammalian jaw, and its concomitant functionality, evolved through time.





**Fig. 1.** Finite element stress plots of *Morganucodon* (left) and *Kuehneotherium* (right) using 3D FE models built from CT scan data (top) vs. 2D extruded FE models: flat (middle) and enhanced (bottom).

**Table 1.** Comparative stress, strain and reaction forces for *Morganucodon* and *Kuehneotherium* using (A) traditional 3D FE models built from CT scan data, (B) flat 2D extruded models, and (C) enhanced 2D extruded models.

	<i>Morganucodon</i>			<i>Kuehneotherium</i>		
	A	B	C	A	B	C
Maximum von Mises stress (MPa)	53.8	46.5	55	82.7	67.8	84.8
Mean von Mises stress (MPa)	3.99	3.05	3.57	4.21	3.26	3.68
Maximum principal strain	3,100	2,827	2594	4,920	4,250	5,400
Reaction force at the bite point	2.00	1.96	1.85	1.14	1.19	1.19
Reaction force at the condyle (N)	2.38	2.05	2.15	3.12	3.1	3.07

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## **Life history partitioning follows phylogeny amongst Middle Jurassic mammaliaforms [oral presentation]**

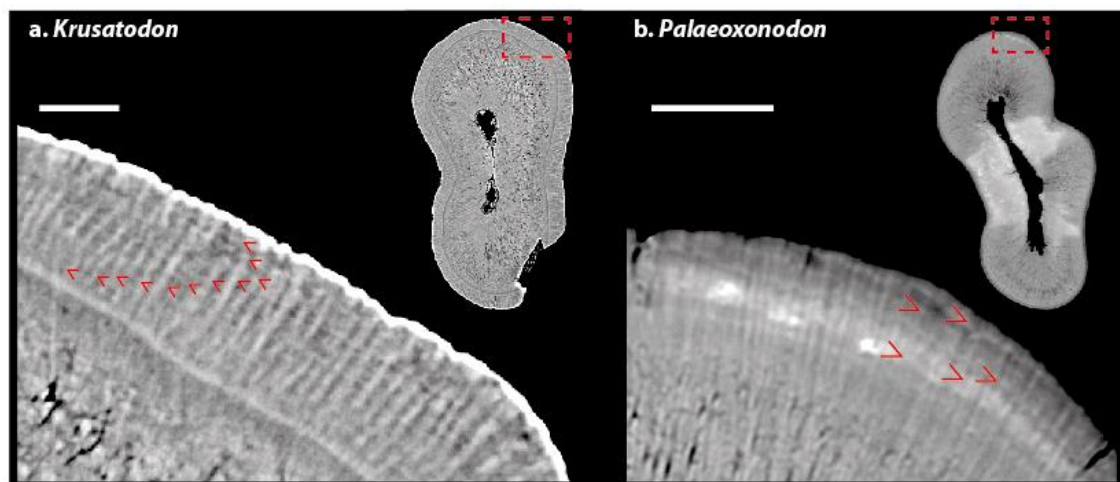
Elis NEWHAM<sup>1</sup>, Pam GILL<sup>2,3</sup>, Philippa BREWER<sup>3</sup>, Philipp SCHNEIDER<sup>1</sup>, Neil GOSTLING<sup>1</sup> & Ian CORFE<sup>4</sup>

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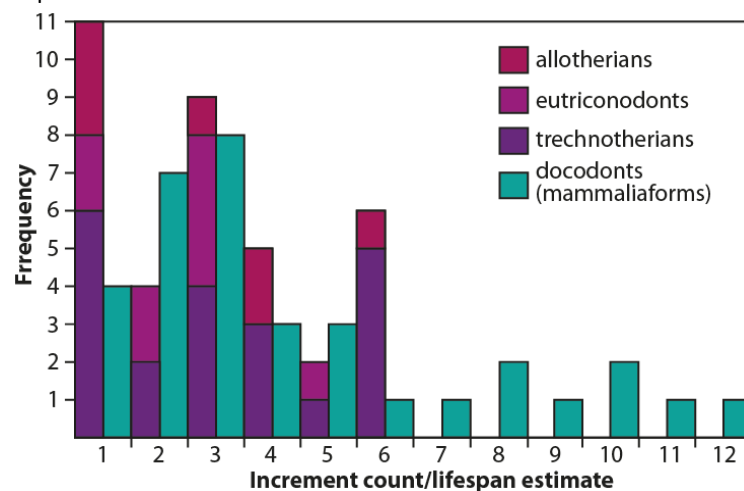
Our understanding of the early radiation of Mammaliaformes during the Late Triassic to Middle Jurassic has rapidly developed over the last decade thanks to a suite of exceptionally preserved fossils (Luo 2007, Han et al. 2017), and the application of state-of-the-art methodologies to explore their phylogenetic and ecological evolution (Newham et al. 2014, Gill et al. 2014, Close et al. 2015). We now have examples of Jurassic mammaliaform taxa occupying an increasingly wide range of highly specialised ecological niches including volant, semi-aquatic, arboreal and fossiliferous forms. Recent studies including these new taxa have suggested that they represent part of a significant adaptive radiation in taxonomic and ecomorphological diversity during the mid-Jurassic, represented by a Mesozoic-wide peak in rates of morphological change during this period (Close et al. 2015). Although the patterns of this diversification are well documented, explanations of its cause remain open to conjecture. It has been hypothesised that the Early-Middle Jurassic adaptive radiation of mammaliaforms may represent the acquisition of a "critical mass" of key anatomical and physiological innovations amongst mammaliaform taxa (Close et al. 2015). This is evidenced anatomically by the independent acquisitions of several critical mammalian anatomical features including pestle-mortar molar occlusion, and mobile "mammalian" middle ear. However, physiological aspects of Jurassic mammaliaform taxa are more difficult to discern.

We have here used synchrotron radiation-based micro-computed tomography (SR CT) to study the fossilised cementum of a large sample of Middle Jurassic mammaliaform taxa from the Bathonian fauna of Oxfordshire (UK), in order to assess and compare aspects of life history. This fauna represents major mid-Jurassic clades, and a split between non-mammalian mammaliaform lineages such as the Docodonta, and crown mammalian clades including Allotheria, Eutriconodonta and Trechnotheria. Cementum is a mineralised dental tissue common to all mammaliaforms found wrapping around the roots of teeth and acting as an attachment complex between teeth and the periodontal ligament. It is unique amongst mineralised dental tissues as its growth is continuous throughout life with a circum-annual periodicity, represented by incremental features of contrasting opacity under transmitted light microscopy (Klevezal 2017). Counts of these increments have been used for decades as a direct estimate of chronological age in extant mammals (Nai et al. 2016).

The finding of cementum increments in SR CT data of Middle Jurassic taxa (Fig. 1) has allowed us to make minimum estimates of maximum lifespan for these groups for the first time, and we find a significant disparity between long-living non-mammalian mammaliaforms (Fig. 1.a) and short-living crown mammals (Figs. 1b, 2). Further, as lifespan has been shown to correlate robustly with basal metabolic rate (Hulbert et al. 2007) and post-natal growth rate (De Magalhães et al. 2007) in extant mammals, the disparity found in these lifespan estimates suggests a dramatic change in metabolic potential between non-mammalian mammaliaform and crown mammal clades. Non-mammalian mammaliaforms retain a metabolically slow life history, with lifespans akin to extant reptiles of similar body mass. Crown mammal lineages in contrast exhibit a life history with significantly lower lifespans and higher inferred metabolic and growth rates, more akin to extant mammals. We suggest that this increase in metabolic potential fostered the rapid rates of evolutionary change found among crown mammals during this period, and so may have facilitated the Early to Middle Jurassic adaptive radiation of crown mammals.



**Fig. 1.** (a) Tomographic reconstruction of a *Krusatodon* (non-mammalian mammaliaform) molar root, with cementum (found wrapping around the root dentine) displaying 11 preserved increments. (b) Tomographic reconstruction of a *Palaeoxonodon* (crown mammal) molar root, with cementum displaying five increments. Scale bars represent 30  $\mu$ m.



**Fig. 2.** Histogram of increment counts for all specimens studied, highlighting the disparity between non-mammalian mammaliaform and crown mammal lifespans.

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## Arthropod damage marks on twigs of the conifer *Patokaea* from the Upper Triassic of Poland [poster presentation]

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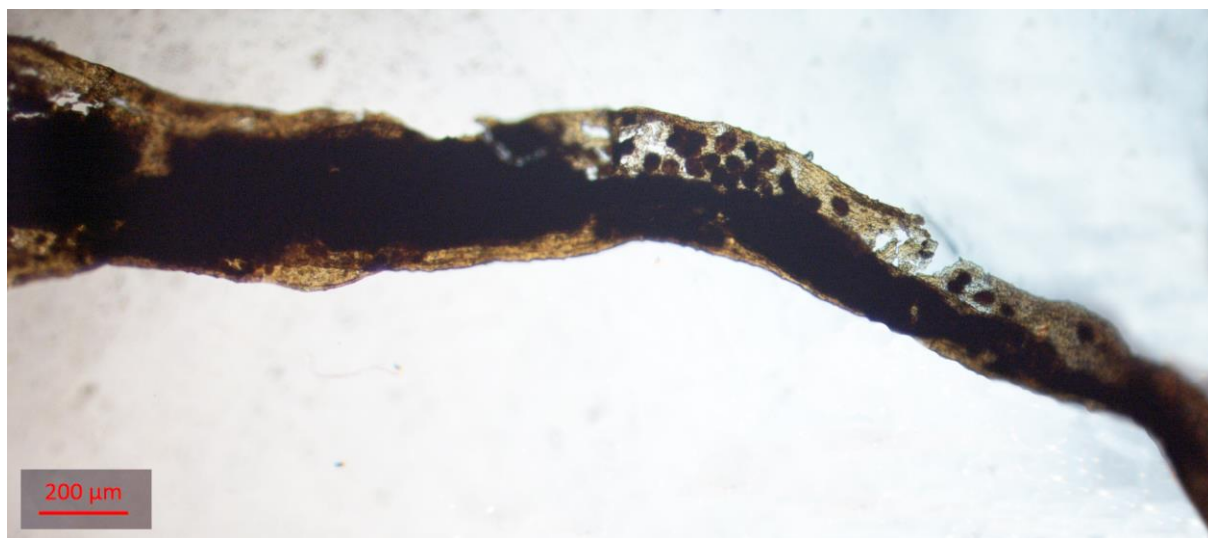
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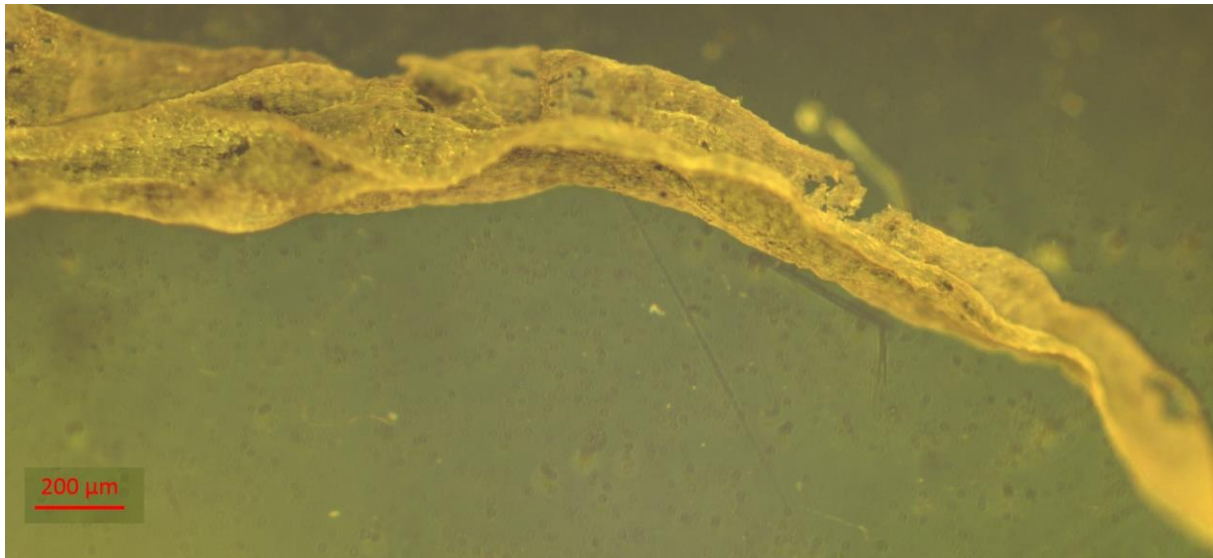
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A new conifer family, Patokaeaceae, comprising one genus and species, *Patokaea silesiaca*, has been recently described from the Upper Triassic of southern Poland (Pacyna et al., 2017). The plant remains are preserved as coalified compressions with well-preserved cuticles. Leafy shoots predominate in the material. The compressed remains were separated from the sediment by treatment with 40% hydrofluoric acid, then washed with distilled water and examined in water using a Leica stereomicroscope. Whilst picking through the leafy shoots, we detected that some were damaged, most probably as a result of arthropod activity. Some leaves are mined and contain elongate masses of frass within the mine that consist of very small, ovoidal coprolites with dimensions of 36µm x 45µm. Also, round holes are sometimes visible on the leaf cuticle, although are absent from mined specimens. Several shoot apices differ from the typical condition described for this species by Pacyna et al. (2017). Altered, atypical shoot apices are shortened, swollen, and their leaves are very densely arranged. This alteration could be an effect of galling by an arthropod, possibly a mite, similar to galls in modern *Picea*. Somehow similarly deformed shoot apices have been described by Amerom (1973) in Carboniferous calamitaleans and are interpreted as galls at the strobilus terminus of calamite axes. The Triassic fossil record of leaf-mining is recorded principally by impressions of galleries and frass on fossil leaves (e.g., Labandeira, 2002; Labandeira et al., 2016), but here we describe frass preserved within leaf cuticles and accordingly interesting new data could be obtained from the *Patokaea* plant.



**Fig. 1.** Apical part of *Patokaea silesiaca* leaf under a light microscope, with the coprolites visible under the translucent cuticle.



**Fig. 2.** The same leaf fragment under epifluorescence, with the cell pattern of the cuticle visible and coprolites inside the cuticle not visible.

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**"Elephant-skin textures" on multiple trackways of ornithopod dinosaurs in Late Cretaceous lake margin deposits, Korea: occurrences and paleoecological implications [poster presentation]**

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The occurrences of "elephant-skin textures" (one of MISS) on multiple trackways of ornithopod dinosaurs and a theropod footprint from Late Cretaceous lake margin deposits, Korea, are described and their origin and paleoecological implications are interpreted. The deposits are well-lithified (hornfelsic) tuffaceous rocks that preserve the footprints. The rocks represent sheetflood deposits consisting of interlaminated fine-grained sandstone to siltstone and mudstone beds with planar- to cross-laminated fine-grained sandstone to siltstone beds. Very thin beds of tuffaceous breccias are intermittently intercalated. The footprint-bearing mudstones are smectitic and in places microbial. Polygonal mudcracks intersecting the footprints are associated and interference ripples with rain prints are observed in the deposits. The paleoenvironment is interpreted as a lake margin where microbial mats could form under semi-arid conditions with alternation of wetting and drying periods. The lake environment might have been influenced by occasional volcanic eruption.

There are five NW-oriented subparallel trackways and one SE-directed trackways of ornithopod dinosaurs. One theropod footprint with opposite direction to those of adjacent ornithopod tracks is also present. Most of the ornithopod footprints are assigned to the ichnogenus *Caririchnium* (Lockley et al., 2006), and some of them to the ichnogenus *Ornithopodichnus* (Kim et al., 2009). The depth of the footprints generally decreases along the trackway, and heel pad prints are more deeply impressed than digital prints, indicating that dinosaurs walked out of a water-saturated area.

The elephant-skin textures occur selectively in the dinosaur footprints. Polygons of the elephant-skin textures are mostly about 1 to 2 cm in diameter, and their flattened ridges are a few mm in width. The polygons are varying in surface morphology: subrhombic polygons with flattened ridges, irregular polygons with flattened ridges, irregular polygons with pointed ridges, subcircular polygons with rounded ridges, sublinear ridges, and regular polygons with flattened ridges. The selective occurrence of the elephant-skin textures in footprints and their variation between footprints of the same trackway suggest that they could be the transformed skin impressions by repetition of swelling and shrinkage of the smectitic muds with microbes due to alternation of wetting and drying. The development of elephant-skin textures in every footprints observed in this area suggests that the multiple trackways with subparallel orientation by ornithopods were printed simultaneously, implying truly gregarious behavior of ornithopods.

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**Preparation methods for ultrastructural and *in situ* chemical and biochemical analyses on carbonaceous compressions using fossil feathers as an example** [oral presentation]

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The skeleton fossil record has the advantage of relative continuity throughout geological time, while the rare "soft-bodied" fossils provide much more complete data for a biological view, not only providing critical morphological characters to test hypothesis of phylogeny of the organism, but also carrying biochemical or molecular data related to the evolution of the organism (Briggs, 2003; Schweitzer, 2011; Briggs and Summons, 2014). Therefore, a combination of morphological, chemical and molecular data gleaned from soft-bodied fossils makes a great contribution to understand the evolutionary history of the organisms.

Soft-bodied fossils are preserved as various types, e.g., impressions, casts, permineralizations, and compressions. Different techniques should be applied to the various preservation modes. Herein, we focus on soft-bodied fossils preserved as carbonaceous compressions (Butterfield, 1990). In compressions, the soft tissues are preserved as a thin carbon film (the film has some thickness, so it is a 3-Dimensional rather than 2-D), and it is usually distinct from underlying sediments in color, texture, and chemistry (Schweitzer, 2011). Besides permineralization, carbonaceous compressions are one of the most common preservation pathways. Most of the plant fossils, which are actually a variety of isolated organs, such as leaves, fruits and seeds, wood, flowers and pollen grains, are preserved as carbonaceous compressions (Gupta et al., 2006; Witkowski et al., 2012). There are also some resistant but not biomineralized tissues of invertebrates, such as cuticles of graptolites, chelicerates and insects, however, that may survive as carbonaceous compressions too (Briggs, 1999; Gupta and Briggs, 2011). In vertebrates, however, the integumentary tissues, such as skins, scales, feathers and fur also commonly occur as carbonaceous compressions in the fossil record (Pan et al., 2013). Although carbonaceous compressions have been known as organic fossils for many years, the unusual material and poor sensitivity and resolution of analytical techniques prevented conclusive study on the ultrastructural and indigenous chemical and molecular characters.

Here, we described methods for preparing carbonaceous compressions for combined microscopic observation and chemical and biochemical analyses, collecting the most information from the least amount of sample destruction. We use fossil feathers preserved as carbonaceous compressions from the Lower Cretaceous Jehol Biota as an example, including six aspects: 1) sampling; 2) microscope and electron microscope observation and documentation; 3) demineralization; 4) embedding with a preferred orientation, and polymerizing; 5) semi-thin sections for histological studies, immunolabelling tests and NanoSIMS analyses; 6) Ultra-thin sections for TEM and immunoelectron labelling tests and ChemiSTEM chemical analyses.

Combining these methods, i.e., electronic microscopy observations on ultrastructures, light microscopy observations on the histological sections, elemental composition mapping, and immunohistochemistry tests only a tiny sample is needed.



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## The mammal-rich freshwater assemblage of the Middle Jurassic Kilmaluag Formation, Isle of Skye, Scotland [oral presentation]

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The Kilmaluag Formation in Scotland represents a predominantly freshwater environment of Bathonian age, with a mixed autochthonous and allochthonous vertebrate assemblage. Vertebrate fossils reveal a diverse Middle Jurassic fauna with similarities to the Forest Marble Formation at Kirtlington Quarry, England (Evans et al. 2006). Ongoing field work on Isle of Skye has expanded upon published faunal lists, and indicates a richer fauna of small vertebrates than previously recognised, including numerous mammals, squamates, and salamanders. Mammal genera represented so far include: *Wareolestes*, *Boreolestes*, *Krusatodon*, *Palaeoxonodon*, and *Phascolotherium*. Unlike at other Middle Jurassic sites, we have yet to recover any multituberculates or haramiyids, suggesting a marked difference in faunal composition between the Kilmaluag Formation and the Kirtlington site and elsewhere.

Unlike Middle Jurassic sites in England, and Late Jurassic sites in Portugal and North America, microvertebrate fossils from the Kilmaluag Formation are most often recovered as associated skeletons or skeletal elements. This is partly preservational, but is also the result of the dense dolomitised limestone of the Kilmaluag Formation, that does not react strongly to acid preparation. Specimens must therefore be found by eye, cut from the exposure, and visualised using micro-CT or synchrotron scans. In situ fossils therefore tend to retain their anatomical associations within the matrix, and with minimal damage - unlike the disarticulated remains picked-through after bulk processing by acid. While spectacular vertebrate fossil skeletons are also being recovered from Jurassic sites in China, specimens in the Kilmaluag Formation are preserved in three-dimensions, with minimal deformation. This makes them of great value for morphological study and quantitative analyses such as geometric morphometrics. Such analyses are hampered in the compressed specimens typical of many Chinese sites.

We provide an updated faunal list including recent finds from fieldwork and publications over the last decade. We compare the composition of the mammalian fauna of the Kilmaluag Formation to those of the Middle Jurassic Forest Marble Formation in England, and the Tiaojishan Formation in China. We also draw comparisons with the Late Jurassic Morrison Formation of the United States and Guimarota Formation of Portugal, highlighting that the mammal fauna of the Kilmaluag Formation shows no multituberculates and haramiyids to date. We discuss the influence of collection bias on the faunal lists: with bias towards more complete, associated remains over single teeth and skeletal elements such as those found in bulk-processed sites such as Kirtlington Quarry. Finally we outline evidence for the taphonomic setting of the Kilmaluag Formation. This includes evidence for a predominantly freshwater lagoon environment without significant current action, with infaunal bioturbation of fossil remains, and the possibility of a scatological source for some of the recovered mammal remains.

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## The earliest known hynobiid (*Liaoxitriton daohugouensis*) from the Jurassic of China [poster presentation]

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*Liaoxitriton daohugouensis* was established on two specimens preserved as ventral impressions from the Middle/Late Jurassic deposits of Inner Mongolia, China (Wang, 2004). The same fossil horizon has yielded exquisite fossils of feathered dinosaurs, pterosaurs, lizards, mammals and invertebrates that are referred to as the Yanliao Biota (or Daohugou Biota) (Carroll and Zheng, 2012; Gao and Shubin, 2003; Evans et al., 2005; Evans and Wang, 2009; Sullivan et al., 2014; Wang, 2004; Wang and Rose, 2005; Zhang, 2002. Zhou and Wang, 2017). Due to preservation conditions, the dorsal anatomy of *L. daohugouensis* is largely unknown and the taxonomic position has varied in different phylogenetic analyses. Recently, five new specimens, preserved as skeletons and impressions on part and counterpart slabs, have been recovered from the same locality and horizon of *Liaoxitriton daohugouensis* and can be referred to the species based on a series of characteristics, such as vomers in contact at the midline and posterolaterally bordering a large palatal fenestra; vomerine tooth row short, slightly arched and transversely oriented; and pterygoid triradiate with a robust anterior ramus; three hyobranchial elements ossified, with Hypobranchial II and Ceratobranchial II paired and rodlike, and Basibranchial II single and trident shaped; the coracoid portion of the scapulocoracoid strongly expanded; and the trunk vertebrae amphicoelous and ribs uncapitate. The new specimens also provide more osteological information and allow us to re-diagnose the species and to re-evaluate its phylogenetic position. The following characteristics can be added to *L. daohugouensis*: dorsal process of premaxilla in contact with nasal; nasals broad with midline contact; lacrimal and prefrontal present; parietal-prefrontal contact absent; quadrate absent; parietals with no midline contact, separated by a narrow slit; angular present. Some characteristics are noteworthy, such as the presence of a separate angular in the mandible, the presence of lacrimals, vomerine tooth row oriented transversely and arched anteriorly, and the presence of uncapitate ribs. All of these morphological characters indicate that *L. daohugouensis* is closely related to the Hynobiidae and may represent the earliest fossil record of this family.

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## Review of the theropod dinosaur fauna from the Late Jurassic – Early Cretaceous of Thailand and Southeast Asia and its biogeographic implications [oral presentation]

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In Southeast Asia, at least fourteen non-avian theropods have been reported so far. They are dominantly found in the northeastern Thailand, however, one bizarre theropod has been described from Laos, one reported from Malaysia and one recently reported from Myanmar. The temporal distribution of Southeast Asian theropod ranges from the Late Jurassic to the Early Cretaceous.

There are two large-bodied metriacanthosaurids (=sinraptorids) from the Phu Kradung Formation (≈Late Jurassic) of Thailand (Buffetaut and Suteethorn, 2007). Seven non-avian theropods from the Sao Khua Formation (≈Late Barremian) of Thailand are described, including a fragmentary, small-bodied compsognathid (Buffetaut and Ingavat, 1984), the spinosaurid *Siamosaurus suteethorni* which based on isolated teeth (Buffetaut and Ingavat, 1986), an ostrich-mimic dinosaur *Kinnareemimus khonkaenensis* (Buffetaut et al., 2009), a partial maxilla of a large-bodied carcharodontosaurid (Buffetaut and Suteethorn, 2012); a probable basal coelurosaur *Siamotyrannus isanensis* (Buffetaut et al., 1996; Samathi, 2003); and two newly reported, undescribed mid-sized megaraptorans which look similar to *Fukuiraptor* from Japan. Two theropods from the Early Cretaceous Khok Kruat Formation (≈Aptian) of Thailand include an undescribed spinosaurid and an undescribed carcharodontosaurian. One spinosaurid from Laos named *Ichthyovenator laosensis* is recorded from the "Grès supérieurs" Formation which is equivalent to the Khok Kruat Formation (≈Aptian) of Thailand (Allain et al., 2012). Recently, two spinosaurid teeth from the late Early Cretaceous of Malay Peninsula are correspondingly reported. One coelurosaur and enantiornithine birds preserved in amber were also reported from the mid-Cretaceous of Myanmar (Xing et al., 2016a; 2016b; 2017; 2018).

All non-avian theropod faunas from Southeast Asia consist of non-maniraptoran tetanurans (with exception of the coelurosaur and birds from Myanmar). They show similarity to Chinese plus Japanese theropods during the Early Cretaceous in broad systematic terms. During this time, megaraptorans can be found only in Japan, Australia, and Thailand, whereas tyrannosauroids can be found in China, Europe, and possibly Brazil and Australia. Spinosaurids, carcharodontosaurians, and some coelurosaurs were almost cosmopolitan. Metriacanthosaurids, on the other hand, were endemic to Asia including China and Thailand and Europe during the Middle to Late Jurassic.

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## A gigantic marine ostracod trapped in Burmese amber (mid-Cretaceous of Myanmar) [poster presentation]

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The Burmese amber (or 'Burmite', ~99 Ma, Myanmar), widely known for exquisite preservation of a mid-Cretaceous terrestrial fauna including dinosaur remains and birds (e.g., Xing et al. 2016, 2017), also yields marine fossils and microfossils which can provide important contextual information on paleoenvironment and amber formation. The first Cretaceous ostracod recorded in amber (Xing et al., 2018) is a 'gigantic' representative of the exclusively marine group Myodocopa. Subsequent resin flows in the amber specimen, containing terrestrial arthropods and insect frass, resolve an enigmatic taphonomic pathway.

Ostracods are aquatic microcrustaceans, with a calcareous, bivalved shell (carapace). They are usually small (0.5–2 mm), with well-calcified carapaces that provide an excellent fossil record extending to at least the Ordovician (~485 million years ago). Ostracods are rarely encountered in amber, and the few examples known derive from Eocene and Miocene amber deposits. While earlier finds concern single non-marine freshwater specimens from the Eocene Baltic amber (Keyser and Weitschat, 2005; Keyser and Friedrich, 2017 and references therein), the multilayered Miocene amber near Chiapas, Mexico, revealed a diverse ostracod fauna with hundreds of specimens dominated by brackish water species (e.g., Matzke-Karas et al., 2017).

Our first finding of a valve of a 'gigantic' (12.9 mm) marine ostracod in a specimen of Burmese amber (Fig. 1) effectively doubles the age of the ostracod amber record but also offers the first representative of the Subclass Myodocopa (Ordovician to recent) in amber, an exclusively marine and weakly calcified group with a poor fossil record (Xing et al., 2018). However, lacking soft parts and the complementary right carapace valve combined with a broader range of carapace features and examples of morphological stasis, restrict our inferences at lower taxonomic level.



**Fig. 1.** Amber specimen DIP-V-17118 (28 x 19 x 17 mm) in natural light with lateral view of ostracod specimen (12.9 mm in length, left valve, anterior end to the left) clearly visible. Orange dot (arrow) represents the eye tubercle, dark brownish spots are insect frass particles (©Lida Xing, China University of Geosciences).

The amber that constitutes our specimen was produced under two distinct sets of conditions. Subsequent resin flows in the amber specimen contain terrestrial arthropods (spider fragments) and insect frass. The 'marine' resin flow that contains the ostracod is relatively clear and is separated by a prominent drying line from a secondary 'terrestrial' resin flow that contains multiple, dark, organic particles of insect frass, as well as the fragmentary remains of spiders. These features resolve an enigmatic taphonomic pathway which seems to be much less elaborate than scenarios for inclusion of aquatic (freshwater mostly) organisms in amber proposed before and support a marginal marine setting for resin production. The resin was probably released underwater or at the water's edge, encapsulating the ostracod, then the resin mass dried subaerially for a significant length of time before a subsequent resin flow captured a range of terrestrial inclusions. This combination of marine and terrestrial resin flows may have been brought about by variation in water levels, a mechanism proposed in the study of modern marine organisms preserved in resin (Schmidt and Dilcher, 2007) and invoked for other Cretaceous ambers with marine contents (Perrichot et al., 2010). While many sites of the mid-Cretaceous Burmese amber exhibit marine influences (marine fossil content), full paleoenvironmental and geological details for the numerous amber-producing sites in the Kachin state of Myanmar have yet to be reported.

In addition to its significance of the Burmese amber deposits as important archive for mid-Cretaceous terrestrial life and biodiversity, our find of the oldest ostracod preserved in amber that also belongs to a marine group with a poor fossil record emphasizes the significance and further potential of these deposits as archive for contemporaneous marginal marine life and biodiversity.

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## Cretaceous non-marine integrated stratigraphy - a view from the ostracodologist's perspective [oral presentation]

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Despite general progress in chronostratigraphic and geochronologic methodology and research in non-marine (here used for 'continental' aquatic or limnic, and terrestrial palaeoenvironments and deposits) Upper Jurassic and Cretaceous deposits worldwide, age assignment as well as regional and particularly supra-regional (inter-basinal to intercontinental) correlation of these remain widely insufficient. While for the youngest Mesozoic marine record stratigraphic resolutions up to Milankovich scales (405, 100 kyr eccentricity cycles) have been achieved, age assignments of Late Jurassic to Cretaceous non-marine successions are, in contrast, often less accurate than stage level, thus implying large errors of several to many million years. This is not at all adequate, particularly as to supra-regional correlation of non-marine deposits among one another, their correlation with marine successions, and their geochronological linking. Late Mesozoic non-marine stratigraphy, therefore, only finds its way into the Global Geological Timescale (GTS) very slowly. As a consequence, tremendous non-marine archives – such as the world's largest Upper Jurassic and Lower Cretaceous highly fossiliferous, non-marine archive, the North American Western Interior foreland basin (e.g., Sames et al., 2010) – remain practically excluded from being considered relevant for the global stratigraphic record, for high-resolution timescales and for progress in global Late Jurassic to Cretaceous stratigraphy. In addition, the existing options and potential of higher-resolution integrated non-marine (ostracod) biostratigraphy have not yet been appropriately recognized.

Non-marine ostracods (Fig. 1) are among – if not *the* – most common microfossils in late Mesozoic non-marine deposits and, consequently, one of the most useful groups for e.g. biostratigraphic and palaeoenvironmental application. This results from the combination of major adaptive radiations of important groups in the Late(st) Jurassic to Early Cretaceous.



**Fig. 1.** Example species of two important genera used for regional and supraregional biostratigraphy in Upper Jurassic, and Lower Cretaceous ('Purbeck–Wealden interval') successions. Left: *Theriosynoecum fittoni*, right: *Cypridea setina*. Scale bar: 100  $\mu$ m, specimens to scale.



The application potential of Late Jurassic–Cretaceous non-marine ostracods, not only but particularly as a tool for (regional) biostratigraphy, has long been known. However, the practical implementation particularly to supra-regional biostratigraphy was and is still strongly hampered by an often confusing and contradictory literature with respect to taxonomy, phylogeny and palaeoenvironmental interpretation, having led to a plethora of regional taxon names to deal with.

During the last decades, modern insights into non-marine ostracod palaeobiology and palaeobiogeography (including considerations of *per se* substantial intraspecific variations in the carapace, and their nature, as well as passive reproductive and dispersal strategies) and new data have expedited the process of taxonomic revision and facilitated new approaches and tests for prior hypotheses of supra-regional to global distribution of certain non-marine ostracods (e.g., Sames, 2010; Sames and Horne, 2012; Trabelsi et al., 2015). Based on this, we can now overcome the previously presumed major drawbacks to the biostratigraphic utility of non-marine ostracods, i.e., their endemism and strong facies control. This allows us to better deal with the immense complexity of the non-marine record in that we can undertake supra-regional correlations, and correlate between different facies. Such approach must include the consideration of the potential diachronic nature of facies correlations, since the local occurrence and stratigraphic distribution of taxa may owe more to local environmental changes than to sequential evolutionary changes. Then correlations based on the ranges of these taxa may be spurious and would hamper (regional) chronostratigraphic correlations at higher resolution; although the repeated occurrence or dominance of taxa might carry potential for cyclostratigraphic use (see below). Therefore, supra-regional correlations work at the cost of (the mostly just presumed high local to regional) chronostratigraphic resolution. However, starting from the resulting supraregional stratigraphic ties, stratigraphic resolution can then regionally be increased in a next step by integration with other chronostratigraphic methods and proxies.

While we make progress in heading for a global biostratigraphic approach, our goal of global taxonomic concepts appears achievable but not to be reached quickly. Based upon the above the next further steps, going hand in hand, are: a) the revision of the ostracod taxonomy at 'classic' (e.g., the English Purbeck–Wealden, West African and Brazilian 'Wealden') and new (e.g., Songliao Basin, China) significant sites of non-marine (ostracod bio-) stratigraphy; b) the utilization of the ostracods themselves for integrated chronostratigraphic analyses in that assemblage changes and certain ecophenotypic features of which the control factors are known, are reanalyzed and tested for cyclostratigraphic use; c) the regional integration of non-marine ostracod data with other stratigraphic and geochronologic data; and d) the interpretation and application of resulting data on a supra-regional to global scale.

With my talk I am going to give a short, critical synopsis on the state-of-the art, ongoing projects, and near future perspectives illustrated by selected examples.

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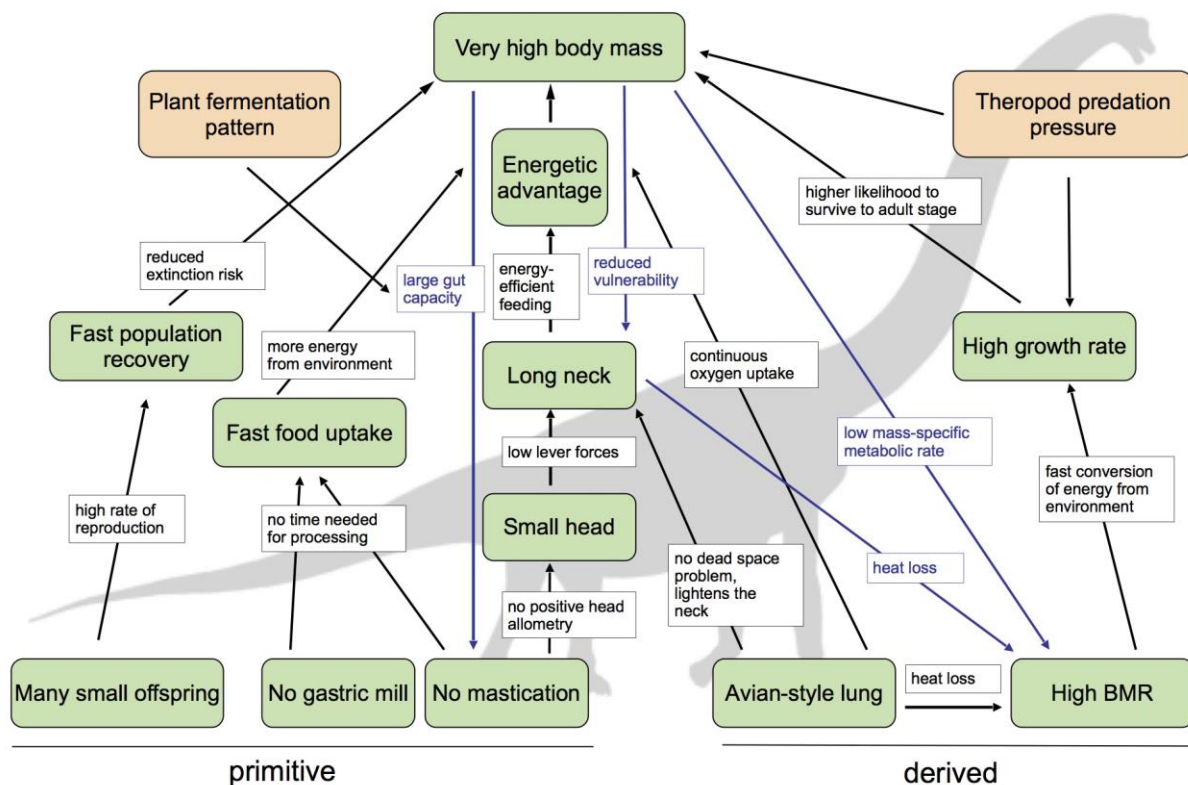
## An evolutionary cascade model for sauropod dinosaur gigantism [oral presentation]

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Sauropod dinosaurs are a group of herbivorous dinosaurs which exceeded all other terrestrial vertebrates in mean and maximal body size. Sauropod dinosaurs were also the most successful and long-lived herbivorous tetrapod clade, but no abiological factors such as global environmental parameters conducive to their gigantism can be identified. These facts justify major efforts by evolutionary biologists and paleontologists alike to understand sauropods as living animals and to explain their evolutionary success and uniquely gigantic body size. Contributions to this research program have come from many fields and can be synthesized into an evolutionary cascade model (ECM; Sander 2013) of sauropod dinosaur gigantism (Fig. 1).



**Fig. 1.** Evolutionary cascade model explaining the gigantism of sauropod dinosaurs, the giant long-necked herbivores of the Jurassic and Cretaceous. The model is divided into three stages of increasing complexity. The green boxes contain observed or inferred biological traits and characteristics. Some traits are plesiomorphic for sauropods, while others are derived. Such traits appear as key innovations in the model. The black arrows indicate hypotheses of evolutionary causation, with selective advantages indicated. The blue arrows are hypotheses of evolutionary feedback loops, and the selective advantages driving the feedback loops appear in blue print. Inter-guild competition is indicated in the model as carnivorous (theropod) dinosaur predation pressure. However, intra-guild competition, that is, competition between individuals and species of the same niche (in this case: herbivores) is the general underlying principle of the model, where improvement of efficiency is overruling feedback loops (escalation *sensu* Vermeij 2013). Note the central position of the small head-long neck cascade. Modified from Sander et al. (2011).

An evolutionary cascade model combines two or more evolutionary cascades that have shaped the evolution of a lineage. The model will reveal the complex interplay of evolutionary constraints and historical contingencies that have allowed a lifestyle or an adaptation to develop (Sander et al. 2011, Sander 2013). Note that an evolutionary cascade model is a flow diagram, and not a network diagram, which is what sets it apart from earlier approaches such as the correlated progression concept of Kemp (2007) in which links between different traits were hypothesized without evolutionary sequence nor causation. However, in an evolutionary cascade model, the interplay of evolutionary cascades is made clear. Each cascade is made up of a sequence of biological traits in which one trait is the logical prerequisite for the next one, indicating the action of natural selection. These traits can be either plesiomorphic, or primitive, at the level of the group in question or represent evolutionary innovations. In evolutionary cascade models with extinct animal groups, which represents the majority in tetrapods, some of the traits need to be inferred from paleobiological evidence. Feedback loops in the ECM consist of selective advantages originating from traits higher in the cascades but affecting lower traits.

The sauropod gigantism ECM (Fig. 1) consist of five separate evolutionary cascades ("Reproduction", "Feeding", "Head and neck", "Avian lung", and "Metabolism"). Each cascade starts with observed or inferred basal traits that either may be plesiomorphic or derived at the level of Sauropoda. Each trait confers hypothetical selective advantages which permit the evolution of the next trait. All cascades end in the trait "Very high body mass". Each cascade is linked to at least one other cascade. Important plesiomorphic traits of sauropod dinosaurs that entered the model were ovipary as well as no mastication of food. Important evolutionary innovations (derived traits) were an avian-style respiratory system and an elevated basal metabolic rate. Comparison with other tetrapod lineages identifies factors limiting body size.

An evolutionary cascade reflects the effects of macroevolutionary constraints and the periodic overcoming of certain constraints by evolutionary novelties or key innovations. The concept of an evolutionary cascade transcends the concept of evolutionary novelties and key innovations because it identifies multiple primitive traits, key innovations, and causations that have shaped the evolutionary history of a group and therefore aims at a comprehensive representation of the interplay between constraints and the overcoming of them in the evolutionary history of a lineage. The evolutionary cascade approach is a historical one, essentially a narrative, and does not claim to predict future evolutionary events. However, the evolutionary cascades approach is of heuristic value because it helps in formulating hypotheses of evolutionary causation. A crucial quality of evolutionary cascades from a paleontological perspective is that they predict the sequence of appearance of traits, which then can be tested against the sequence observed in the fossil record and inferred from phylogenetic analysis.

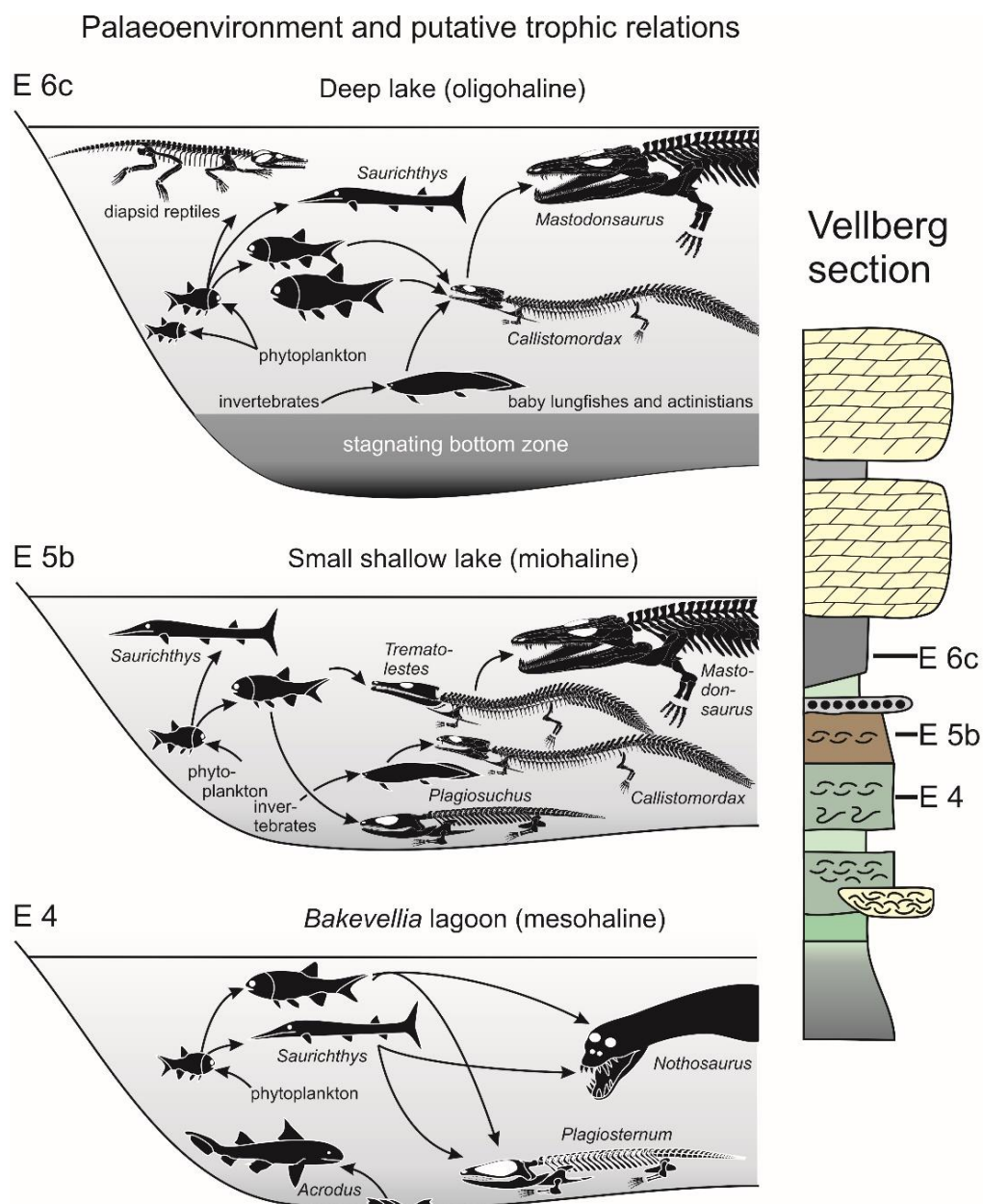
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**The vertebrate deposits of Vellberg (Middle Triassic, Germany) [oral presentation]**Rainer R. SCHOCH<sup>1</sup>

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The Middle Triassic was a crucial time for the evolution and diversification of tetrapods, but few vertebrate deposits are known from that time window. The Lower Keuper of Southern Germany, which is of Ladinian age, has contributed many new tetrapod taxa in the last three decades. Next to the rich deposits of Kupferzell, the most productive *fossilagerstaette* is the limestone quarry near Vellberg-Eschenau, some 25 km SE of Kupferzell. There, a sequence of 30 cm (Fig. 1, E4–6) yielded rich fish, temnospondyl, and reptile faunas in three successive lake horizons (Schoch and Seegis, 2016). The sequence starts with a lagoonal deposit (E4) bearing a brackish fauna that includes *Nothosaurus*, *Plagiosternum*, sharks and euhaline bivalves. Locally, the lagoon was replaced by a small eutrophic and miohaline lake (E5) inhabited by the temnospondyls *Mastodonsaurus* (top predator), *Kupferzellia*, *Trematolestes*, *Callistomordax*, and *Plagiosuchus*, in addition to some 15 bony fish taxa. In that lake, temnospondyls evidently hatched and grew up, but this water body was small and laterally replaced by swamps. In the top of the sequence, a stronger stratified, probably somewhat deeper lake (E6) contained a similar temnospondyl fauna, but in addition to the fishes and amphibians it was inhabited or frequently visited by diapsid reptiles, such as a 40 cm long choristodere, the archosauriform *Jaxtasuchus*, the stem-turtle *Pappochelys*, and the rauisuchian *Batrachotomus*, among other still undescribed taxa (Schoch, 2015; Schoch and Sues, 2015). This lake deposit also preserves numerous terrestrial tetrapods, such as owenettid parareptiles, lepidosauromorphs, rhynchocephalians, and a variety of archosauriforms; the absence of synapsids and rhynchosaurs is noteworthy, as is the abundance of putative fish-eaters. The lake measured at least 5 km, was populated by lungfish and coelacanthid babies, and many skeletons show extensive evidence of predation. At the top of the sequence, a carbonatic shore facies was deposited, in which occasional skeletons of *Batrachotomus* occur. Repeated drying of water bodies is evident in the lagoonal (E4) as well as the stratified lake (E6) deposit, whereas bonebeds indicate prefossilization and reworking.



**Fig. 1.** Studied section at Vellberg quarry (~1 m), with three main fossiliferous beds indicated (right). Putative lake properties and reconstructed trophic relations mapped for each water body.

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**Reconstruction of mandibular shape in *Docodon victor* and testing of different chewing motions using 3D virtual simulation software Occlusal Fingerprint Analyser (OFA) [oral presentation]**

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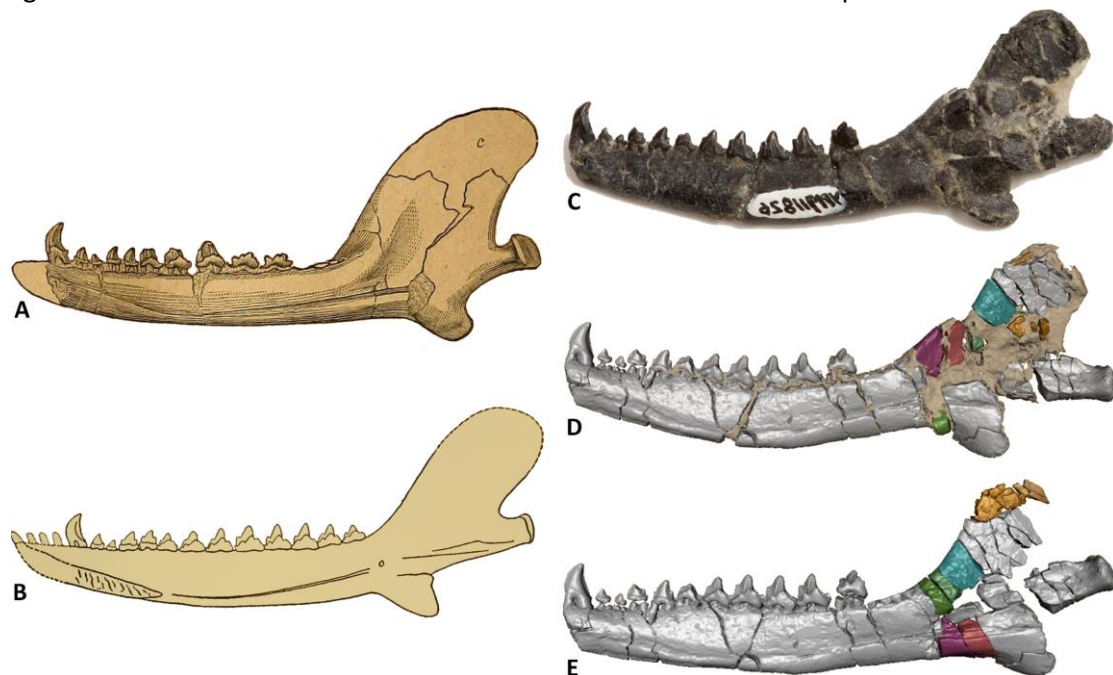
Docodonts were widely distributed geographically in the Middle Jurassic and their remains are relatively common in fossil sites of Europe and Asia (e.g., Kermack et al. 1987; Sigogneau-Russell 2003; Martin and Averianov 2004, Meng et al. 2015). During the Late Jurassic, docodonts further expanded to other parts of the Laurasian landmass (e.g., Lillegraven and Krusat 1991; Pfretzschner et al. 2005; Rougier et al. 2015). Although less diverse, some docodonts survived into the Early Cretaceous (e.g., *Sibirotherium* Averianov and Lopatin 2015). Docodont fossils discovered in the last twenty years reflect high ecomorphological diversity within this group (e.g., Ji et al. 2006; Ruf et al. 2013; Luo et al. 2015).

*Docodon* has been a key taxon of comparative, functional, and morphological studies of mammaliaform mandibles and teeth. We therefore re-examined dental and mandibular remains of *Docodon* from Yale Quarry 9 of the Morrison Formation at Como Bluff, Wyoming (Late Jurassic), using Computed Tomography (CT) scans and 3D image analyses. Our results support a long-held notion that the multiple species of *Docodon* from the same quarry were over-split. We thus formally propose that the specimens examined in this study should be synonymized under *Docodon victor*. The OFA analysis of *Docodon* supports the hypothesis that its lower jaw had a significant palinal (backward directed) component in a distolingual chewing movement. *Docodon* very likely shows a derived chewing pattern evolved within Docodonta. The posterior-directed component in the occlusal trajectory of *Docodon* is functionally convergent to the one found in unrelated traversodontid cynodonts, tritylodontids, and multituberculates.

In addition, our CT-based forensic analysis demonstrates that the peculiar mandibular shape of the *Docodon* holotype YPM-VP011826, as previously illustrated, is mainly caused by the inaccurate restoration of tiny fractured fossil pieces, manually glued back together. After identifying the correct positions of the pieces and matching the fractures virtually, the restored mandible of *Docodon* is very similar to better-preserved mandibles of other docodonts. Thus, mandibles of Late Jurassic docodonts varied far less than previously believed. We were able to trace the ontogenetic change of the Meckel's sulcus in mandibles having different stages of tooth eruption. In the youngest juvenile mandible, the Meckel's sulcus extends into the symphyseal region, but retreats posteriorly in adult mandibles, suggesting a change of Meckel's element during the ontogeny. The last molar of adult individuals erupts anterior to the base of the coronoid process, while the succeeding teeth erupt lingual to the coronoid in younger individuals. We interpret the medial ridge protuberance overhanging the postdentary trough to be the attachment site for M. temporalis profundus. The position of the ectotympanic notch on the posterior aspect of the mandibular angle indicates a different structural relationship of ectotympanic and mandible from those of other non-mammalian mammaliaforms.

We tested two alternative historical interpretations of chewing motions in *Docodon* using the OFA. The virtual reenactment of the palinal (distolingual) chewing movement postulated by Gingerich (1973) shows large wear surfaces matching during occlusion and less shift in the direction

and inclination of the movement. In comparison, the virtual reenactment of a proal (forward) chewing movement as postulated by Jenkins (1969) shows less matching contact areas for the same upper and lower molars. The latter movement also requires stronger deflections in the jaw trajectory during the transverse movement out of occlusion after maximum intercuspatation.



**Fig. 1.** The lower jaw of *Docodon victor*. A) Illustration from Marsh (1887), B) illustration from Simpson (1929), C) photograph of glued specimen YPM-VP011826 in the Peabody Museum of Natural History collection (mirrored), D) 3D surface of YPM-VP011826, grey = bone, light brown = glue, colored pieces = misplaced pieces, and E) corrected positions of colored pieces.

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**Vertebrate fauna of a fissure filling from the Lower Cretaceous (Barremian–Aptian) of Balve, Westphalia, Germany** [poster presentation]

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The Sauerland area in the southern part of Westphalia is dominated by Devonian deposits including reef limestones ('Massenkalk') from the Middle to Upper Devonian. The Massenkalk underwent fundamental karst processes during the Mesozoic and Cenozoic. Although karst fissures and caves are not rare in the Sauerland, most of their pre-Pleistocene fillings are barren. Some are known to yield fossils, but these cases are heterogeneous in their ages: examples include a Pliocene site near Eisborn (Wirth 1970), a spore-pollen assemblage dating another locality in the same region as Miocene (Richter et al. 2014), and a terrestrial filling at Brilon-Nehden, correlated with the Lower Cretaceous (Norman 1987, Norman and Hilpert 1987).

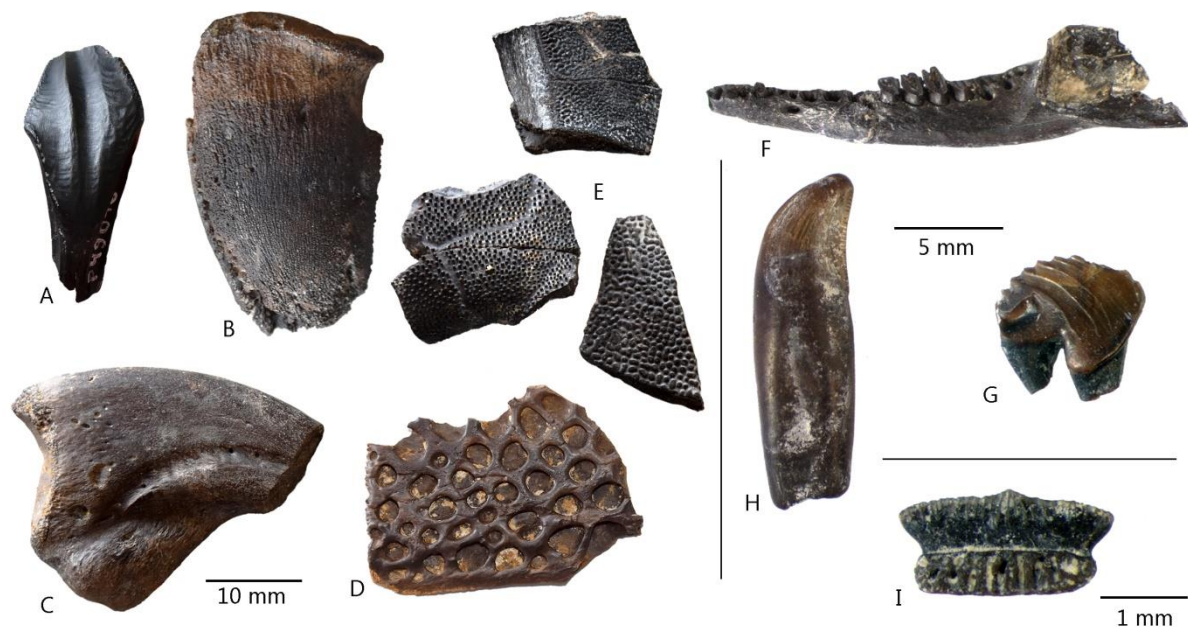
This study is based on fossils from a Lower Cretaceous fissure filling at another promising site, Balve, also at the northern edge of the Sauerland. The karst cavity was formed hydrothermally, probably prior to the Jurassic (Drozdowski et al. 2017). The filling mainly consists of clayey-silty sediments and sandy layers. Herein, we compare fossils collected to date (excavations at Balve are ongoing) with those from other renowned sites in Europe, including the localities in nearby Brilon-Nehden, as well as Bernissart, southwestern Belgium. Excavations at the Bernissart coal were made more than 100 years before those in the Sauerland/Brilon-Nehden, but both sites are well known for their well-preserved and articulated *Iguanodon* and *Mantellisaurus* skeletons (Godefroit 2012, Norman and Hilpert 1987). The vertebrate fauna of Bernissart also includes several osteichthyan taxa, a few amphibians, turtles (e.g., *Peltochelys duchastelii*, *Chitrasephalus dumonii*), and crocodiles (e.g., *Goniopholis* and *Bernissartia*), as well as a number of unidentified theropod remains. In contrast, the Brilon-Nehden site yielded a less diverse array of vertebrates: fragmented fish-specimens, a few postcranial fragments of chelonians, rare and poorly preserved elements of *Goniopholis*, and one disarticulated specimen each with affinities to hypsilophodontid and theropod dinosaurs.

The fissure filling of Balve includes both floral and faunal elements. Thus far, the flora is restricted to spore and pollen remains, as well as fragments of charcoal. Based on the former, a late Barremian–Aptian age is proposed for the filling (Lanser and Heimhofer 2015). The vertebrates are represented mainly by disarticulated bones and teeth belonging to diverse assemblage including a wide range of taxa. The record so far includes hybodontiform chondrichthyans (Lonchidiidae), osteichthyans, amphibians, small reptiles, turtles (*Helochelydra?*), crocodiles (Goniopholididae, Bernissartiidae, Atoposauridae), pterosaurs (Ornithocheiridae?; cf. Lanser 2015), saurischian (Coelurosauria; Tyrannosauroidae, Dromaeosauridae; Lanser and Heimhofer 2013) and ornithischian (Iguanodontia, Hypsilophodontidae, Ankylosauria) dinosaurs as well as mammals (Dryolestidae, Multituberculata, and symmetrodont taxa).

A striking taphonomic filter significantly constrained the fossils to sizes less than about a decimeter in maximum dimension. The vertebrate remains consequently display a size ranging from sub-millimeter to several centimeters. Most bones are preserved as fragments only. Whereas the vertebrate fossils from the fissure filling at Balve are incomplete and have limited morphological information, their quantity and high diversity of the fossils are remarkable. A detailed systematic analysis will reveal faunal correlations not only with the sites mentioned above but also with the English Wealden and with other European sites. In this context, the diverse fossil fauna and flora



from Balve stands to become an important element of the Lower Cretaceous ecosystems of Western Europe, and basis for assessing palaeobiogeographical patterns in the Northern Hemisphere.



**Fig. 1.** Vertebrate remains from the Barremian-Aptian of Balve: A *Iguanodon* tooth, B *Iguanodon* phalange, C theropod phalange (aff. *Eotyrannus*), D crocodile dermal scute, E chelonian fragments (*Helocheilydra?*), F dryolestid lower jaw with three preserved teeth, G multituberculate premolar, H theropod tooth, I Lonchidiidae tooth.

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**A high-latitude Early Cretaceous vertebrate fauna from Yakutia, Russia** [oral presentation]

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Although there are hundreds of localities that have yielded dinosaurs and associated vertebrates (dinosaur faunas) around the world, only few of them derive from Mesozoic polar or sub-polar paleolatitudes (Rich et al., 2002). Most of these localities are from the Late Cretaceous, and only four are Late Jurassic-Early Cretaceous in age; of these, three are situated in the Southern Hemisphere. The only Early Cretaceous locality from the Northern Hemisphere is the Teete site in northern Yakutia, Russia, which was previously known for subpolar dinosaurs (Rich et al., 1997, 2002). The high latitude (polar) dinosaur faunas of the Southern Hemisphere are comparably well studied, while the vertebrate assemblage from Teete is poorly known (Rich et al., 2002). So far, primitive actinopterygian fishes, frogs, salamanders, lizards, choristoderes, various dinosaur groups (ankylosaurs, theropods, sauropods, and stegosaurs), and tritylodontid synapsids had been recognized in the Teete vertebrate assemblage (Kurzanov et al., 2003; Lopatin, Agadzhanyan, 2008; Kolosov et al., 2009). The fishes, amphibians, lizards, and choristoderes from Teete have remained undescribed and their affinities are uncertain. The assignment of the dinosaur specimens to particular taxa (e.g., ?*Stegosaurus* sp., cf. *Camarasaurus*, *Allosaurus* sp., *Coelurosauria* fam. indet.) was based on the study of few isolated teeth (Kurzanov et al., 2003) and requires a reassessment on the basis of more reliable material. The only named vertebrate taxon from Teete — the tritylodontid synapsid *Xenocretosuchus kolosovi* Lopatin and Agadjanian, 2008 — was recently attributed to the genus *Stereognathus* Charlesworth 1855 (Lopatin and Agadjanian, 2008; Kolosov et al., 2009; Averianov et al., 2017). Remains of choristoderes from Teete have been identified as *Choristodera* indet. (Skutschas and Efimov, 2015; Skutschas and Vitenko, 2017).

In 2017, P. Skutschas, R. Schellhorn, and D. Vitenko conducted new field work at the Teete locality. They screen-washed 500 kg of fossiliferous matrix and recovered numerous vertebrate microfossils. According to previously known and newly collected material, the high latitude assemblage of Teete includes palaeonisciform and amiid fishes, two salamander taxa (a large stem salamander and a small crown salamander), lizards, primitive (= non-neochoristoderan) choristoderes, turtles, various dinosaurs (stegosaurs, ornithomimids, theropods, and sauropods), the tritylodontid synapsid *Stereognathus kolosovi*, and three mammalian taxa (haramiyid cf. *Sineleutherus* sp., a new genus and species of tegotheriid docodont and a new genus and species of eutriconodontan). The purported Lower Cretaceous age of the fossiliferous sediments at the Teete locality is inconsistent with the mammalian, tritylodontid, salamander and dinosaur components of vertebrate assemblage. These elements have a distinctive Jurassic appearance, being similar to the Middle-Late Jurassic vertebrate assemblages known from Siberia (Russia), Xinjiang (China), and Great Britain. If the dating of the Teete locality proves to be correct, this may be explained by stable environmental conditions in North Asia and a smooth transition from the Jurassic to Cretaceous

biotas, in contrast to the environmental perturbations that occurred in other regions at the Jurassic/Cretaceous boundary (Tennant et al., 2017).

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## Plant-fungal interactions in Mesozoic forest ecosystems - evidences from China [oral presentation]

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In extant terrestrial ecosystems, fungi as saprotrophs, mutualistic symbionts, parasites and pathogens, establish series of ecological and co-evolutional interactions with other organisms (Kiers and Denison, 2008; Perotto et al., 2012). Among those complicated interactions, plant-fungal interactions occur at multiple levels and contribute to shape plant communities and the ecosystems they comprise (Krings et al., 2012). As a large part of the extant biological world, fungi have a remarkably long evolutionary history (Tiffney and Barghoorn 1974; Taylor and Krings, 2005, 2010; Taylor et al., 2014). Interestingly, many of the fungal fossil records are associated with permineralized plant remains (Taylor et al., 2009). Structurally preserved petrified woods not only play roles in understanding the floristic composition and evolution of the plant kingdom in geological history, but also contribute to revealing the complex interactions between plant and other organisms in terrestrial ecosystems, including fungi. Abundant and diverse Mesozoic petrified wood has been described in China (Zhang et al., 2006; Wang et al., 2009, 2017; Yang et al., 2013). Most of these previous studies on Chinese Mesozoic petrified wood focused mainly on their anatomy and systematics; whereas, rare attention has been paid the fungal remains associated with them and their interactions with the host (Hsü, 1953; Feng et al., 2015).

In the past few years, numerous well-preserved fungal remains represented by fungal mycelia were found within Mesozoic petrified wood from various horizons throughout China, including the Lower Triassic of Inner Mongolia, the Middle Jurassic of west Liaoning Province, Chongqing City and Tibet, in the Lower Cretaceous of west Liaoning, Heilongjiang and Zhejiang Provinces. Besides fungal hyphae, some fungal mycelia also bear delicate asexual spores (e.g., intercalary/terminal chlamydospores and conidiospores), which contribute to understanding the evolution of asexual reproduction of the fungi. Taxonomically, some of these fungal remains are referable to the Basidiomycota, since they bear typical clamp-connections; while some other are difficult to determine. Palaeoecologically, most of them are interpreted as saprobes of the forest ecosystem, since typical wood decay characters can be recognized in the wood tissues of their host. Judging from wood-rotting characteristics, some of them are white-rot fungi, while some others are brown-rot fungi. Of interest, in an Early Cretaceous coniferous wood from western Liaoning Province, numerous tyloses of different developmental stages were found. The formation of these tyloses is presumed to be triggered by fungal infection as a physiological restraint to the invasion of the fungus. In other words, such a fungus might be a pathogen.

In conclusion, the current new findings of fungal remains in China contribute to understanding the diversity and asexual reproductive behaviors of Mesozoic fungi, and shed light on revealing complex plant-fungal interactions in Mesozoic forest ecosystem.

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## Diet and trophic level reconstruction of extinct avian and non-avian dinosaurs using Ca isotopes [oral presentation]

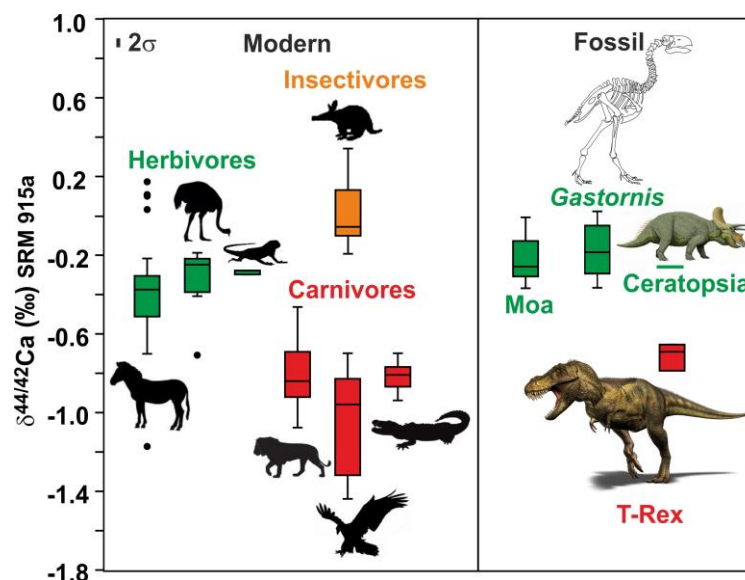
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Bones, teeth and eggshells are valuable chemical archives that record the isotope compositions of food and water ingested by the animal. If their isotope composition is not biased by chemical alteration during fossilisation processes, it can provide valuable insights into the palaeobiology and palaeoecology of extinct vertebrates. Non-traditional stable isotope systems (e.g., Ca, Mg, Zn) were recently applied to distinguish between faunivorous and herbivorous taxa and determine the trophic level in food webs (Skulan et al., 1997; Heuser et al., 2011; Jaouen et al., 2016; Martin et al., 2015a, 2015b, 2017; Hassler et al., 2018). Especially calcium isotopes ( $^{44}\text{Ca}/^{42}\text{Ca}$  expressed as  $\delta^{44/42}\text{Ca}$  value) are a promising deep time diet proxy that is resistant to diagenetic alteration because with 38wt% Ca is the major element in bioapatite of bones and teeth, therefore (unlike for all other trace elements), even fossil bone can preserve original isotope compositions (Heuser et al., 2011; Martin et al., 2017). Calcium isotopes enable us to distinguish both meat- and even insect-feeders from plant-feeders (Fig. 1). Consumption of bone rich in light calcium isotopes as well as the fractionation of calcium isotopes during bone biomineralization results in lower bone  $\delta^{44/42}\text{Ca}$  in carnivores than in herbivores (Skulan and DePaolo, 1999). The consumption of animal tissues (i.e., bone) causes consumer  $\delta^{44/42}\text{Ca}$  values to decrease systematically with each trophic level along the food chain (Skulan et al., 1997; Clementz et al., 2003, Martin et al., 2015b). Calcium isotope analysis of bones and teeth thus enables us to reconstruct the diet of extinct vertebrates, their niche partitioning, the length of food chains and fossil food webs as well as to identify apex predators (Heuser et al., 2011; Hassler et al., 2018; Fig. 1).



**Fig. 1.** Bone  $\delta^{44/42}\text{Ca}$  values of modern and fossil vertebrates from different feeding categories and ecosystems all measured at the MPI for Chemistry in Mainz. A similar trophic level effect ( $-0.5 \pm 0.1\text{‰}$ ) between herbivores and carnivores was found for modern mammals, birds and reptiles. Faunivores and herbivores can thus be distinguished by  $\delta^{44/42}\text{Ca}$ : Insect-feeders > plant-feeders (both browsers and grazers) > carnivores. Fossil bones from two extinct giant flightless birds (Moa and *Gastornis*) have herbivore-like  $\delta^{44/42}\text{Ca}$  while enamel  $\delta^{44/42}\text{Ca}$  confirm T-Rex as apex-predator.

Here, we assess whether extinct non-avian and avian dinosaurs ingested bone by analyzing the calcium isotope compositions of their bones and teeth, comparing them with those of sympatric carnivorous and herbivorous taxa as well as modern-day mammals, birds and reptiles. Our  $\delta^{44/42}\text{Ca}$  data for the extinct *Gastornis*, traditionally viewed as a giant terror bird, demonstrate that it was in fact a herbivore similar to a Moa, and not a bone-crushing carnivore like T-Rex (Fig. 1). The Late Cretaceous theropods *Tyrannosaurus rex* and *Albertosaurus* were consuming significant amounts of isotopically light bone tissue and have compared to sympatric plant-eating dinosaurs lower  $\delta^{44/42}\text{Ca}$  values. T-Rex has the lowest  $\delta^{44/42}\text{Ca}$  similar to those of extant carnivorous mammals, birds and reptiles (Fig. 1) confirming its role as top predator in Maastrichtian ecosystems. In contrast, *Allosaurus* from the Late Jurassic Morrison Formation has  $\delta^{44/42}\text{Ca}$  values overlapping with those of sympatric sauropods, suggesting that this theropod presumably ingested predominantly meat and less than 1-2% bone. This is in line with morphological, biomechanical and faecal evidence demonstrating that *T-Rex* had a very high bite force and clearly was capable to crush and ingest bone while in contrast the skull of *Allosaurus* was more fragile and he probably avoided bone.

After the dinosaur extinction the ecological niche of terrestrial apex-predators was vacant and filled (at least in the Palaeogene of South America) by large, carnivorous "terror birds", the Phorusrhacidae. The giant flightless ground bird *Gastornis* was one of the largest tetrapods in Paleocene-Eocene terrestrial ecosystems in both Eurasia and North America. Based upon its huge skull and ferocious beak, capable of exerting a bite forceful enough to crush bone, it has mostly been reconstructed as a fearsome predator similar to a terror bird. However, its diet is controversial and plant-feeding has also been suggested. Here we demonstrate that *Gastornis* has bone  $\delta^{44/42}\text{Ca}$  similar to those of herbivorous ground birds, such as extant ratites and the extinct moa, but much higher than modern-day most carnivorous raptors (except the griffon vulture, which avoids bone), indicating that it did not ingest any significant amount of bone. Clearly, *Gastornis* was an herbivore and not the carnivorous apex predator often-portrayed in Paleocene-Eocene terrestrial food webs. Thus, *Gastornis* did not replace theropod dinosaurs as a hypercarnivore in Paleogene terrestrial ecosystems.

Overall, calcium isotopes are a promising dietary proxy to investigate transitions from animal- to plant-feeding in the Permo-Triassic, to reconstruct Paleozoic/Mesozoic key food webs and the evolution of herbivory. This is ongoing research funded by the ERC under the European Union's Horizon 2020 research and innovation programme (ERC CoG grant agreement No 681450).

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**Cretaceous Burmese amber biota** [poster presentation]Bo WANG<sup>1</sup>

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Burmese amber (amber from northern Myanmar) contains the most diverse biota of all Cretaceous amber so far. During the last 100 years, Burmese amber has received worldwide scientific interest; more than 300 families of arthropods plus diverse plants and vertebrates have been reported.

Burmese amber has been known for nearly 2000 years, and it has been traded with China since Han Dynasty times (202 B.C. to 220 A.D). The first reported animal inclusions in Burmese amber were presented between 1917 and 1922 by Dr. Cockerell in the Natural History Museum, London. The renaissance in Burmese amber research started at the very end of 20th century and the investigations on inclusions of Burmese amber are now in full bloom. Recently, amber and its inclusions have been thoroughly investigated, with international collaborations that have resulted in prolific papers and reports published on the identification and description of numerous fossil inclusions.

We have re-investigated this biota based on new, abundant fossils and got some new and surprising discoveries. We found a number of arthropod groups that are rare or extremely rare in amber, e.g. crabs (Brachyura), camel spiders (Solifugae), whip-scorpions (Thelyphonida), and onychophorans (Onychophora). Insects are the most common group in Burmese amber and show a remarkable mixture of basal and derived forms. Flowering plants were flourishing and diversifying, the insects that fed on the flowers were also flourishing and diversifying, and the predators that fed on the insects (spiders, lizards, mammals, and birds) were flourishing and diversifying. The stories of plants, insects and other invertebrates, and predator interactions documented in Burmese amber offer an unprecedented view into the co-evolution of insects and plants, the evolution of pollination, adaptations to various types of food and habitats, and the formation of recent ecosystems and biotas.

Although the list of exciting discoveries is long, only about 20% of the inclusions have been formally described from Burmese amber. Therefore the Burmese amber biota requires much more extensive and detailed taxonomic investigation.



## A new eobaatarid multituberculate from the Jehol Biota and implications for multituberculate phylogeny [poster presentation]

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Fossil record of Eobaataridae is relatively sparse despite its world-wide distribution (Kielan-Jaworowska et al., 2004). A few well-preserved eobaatarid specimens have been recovered in the Jehol Biota and the Fuxin Biota to date (Hu and Wang, 2002; Kusuhashi et al., 2009, 2010). Recently, a new multituberculate specimen (IVPP V17949), preserved as half skeleton (including skull and forelimbs), has been discovered in the Jiufotang Formation at the Xiaotaizi site, Jianchang County, Liaoning Province, China (Fig. 1). The specimen shows many characteristics of eobaatarids, such as a dental formula of  $3\cdot0\cdot5\cdot2/1\cdot0\cdot3\cdot2$ , lower incisors gracile, 9 serrations of p4, asymmetric tooth crown of m1–2 with lingual margin shorter than labial and with coalescing cusps, M1 with a distinct posterolingual ridge, I3 transversely wide. The specimen differs from all known eobaatarids in having a unique combination of dental features: 9 serrations of p4, m1–2 cusp formula 3:2, two rows of cusps in P5 with three large cusps in lingual row and 3–5 low cusps in the labial row, I2 with a posterior cuspule. The new taxon displays cranial features that are shared with *Sinobaatar lingyuanensis*, including relatively slender nasals, narrow frontals, large lacrimals, V-shaped frontoparietal suture, and transversely wide parietals. The magnum contacts Mc III and IV, and the unciform contacts Mc IV and V in the specimen, as they do in *Sinobaatar lingyuanensis*. The cuneiform contacts Mc V, similar to *Kryptobaatar* and different from *Sinobaatar lingyuanensis* (Hu and Wang, 2002; Minjin, 2008). Based on the comparisons of manual morphology and phalange indices with extant terrestrial and arboreal mammals, the manual digit III in new taxon has a phalange index of 105%, larger than Late Cretaceous *Kryptobaatar dashzevegi* (81%) and close to that in *Sinobaatar lingyuanensis* (108%) and *Rugosodoan eurasiaticus* (117%) (Luo et al., 2016). We hypothesize that the new multi was a terrestrial mammal with a moderate phalange index among multituberculates. Based on a new character matrix, phylogenetic analysis reveals that the new taxon has affinity to eobaatarids and that it is closely related to *Sinobaatar*. Phylogenetic results also yield better resolution of both plagiaulacidan and cimolodontan phylogeny.



**Fig. 1.** New eobaatarid specimen (IVPP V17949). A, skeleton in dorsal view; B, skull in ventral view; C, left forelimb in dorsal view.

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**Ostracods from the Upper Cretaceous Jiaozhou Formation of Zhucheng, Shandong, China and their biostratigraphical and palaeoenvironmental significance** [poster presentation]

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Abundant fossil ostracods have been recovered from Mesozoic non-marine sediments over a vast area of China including the Jiaolai Basin, a late Mesozoic fault basin in the Jiaodong Peninsula, East China. Cretaceous strata are well developed in the Jiaolai Basin, yielding abundant fossils such as hadrosaurids, tyrannosaurs, various types of dinosaur eggs, bivalves, gastropods, ostracods, clam shrimps, insects and plants. However, few studies have focused on the ostracods. During a geological investigation in Zhucheng City, eastern Shandong Province, East China, we found a new exposure of the Jiaozhou Formation, which constitutes the uppermost part of the Cretaceous–earliest Paleogene strata (encompassing the K/Pg boundary) in the Jiaolai Basin. Samples from the exposed Jiankou section near Jiankou Village, Zhucheng City, yielded abundant ostracods assigned to twelve genera and twenty-seven species, reported for the first time from the Jiaozhou Formation in this area. The assemblage is composed entirely of non-marine taxa, including species of *Cypridea*, *Talicypridea* and *Candoniella*. An ostracod biostratigraphical study indicates this section to be Campanian–early Maastrichtian in age; the upper part of the Jiaozhou Formation therefore potentially contains the K/Pg boundary, but unfortunately it is not exposed at present. A palaeoenvironmental analysis of the species composition of the assemblages obtained, combined with a study of valve ornamentation, suggest fresh to oligohaline water with an increase in water depth and salinity through the Jiaozhou Formation during the Campanian.

**A long-armed confuciusornithid bird from the Early Cretaceous Jehol Biota further increases ecomorph diversity of the Confuciusornithidae [oral presentation]**

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Confuciusornithidae arguably is the most specimen-rich clade of Mesozoic birds with thousands of individuals in public and private collections worldwide. This avian group plays a central role in understanding the evolution of the avian horny beak and pygostyle. The known specimens of confuciusornithids are mainly from the Early Cretaceous Jehol Biota in northeastern China, with a few specimens from contemporaneous deposits in North Korea, showing that this clade persisted at least 11 million years (130.7 Ma-120 Ma). The numerous specimens reveals that this avian group is readily distinguishable from other basal birds in having robust toothless upper and lower jaws, a fused scapulocoracoid, and a tiny claw on the middle manual digit, among other features. Here, we report a new taxon of the Confuciusornithidae from the Early Cretaceous Jehol Biota, northeastern China. This new bird, surprisingly, has a normal major digit claw as in other basal birds, which was likely independently regained during the course of the evolution of the Confuciusornithidae based on our phylogenetic study. Unfortunately, the biological significance of this trait is unclear due to the lack of analogues in modern birds, in which manual claws completely lost in adults. The taxon is further differentiated from other confuciusornithids in having proportionally much longer forelimbs. Our morphometric analysis indicates that the morphospace of the Confuciusornithidae, with the addition of the new taxon, is greatly broadened to a degree that it overlaps with that of Early Cretaceous Ornithuromorpha and Enantiornithines, indicating that the morphological diversity of confuciusornithids is greater than previously thought.

## Advances in the study of the herpetological fauna from the Lower Cretaceous of the Greater Khingan Mountains in NE China [oral presentation]

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In the past five years, numerous vertebrate fossils (amphibians, reptiles, and birds), especially many well-preserved amphibian specimens (Anura and Caudata), have been discovered from a new locality in the Greater Khingan Mountains area of Nei Mongol in northeastern China (Wang et al., 2014; Wang et al., 2015; Jia and Gao, 2016; Gao and Chen, 2017). Typical elements of the well-known Jehol Biota, *Eosestheria*, *Ephemeropsis trisetalis* and *Lycoptera*, are found at this locality, indicating the fossil horizon is of similar age to the Jehol Biota (i.e., Early Cretaceous) and that the fauna is probably part of the biota (Wang et al., 2017). This new locality expands the distribution of the Jehol Biota far to the north, and the faunal composition is slightly different from that of Jehol Biota in western Liaoning and northern Hebei. To date, two vertebrate taxa, *Genibatrachus baoshanensis* (Anura) and *Nuominerpeton aquilonaris* (Caudata), have been named and described from the new locality (Gao and Chen, 2017; Jia and Gao, 2016). *G. baoshanensis* was established based on eight specimens and, as a stem member of the Pipanura, it differs from the frogs (*Liaobatrachus*) of western Liaoning. *N. aquilonaris*, although given an extensive morphological and ontogenetic description, was not discussed in detail in terms of its systematic position. Many well-preserved articulated specimens of *Genibatrachus baoshanensis* and *Nuominerpeton aquilonaris*, of different developmental stages, were discovered in the past two years. These have the potential to provide detailed data on the morphology and ontogeny of these species, and to better evaluate their phylogenetic position. Moreover, several turtle specimens were also discovered, enriching the faunal diversity of this locality.

All the studied material was collected from the Pigeon Hill locality, Baoshan Town, Molidawa Qi, Nei Mongol, including 124 frog, 86 salamander, and 10 turtle specimens. These are now deposited in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing. All the specimens were examined by microscope (Nikon SMZ1500), and photographed with a Nikon D7000. To determine the vertebral centrum type, some amphibian specimens were scanned by Computed Laminography (160-Micro-CL) at the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences. The image volumes were visualized using ImageJ software. Measurements were made with Vernier calipers.

The preliminary study on the anuran specimens indicates that: 1) the centrum type of *G. baoshanensis* is not certainly procoelous as Gao et Chen (2017) described, whereas CT scans revealed both procoely and opisthocoely; 2) the juveniles and adults all have a V-shaped parahyoid bone, contrary to the original description; 3) the neural arches of the presacrals are imbricated rather than non-imbricate as described previously; 4) the vomerine teeth are aligned in one transverse row, not as "a small patch of vomerine teeth" as suggested in the original paper.

Current research on the salamander material identified a possible new taxon. It has a unique combination of features including: a rounded rostrum, a small patch of vomerine teeth, a triradiate pterygoid with a short anterior ramus, and a notably expanded coracoid end on the scapulocoracoid.

Preliminary study of the turtle fossils reveals similarities with other fossil turtles from the Jehol Biota, such as *Manchurochelys*, *Liaochelys* and *Xiaochelys*, which are all members of the family

Macrobaenidae. However, the new material may represent a new taxon of the family. The turtle material provides new evidence for the biotic relationship between the Pigeon Hill locality and the typical Jehol localities.

In summary, the amphibian and reptile material mentioned above not only enriches our knowledge of the vertebrate biodiversity at that time, but also provides a new and important perspective to the study of the morphology, ontogeny, systematics, and biogeography of Early Cretaceous amphibians and turtles, further helping to reconstruct the early evolutionary history of these herpetological lineages. Moreover, the relationship of the new assemblage with the typical Jehol Biota, as well as the similarities and differences between the faunas, is relevant to the study of the faunal migration and evolution and related environmental constraints.

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## **Review of the horizons and localities yielding mammals of the Middle-Late Jurassic Yanliao and the Early Cretaceous Jehol Biotas, China [oral presentation]**

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In the past two decades, mammalian fossils from the Late Mesozoic deposits of northeastern China have provided significant information for understanding the phylogeny of several major clades of mammals. These fossils belong to two well-known biotas: the Middle-Late Jurassic Yanliao Biota and the Early Cretaceous Jehol Biota. The mammal specimens from the Yanliao Biota were collected from the Haifanggou and Tiaojishan formations at four localities: Daxishan, Linglongta, Jianchang County, Liaoning Province; Nanshimen, and Mutoudeng, Qinglong County, Hebei Province; and Daohugou, Ningcheng County, Nei Mongol Autonomous Region (Sullivan et al., 2014). They have been identified as 14 species representing 12 genera, referred to Docodonta, Eutriconodonta, Haramiyida, Multituberculata and Eutheria. The mammals of the Jehol Biota were collected from the Yixian and Jiufotang formations at seven localities: (in Liaoning Province) Dawangzhangzi, Lingyuan City; Lujiatun, Beipiao City; Jianshangou, Beipiao City; Sihetun, Beipiao City; Xiaotaizi, Jianchang County; and Shangheshou, Chaoyang City; and Daluozigou, Fengning County, Hebei Province (Bi et al., 2016; Luo et al., 2007; Meng et al., 2011; Wang et al., 2006). They have been classified into 20 species representing 17 genera, which are referred to Eutriconodonta, Multituberculata, Symmetrodonta, Eutheria, and Metatheria.

The locality and horizon information of the fossil mammals of both biotas are summarized in table 1 (next page).

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**Table 1.** Fossil mammals from the Yanliao and Jehol Biotas.

Biota	Species	Locality	Horizon
Yanliao Biota	<i>Juramaia sinensis</i>	Daxishan, Jianchang, LN	Tiaojishan Fm., J <sub>3</sub>
	<i>Rugosodon eurasiaticus</i>	Daxishan, Linglongta, Jianchang, LN	Tiaojishan Fm., J <sub>3</sub>
	<i>Shenshou lui</i>	Daxishan, Linglongta, Jianchang, LN	Tiaojishan Fm., J <sub>3</sub>
	<i>Xianshou linglong</i>	Daxishan, Linglongta, Jianchang, LN	Tiaojishan Fm., J <sub>3</sub>
	<i>Xianshou songae</i>	Daxishan, Linglongta, Jianchang, LN	Tiaojishan Fm., J <sub>3</sub>
	<i>Vilevolodon diplomylos</i>	Nanshimen, Gangou, Qinglong, HB	Tiaojishan Fm., J <sub>3</sub>
	<i>Maiopatagium furculiferum</i>	Daxishan, Linglongta, Jianchang, LN	Tiaojishan Fm., J <sub>3</sub>
	<i>Arboroharamiya jenkinsi</i>	Mutoudeng, Qinglong, HB	Tiaojishan Fm., J <sub>3</sub>
	<i>Arboroharamiya allinhopsoni</i>	Nanshimen, Qinglong, HB	Tiaojishan Fm., J <sub>3</sub>
	<i>Megaconus mammaliaformis</i>	Daohugou, Ningcheng, NM	Haifanggou Fm., J <sub>3</sub>
	<i>Pseudotribos robustus</i>	Daohugou, Ningcheng, NM	Haifanggou Fm., J <sub>3</sub>
	<i>Volaticotherium antiquus</i>	Daohugou, Ningcheng, NM	Haifanggou Fm., J <sub>3</sub>
	<i>Castorocauda lutrasimilis</i>	Daohugou, Ningcheng, NM	Haifanggou Fm., J <sub>3</sub>
	<i>Docofossor brachydactylus</i>	Nanshimen, Gangou, Qinglong, HB	Tiaojishan Fm., J <sub>3</sub>
	<i>Agilodocodon scansorius</i>	Daohugou, Ningcheng, NM	Haifanggou Fm., J <sub>3</sub>
Jehol Biota	<i>Akidolestes cifellii</i>	Dawangzhangzi, Lingyuan, LN	Yixian Fm., K <sub>1</sub>
	<i>Zhangheotherium quinquecuspidens</i>	Jianshangou, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Lactodens sheni</i>	Shangheshou, Chaoyang, LN	Jiufotang Fm., K <sub>1</sub>
	<i>Anebodon luoi</i>	uncertain, Beipiao, LN	K <sub>1</sub>
	<i>Maothierium sinensis</i>	?Sihetun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Maothierium asiaticus</i>	Lujiatun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Repenomamus robustus</i>	Lujiatun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Repenomamus giganticus</i>	Lujiatun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Gobiconodon zofiae</i>	Lujiatun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Gobiconodon luoi</i>	Lujiatun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Meemannodon lujiatunensis</i>	Lujiatun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Juchilestes liaoningensis</i>	Lujiatun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Jeholodens jenkinsi</i>	Sihetun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Yanoconodon alleni</i>	Daluozigou, Fengning, HB	Yixian Fm., K <sub>1</sub>
	<i>Liaoconodon hui</i>	Xiaotaizi, Jianchang, LN	Jiufotang Fm., K <sub>1</sub>
	<i>Chaoyangodens lii</i>	Dawangzhangzi, Lingyuan, LN	Yixian Fm., K <sub>1</sub>
	<i>Sinodelphys szalayi</i>	Dawangzhangzi, Lingyuan, LN	Yixian Fm., K <sub>1</sub>
	<i>Acristatherium yanensis</i>	Lujiatun, Beipiao, LN	Yixian Fm., K <sub>1</sub>
	<i>Eomaia scansoria</i>	Dawangzhangzi, Lingyuan, LN	Yixian Fm., K <sub>1</sub>
	<i>Sinobaatar lingyuanensis</i>	Dawangzhangzi, Lingyuan, LN	Yixian Fm., K <sub>1</sub>



**Insect herbivory on broadleaved conifers from the paralic Cenomanian Lagerstätte of Puy-Puy (Tonnay-Charente, Charente-Maritime, SW, France) [oral presentation]**

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Plants and insects are the two most species-rich groups, and together they make up most of Earth's biodiversity. Given the strong positive correlation between the regional richness of plant and insect species, and the fact that phytophagous insects constitute over a quarter of all macroscopic organisms it is apparent that interactions between these two groups are very important. As previous studies focused on the complexity of plant/insect associations during the Palaeogene, data about Cretaceous damages are much scarcer. Such data would be interesting in the light of the transition from the Mesophytic to the Cenophytic and the global turnover of insect assemblages in the mid-Cretaceous, which is thought to be associated with this transition.

The Puy-Puy quarry, at Tonnay-Charente (Charente-Maritime, SW France) is a sand exploitation of uppermost Albian-lowermost Cenomanian age, preserving an outstanding accumulation of conifer and angiosperm remains associated to exceptionally preserved invertebrates, vertebrates, and ichnofossils. Insect mediated damage was examined on 1605 specimens. Of the total analyzed leaf-damage collection 357 leaves/leaf fragments, representing 22.1%, exhibit some kind of damage. Of these, 301 (84.3%) were damaged in one way, while the remaining 56 (15.7%) showed two or more forms of damage. Second in rank order is the broad-leaved coniferous foliage *Dammarophyllum* sp., representing in fact a lower proportion of damaged leaves (23.4%) but also with an elevated level of consumption (34 DTs). Interestingly, harboring specialized interaction (DT280), representing a leaf miner targeting the parenchyma is also preserved on the broad-leaved coniferous foliage. So far only known from the broad-leaved conifer *Liaoningcladus boii* from the mid Early Cretaceous Yixian Formation.

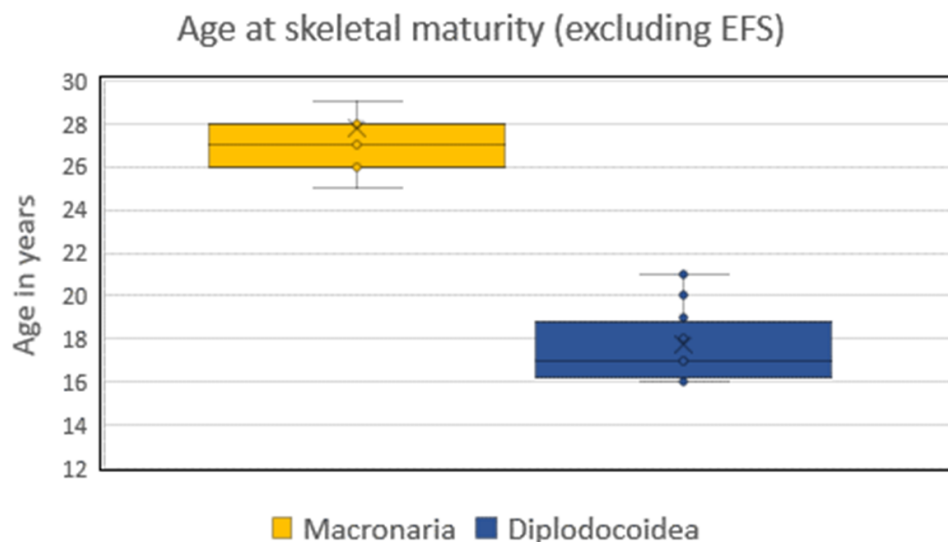
**Growth rates and age distribution of different Jurassic sauropod taxa – implications for life history traits and ecology in normal-sized and dwarfed populations based on dorsal rib histology [oral presentation]**

Katja WASKOW<sup>1</sup> & P. Martin SANDER<sup>1</sup>

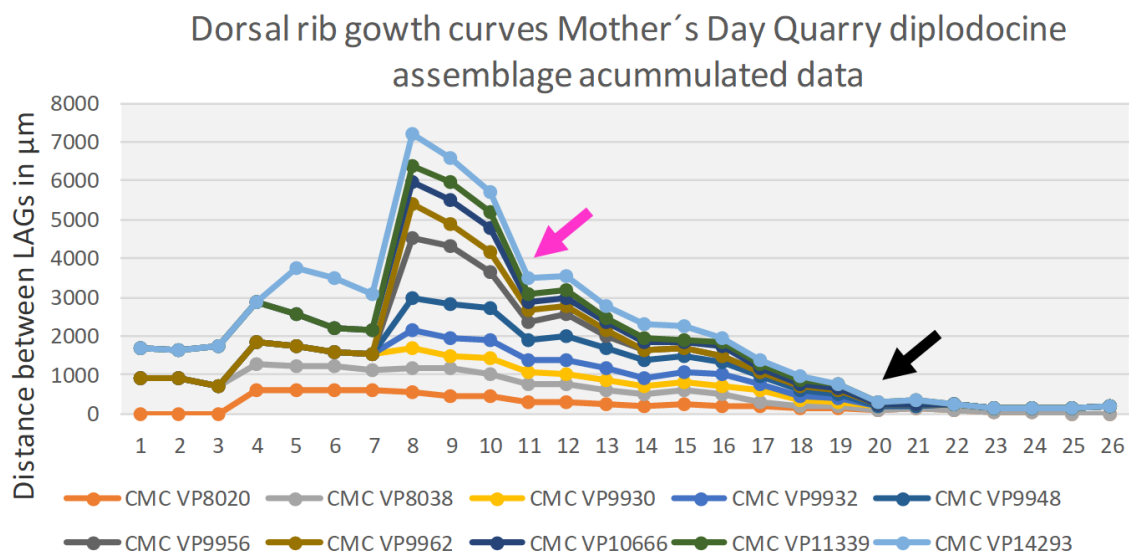
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Sauropod dinosaurs are not only the largest terrestrial vertebrates that ever lived, they also had the largest size difference between hatchlings and adults among amniotes. Therefore, their life history traits and growth rates are of special interest to evolutionary ecologists. Skeletochronology, using histological growth marks in long bones like humeri and femora, is frequently used to construct growth curves in dinosaurs and other tetrapods, plotting age vs. bone size. However, this approach is difficult in sauropods because formation rates of primary and secondary bone tissue in the long bones are too high to produce and preserve lines of arrested growth (LAGs) in all but the outermost cortex (Klein and Sander, 2008). Previous studies have shown in contrast that sauropod dorsal ribs commonly preserve a remarkably complete growth record (Waskow and Sander, 2014). We analyzed the growth record preserved in ribs of 15 Jurassic diplodocoid and macronarian sauropod taxa represented by 66 individuals (including 13 type specimens) from 14 localities. The samples were taken from the proximal shaft of anterior dorsal ribs 2-4. In specimens where the exact position within the rib cage was not known based on articulation it was inferred by the morphology of the rib head region. In articulated specimens size estimations are based on femur length. Sexual and skeletal maturity, two major life history events, are clearly visible in each individual rib growth record, expressed as two successive significant decreases in annual bone apposition rate and thus growth rate. The formation of an external fundamental system (EFS) represents the second decrease. The cycles in the EFS itself, however, were excluded from skeletal maturity estimates because EFS cycles were formed after skeletal maturity was reached and do not record a significant body size gain. Independent of body size, the analysis shows that diplodocoid sauropods have higher growth rates and shorter growth times than their sister taxon, the macronarians. On average, diplodocoids reached sexual maturity after 11 to 13 years of growth and skeletal maturity at 17 to 19 years of age, while macronarians took 16 to 18 years to become sexually mature, reaching skeletal maturity at age 26 to 28 (Fig. 1). This difference is useful for taxonomic assignment of indeterminate sauropod rib material to one of the sister clades. The age distribution in our sample is adult-dominated, suggesting that large sauropods may have inhabited different environments than their juveniles, more conducive to fossil preservation. Independent of taxonomic assignment, geological age or locality the enormous size range from hatchling to adult in sauropods requires that sauropods inhabited different ecological niches at different ages. This assumption has been made before (Foster, 2010) and is corroborated by this study. The only exception showing a heterogeneous age distribution is an assemblage of small sauropods from the Mother's Day Quarry (Wyoming, USA), a low-diversity bone bed of over 2000 mainly small diplodocoid bones. The quarry yielded diverse skeletal elements in complete disarticulation and was previously interpreted as drought-induced mass mortality event killing only juveniles (Storrs et al., 2012). Surprisingly, histological analysis of the rib cross sections revealed an older ontogenetic stage in 15 of the 19 samples. They show an External Fundamental System (EFS), at least two to three generations of secondary osteons and a decrease in vascularization, indicating a subadult to adult ontogenetic stage. Two distinct decreases in growth indicate the points of sexual and skeletal maturity (Fig. 2). All rib samples likely represent different individuals and not different bones of the same individual because the growth record is different

from rib to rib. Additionally, long bone samples of humeri and femora were taken, also indicating the subadult to adult ontogenetic stage of half of the sampled bones. This suggested the presence of a dwarf taxon among Morrison diplodocoid sauropods because all previously known taxa are of large to very large adult size. Island dwarfing, as it occurs in, e.g., *Europasaurus* from the Late Jurassic of Germany and *Magyarosaurus* from the Late Cretaceous of Romania, as an explanation appears inconsistent with the terrestrial habitats of the Morrison Formation, however. The dwarfs may have evolved rapidly on a transient island formed by the transgression of the epicontinental sea from the north. The heterogeneous age distribution of the assemblage of dwarfed sauropods (most likely representing a biological population) suggests that niche partitioning between ontogenetic stages might have been triggered by body size rather than by phylogeny.



**Fig. 1.** Age at skeletal maturity (Excluding LAGs in the EFS) in the two major sauropod clades based on histological growth cycle counts in dorsal ribs.



**Fig. 2.** Growth curves of CMC (Cincinnati Museum Center) diplodocines from the Mother's Day Quarry based on dorsal rib histology. Pink arrow indicates point of sexual maturity, black arrow indicates point of skeletal maturity.

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## The Langenberg Quarry in Northern Germany: a peculiar terrestrial Late Jurassic biota in marine limestones [oral presentation]

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Despite abundant outcrops, terrestrial fossils from Late Jurassic strata in Lower Saxony, Northern Germany, are very rare. This is because the Lower Saxony Basin was covered by a shelf sea that was surrounded by large paleo-islands 150 million years ago. The most outstanding exception to this pattern is the terrestrial fauna and flora found in the Langenberg Quarry near Goslar, a classic outcrop of late Oxfordian to late Kimmeridgian marine limestones and marls at the northern rim of the Harz Mountains in Northern Germany (Wings and Sander, 2012). The quarry is best known as the type locality for the dwarfed basal macronarian sauropod dinosaur *Europasaurus holgeri* (Sander et al., 2006), but has also yielded remains of numerous other organisms from this Late Jurassic island.

Land plants from the Langenberg include twigs and very rare cones of araucarian conifers. Well-preserved leaf cuticles indicate identification as *Pagiophyllum* (likely Araucariaceae). Abundant remains of *Europasaurus* dominate the dinosaur assemblage, which also includes three bones of a diplodocid sauropod (possibly also dwarfed), a stegosaur tooth, very few theropod bones with possible affinities to Ceratosauridae and several theropod teeth. A general survey of more than 80 Late Jurassic theropod teeth from several localities in Northern Germany via a character-based study and a morphometric analysis (discriminant function analysis) indicates that the Late Jurassic islands of Northern Germany provided habitats for a diverse variety of theropod groups including basal Tyrannosauroidae, Allosauroidae, Megalosauroidae cf. *Marshosaurus*, Megalosauridae cf. *Torvosaurus*, and probably Ceratosauria (Gerke and Wings, 2016).

*Europasaurus* provides the largest sample size of skull material for an ontogenetic study in any sauropod taxon (Marpmann et al., 2014). The puzzling taphonomy of *Europasaurus* is unique because the abundant and exquisite three-dimensionally preserved bones – ranging from disarticulated elements to associated partial skeletons – were buried in the shallow marine environment. At least 21 *Europasaurus* individuals belonging to different ontogenetic stages have been identified up to now. The high number of individuals renders taphonomical hypotheses such as drifting carcasses, or swimming or rafting animals implausible. The most parsimonious interpretation is that a herd of *Europasaurus* migrated within the tidal zone and died during the crossing. About one third of the prepared bones bear marks of smaller scavengers. These probable tooth marks are tentatively assigned to invertebrates, small fish or, less plausibly, crocodilians. Taphonomic research is also benefiting from ongoing studies of the sedimentology and microfacies of the Late Jurassic

shallow-water carbonates in Lower Saxony and a high-precision stratigraphic framework based on isotope-geochemical analyses (Zuo et al., 2017).

Non-dinosaurian terrestrial vertebrates include 3D-preserved remains of several pterosaurs, a paramacellodid lizard, and the type specimens of the small atoposaurid crocodilian *Knoetschkesuchus langenbergensis* (Schwarz et al., 2017). Among the 15 pterosaur specimens are four gnathosaurine pterodactyloids, several possible rhamphorhynchid teeth, and the basal-most and oldest member of Eupterodactyloidea. Microvertebrate remains recovered by screen-washing are dominated by fish and crocodilian teeth but also included an astonishing variety of mammal teeth. Multituberculata are represented by several isolated molariform teeth and include the type specimens of *Teutonodon langenbergensis* (Martin et al., 2016). Langenberg docodonts and dryolestids are the easternmost European representatives of these groups. Docodonts only are represented by indeterminate fragments of molars. Three dryolestid molars exhibit a close relationship to those in the English Purbeck Group. Triconodonta are represented by an eutriconodont molariform with a distinct cingulum.

Dinosaur tracks discovered stratigraphically only five meters above the *Europasaurus*-bearing layer are the earliest unequivocal evidence for emergence in the Langenberg section, indicating a sea level fall (Lallensack et al., 2015). The tracks were produced by theropod dinosaurs larger than any animal known from the dwarfed island fauna, indicating a faunal interchange  $\leq 35,000$  years after the *Europasaurus* bone accumulation (Lallensack et al., 2015).

The Langenberg discoveries provide unique insights into a Jurassic European insular ecosystem and close a significant gap in our knowledge of early mammal evolution. Paleobiogeographically, close relationships to the contemporaneous Guimarota (Portugal) vertebrates exist. This is not only true for the mammals, especially the multituberculates, but also for *Knoetschkesuchus langenbergensis*, which is closely related to *K. guimarotae*, and for the basal scincomorph lizard that shows close affinities to the Guimarota paramacellodids.

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## The Rhaetian mystery bones – a histological approach to test several hypotheses [oral presentation]

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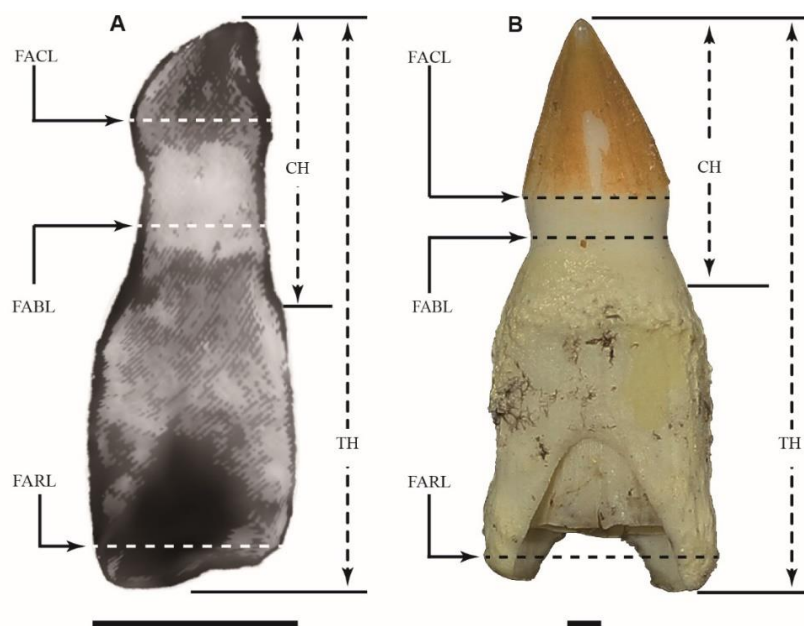
During the Late Triassic (Rhaetian), a rich and unique fauna is recorded. The Rhaetian bone beds of Aust Cliff in England and Bonenburg (City of Warburg, eastern Westphalia) in Germany sample a great diversity of habitats, from open marine to freshwater and terrestrial and contain one of the most peculiar finds from this fauna: giant bone shafts and broken parts of their outer cortex. Estimates of the original size of these bones and fragments suggest that dinosaur-like gigantism had already evolved in the Late Triassic (Galton 2005, Redelstorff et al. 2014). Based on the geological age and on bone size, these bones have been considered to belong to either sauropodomorphs or to large pseudosuchian archosaurs (Galton 2005, Redelstorff et al. 2014). However, bone histology appears inconsistent with both clades (Redelstorff et al. 2014). Since bone histology correlates with phylogeny and is a mature technique, other affinities of the bone should be considered. Here we employ histological comparison to test several hypotheses regarding the identity of the bone shafts and bone fragments. All sauropodomorphs have fibrolamellar bone with a laminar vascular architecture, whereas pseudosuchians lack fibrolamellar bone. The unique bone histology of the Rhaetian Bone Bed fragments, on the other hand, encompasses fibrolamellar bone with longitudinal primary osteons, most of which are modified by secondary re-modeling. Growth marks are common as either LAGs or annuli, indicating cyclical growth (Redelstorff et al. 2014). Although, there may be slight variations in type of growth marks in combination with body size, which may indicate stronger and weaker interruptions of growth as a response to ecological variation or sexual dimorphism. Nevertheless the bone histology of the Rhaetian mystery bones does not fit to the histology of all known dinosaurs so far as well, nor does it fit to pseudosuchian at all. A recently advanced hypotheses based on morphology is that these bone shafts and fragments belong to gigantic ichthyosaurs, representing the surangular of the lower jaw (Lomax et al. 2018). We are in the process of testing this hypothesis because the surangular is known in the bona fide giant ichthyosaur *Shastasaurus sikanniensis* (Nicholls and Manabe 2004). Preliminary histological results reject the Lomax et al. (2018) interpretation. Finally, certain newly recognized histological features of the Rhaetian bones shafts, such as an abundance of structural fibers, are not seen in amniotes but in temnospondyl amphibians (Konietzko-Meier et al. 2013, 2014). Among these, brachyopoids can be extremely gigantic, and bona fide temnospondyl remains occur in the Bonenburg bone bed.

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**Negligible effect of tooth reduction on body mass in Mesozoic birds [poster presentation]**Ya-Chun ZHOU<sup>1,2</sup>, Corwin SULLIVAN<sup>3,4</sup> & Fu-Cheng ZHANG<sup>5</sup><sup>1</sup> Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China; [zhouyachun@ivpp.ac.cn](mailto:zhouyachun@ivpp.ac.cn)<sup>2</sup> University of Chinese Academy of Sciences, Beijing 100049, China<sup>3</sup> Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada<sup>4</sup> Philip J. Currie Dinosaur Museum, Wembley, Alberta T0H 3S0, Canada<sup>5</sup> Institute of Geology and Paleontology, Linyi University, Linyi, Shandong 276000, China; corresponding author: [zhangfucheng@ivpp.ac.cn](mailto:zhangfucheng@ivpp.ac.cn), [zhangfucheng@lyu.edu.cn](mailto:zhangfucheng@lyu.edu.cn)

Tooth reduction and loss was an important evolutionary process in Mesozoic birds (Dilger, 1957; Proctor and Lynch, 1998; Feduccia, 1999; Wang et al., 2017; Zheng et al., 2011, 2014a; Zhou et al., 2009; Louchart and Viriot, 2011). Analysis of evolutionary trends in the total mass of the dentition, a function of tooth size and tooth number, has the potential to shed light on the evolutionary pattern of tooth reduction and loss, and on the causes of this pattern. Because modern birds lack teeth, however, they cannot provide the basis for a model that would allow estimation of tooth masses in their Mesozoic counterparts. We selected the teeth of crocodilians as analogues of those in Mesozoic birds (Fig. 1) because the former are the closest living relatives of the latter, and the two groups are similar in tooth morphology, tooth implantation, and tooth replacement pattern (Martin et al., 1980). To estimate tooth masses in Mesozoic birds, we formulated four regression equations relating tooth mass to various linear dimensions, which were measured in 31 intact isolated teeth from eight individual crocodiles (*Crocodylus siamensis*). The results for Mesozoic birds show that dental mass as a proportion of body mass was negligible, at least from the perspective of flight performance, suggesting that selection pressure favoring body mass reduction was probably not the primary driver of tooth reduction or loss. Variations in dental mass among Mesozoic birds may reflect the different foods they ate, and the different types of feeding behavior they displayed.



**Fig. 1.** Linear measurements applied to bird and crocodilian teeth in this study. A. isolated left premaxillary tooth of *Archaeopteryx lithographica* (London specimen; modified from Wellnhofer, 2009); B. isolated posterior tooth of *Crocodylus siamensis* (IVPP uncatalogued specimen). Dotted line: measurement line, solid line: indication line. Abbreviations: CH, crown height; FABL, fore-aft base length; FACL, fore-aft crown length; FARL, fore-aft root length; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology; TH, tooth height. Scale bars=1 mm



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## **Geological background for the Yanliao and Jehol Biotas in Northeast China [oral presentation]**

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The Middle-Late Jurassic Yanliao Biota and the Early Cretaceous Jehol Biota have been two of the most famous Mesozoic terrestrial lagerstätten in China. In addition to the discovery of many evolutionary important fossils, e.g., feathered dinosaurs, birds, pterosaurs, mammals, lizards, amphibians, fishes and angiosperms, the two biotas are also well known for their extraordinary preservation of soft tissues, such as skins, feather melanosomes, eggs, ovary follicles, crop etc. Then, what is the geological background that had helped shape the evolution and preservation of the Yanliao and Jehol biotas?

The past twenty years have witnessed the significant progress of our understanding of the geochronological framework of the Yanliao and Jehol biotas. This is largely due to the extensive dating of tuffs interbedded in the fossil-bearing deposits as well as the volcanic rock. The Yanliao Biota is now generally accepted to be Middle and Late Jurassic, ranging from about 167 to 159 Ma while the Jehol Biota is between 131 to 120 Ma. The Yanliao and Jehol biotas share a roughly similar paleogeographic distribution in northeastern China although the Early Cretaceous Jehol Biota has a more extended distribution in northern China and beyond.

It is notable that the flourishing times of the Yanliao Biota (160 Ma) and the Jehol Biota (125 Ma) appear to be coincident with the initiation and peak time of the destruction of the North China Craton respectively. The destruction of the North China Craton has also been generally believed to be associated with the subduction of the Paleo-Pacific plate underneath the Asian continent that resulted a series of tectonic and palaeogeographic and palaeoenvironmental changes. Although it remains yet unclear whether or not such coincidence between the evolution of the two biotas and the tectonic events are due to preservational biases (i.e., the frequent volcanic activities were accountable for the exceptional preservation of the two lagerstätten), we suggest that the unique and active tectonic background, the development of the rift basins and the local paleoenvironmental changes must have made an important impact on the evolution of the Yanliao and Jehol biotas.

Finally, recent work on the distribution of the Early Cretaceous volcanic eruptions and the evolving history of the Mesozoic basins in Northeast China and neighboring areas may provide further information for our understanding of the evolution of the Yanliao and Jehol biotas in terms of temporal distribution.

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- 2012/2 Potrok Aike Maar Lake Sediment Archive Drilling Project – PASADO.** 4<sup>th</sup> International PASADO Workshop, Bremen (Germany), August 27-29, 2012, Program and Abstracts. Bernd Zolitschka (editor). – 48 S. – *Verkaufspreis: € 7,-*
- 2012/3 Centenary Meeting of the Paläontologische Gesellschaft.** Programme, Abstracts, and Field Guides. 24.09.-29.09.2012, Museum für Naturkunde Berlin. Edited by Florian Witzmann and Martin Aberhan. – 242 S. – *Verkaufspreis: € 20,-*
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