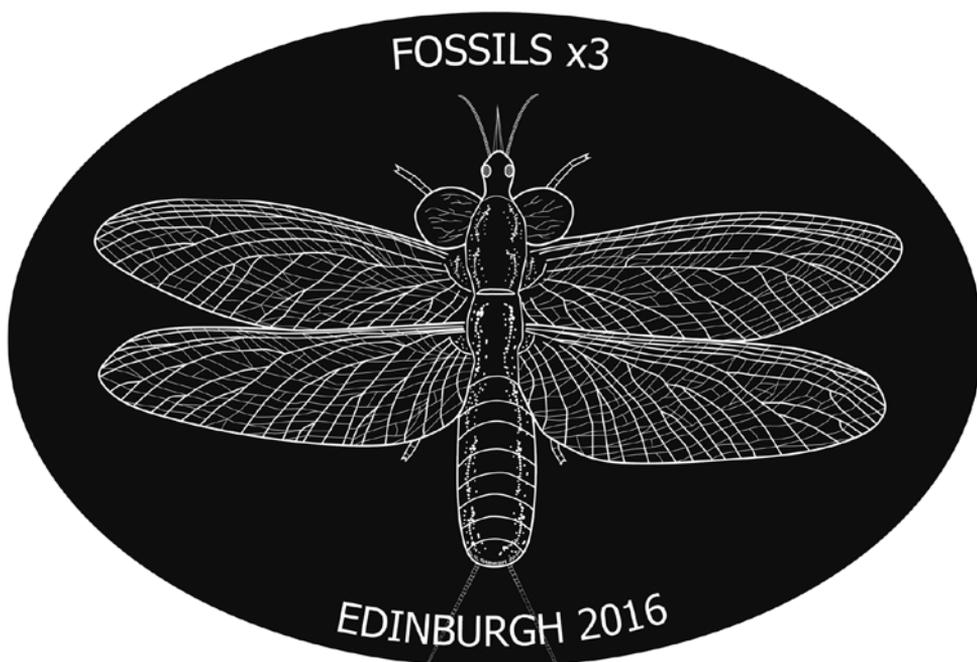




# 7<sup>th</sup> INTERNATIONAL CONFERENCE ON FOSSIL INSECTS, ARTHROPODS AND AMBER

## ABSTRACTS

*Edited by*  
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## **Plant–insect interaction at Willershausen (~3 Ma, Germany): insights into the structuration of an important late European palaeoecosystem**

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The relationships between plants and insects have been essential for the functioning of terrestrial food webs for millions of years. Plenty of palaeontological studies have focused on some key moments during which important climate changes or massive perturbations occurred (such as the K–T [K–Pg] crisis or PETM event). However, only a few of these studies focused on plant–insect interactions during these specific periods and it has been shown that climatic fluctuations could drastically affect trophic interactions. No study has focused on more recent periods that are marked by very important climatic oscillations (glacial–interglacial cycles [Pliocene–Pleistocene boundary]) that influenced the development of different modern ecosystems and forests.

Our study focused on the famous Upper Pliocene (3.2–2.4 Ma; MN 16/17) fossil Lagerstätte of Willershausen, situated in the western foreland of the Harz Mountains, Germany. The fossil richness of this Pliocene palaeolake has been known about since the beginning of the 20<sup>th</sup> century. It has yielded both faunal and floral elements, represented by more than 25,000 fossils. Thus, it provides an ideal setting to examine the correlations between climatic parameters, such as temperature or precipitation, palaeoperturbations, or also forest succession stages and changes in herbivory patterns. Investigations on plant–insect interactions at Willershausen, in a warmer context but with the same palaeogeographic configuration as today, will facilitate reconstruction of the palaeoecosystem and will highlight ecological differences from the present.

In this context, the Willershausen locality will enable us to understand a part of the European ecosystem structuration over 3Ma. Furthermore, it will allow some comparisons with other European localities (e.g. Bernasso, southern France) and with some recent plants species. These comparisons may allow us, in part, to interpret changes in European forests over the last 3 Ma. Thus, it will be possible to characterise these palaeoecosystems during the onset of the glacial–interglacial cycles and to statistically compare plant–insect interactions with respect to environmental parameters.

## **Application of EDXRF to directly measure vertebrate blood (via iron in heme from haemoglobin or haemoglobin-derived porphyrins) in two engorged ticks (Acari: Ixodida) in 100-million-year-old Burmese amber**

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Within the last few years, surface chemistry techniques such as energy dispersive X-ray spectrometry (EDS) mapping and time-of-flight secondary ion mass spectrometry (ToF-SIMS) have been used to measure high iron concentrations and/or the presence of porphyrin molecules from haematophagous insect compression fossils to identify residual blood meals. These techniques are not applicable to insects preserved in amber because they require the specimen to be exposed at the surface, and most amber specimens are contained within the amber matrix (or have been vacuum-entombed). For specimens located within a few millimetres of the amber surface, energy dispersive X-ray fluorescence (EDXRF) can be used to estimate iron concentrations to directly measure potential residual blood meals. In this study, an engorged hard tick (Ixodidae) and an engorged basal lineage Nuttalliellidae tick in 100-million-year-old Burmese amber were studied with EDXRF to semi-quantitatively demonstrate that residual blood meals are present based on elevated iron concentrations. Analysis was completed using a hand-held Niton™ XL2 GOLDD XRF analyser focused on light- to high-weight elements with a 3-mm window. In addition to the two engorged ticks, 185 specimens representing 12 insect orders, including mineral inclusions and fractures (clean and mineral covered), in Burmese amber were also examined using EDXRF. This evaluation provided a database of iron results for comparison to the engorged specimens to determine whether iron detected in the engorged specimens was potentially from blood meals or was simply mineral deposition (primary or secondary). The abdomens of the two engorged ticks were shown to contain high levels of iron compared to the amber matrix and with respect to other non-haematophagous insect specimens, minerals and fractures. To further validate that the high iron concentrations observed in the abdomens of the two engorged ticks originated from vertebrate blood meals, dried human blood and extant hard ticks (Ixodidae) exhibiting various degrees of engorgement, ranging from un-engorged to nearly fully engorged, were also examined with EDXRF. Comparisons of the dried human blood and extant hard tick iron concentrations showed that the elevated iron concentrations observed in the two engorged specimens were consistent with their modern counterparts and that the concentrations were consistent with concentrated blood ratios for hard ticks. Although it is not known whether the iron originated from heme or a haemoglobin-derived porphyrin molecule, the iron concentrations were distinctly measurable and consistent with modern specimens. Therefore, for the first time, direct evidence of vertebrate blood has been found in dinosaur-era amber.

## Arthropod haematophagy and vertebrate remains in Cretaceous Spanish amber

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Haematophagy is a relatively rare feeding habit among Insecta and Acari that has evolved independently several times. In the fossil record, haematophagy usually can only be indirectly inferred through functional morphology. The best medium of preservation with which to trace this feeding habit is amber. In our collection of Spanish amber bioinclusions (upper Albian) some pieces provide information about that behaviour. Biting-midges (Ceratopogonidae) belonging to the genus *Leptoconops*, whose females feed today on reptile, bird and mammal blood, are common in Spanish amber and are sometimes found as blood-engorged individuals. For the first time we have recorded soft ticks belonging to the family Argasidae, which are also Recent vertebrate blood feeders. This finding represents not only the oldest appearance of the family Argasidae in the fossil record, but also the oldest record of the whole order Parasitiformes (the oldest previous record of Argasidae is from Turonian New Jersey amber). Remains of vertebrates are scarce in the Spanish amber collection, but diverse types of feathers and a possible fragment of reptile skin have been recorded. Mammal remains are still absent in Spanish amber, but are known from some older Mesozoic Spanish outcrops, such as Uña, Galve and Las Hoyas (Barremian).

This work is a contribution towards the project CGL2014-52163 “Iberian amber: An exceptional record of Cretaceous forests at the rise of modern terrestrial ecosystems” of the Spanish Ministry of Economy and Competitiveness.

ADDRESS OF THE IPS PRESIDENT  
**The International Palaeontological Society:  
finally, we exist!**

**Dany Azar**

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The first of October, 2015 was a historical and glorious day for all of us, and represents a date to be remembered because it witnessed the official existence of IPS: The International Palaeontological Society. Since the Second International Palaeontological Congress (held in Krakow, Poland) in September, 2001 (during which the IPS was created), and after more than fourteen years passed with several unsuccessful attempts at getting formal registration in different countries, the society now officially exists (with the reference number W751230990 and headquarters at 45 rue Buffon, 75005 Paris, France). Furthermore, following on from the successful Sixth Fossils x3 meeting, held in Byblos (Lebanon), the society has developed a new website, which includes a large database of literature references (around 30,000 pdfs) accessible to all members.

Today we are having our Seventh International Conference on Fossil Insects, in Edinburgh, Scotland, following on from a series of nice meetings since 1998, in various cities around the world: Moscow (Russia, 1998), Vittoria-Gasteiz (Spain, 1998), Ribeirao Preto (Brazil, 2000), Krakow (Poland, 2001), Pretoria (South Africa, 2005), Vittoria-Gasteiz (Spain, 2007), Beijing (China, 2010) and, most recently, in Byblos (Lebanon, 2013). It will no doubt be a successful and profitable congress like its predecessors.

Nowadays, palaeontology (and its related activities) is a growing field and the forthcoming years look very promising. An increasing number of neontologists are gradually integrating with palaeontological teams, augmenting the diversity and quality of research and our knowledge of the historical evolution of many groups. Furthermore, many specialised PhDs have been recently completed or are currently in progress. Moreover, technological advances in communication and new imaging techniques have enabled multiple interdisciplinary collaborations on an international level, which has resulted in an enormous increase in the quality and quantity of very high ranked publications. Consequently, I envisage an exceptionally prosperous and a fruitful future for our research discipline, and I look forward to the ever increasing success of our talented community.

## **State of the art and latest news on Lebanese amber**

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Amber is one of the greatest natural treasures of Lebanon, where more than 450 outcrops have been discovered recently as a result of intensive geological field research. Amber outcrops cover nearly 10% of the Lebanese territory. All outcrops are Lower Cretaceous, except for twenty-two: twenty-one are Late Jurassic (Kimmeridgian) and one is Cenomanian. Most of the amber in this country is found in lenses of dark clay or shale associated with lignite and plant debris, sometimes in a purely fluvial deposition system, i.e. in channels or riversides, and sometimes the deposition was subject to marine influences, i.e. in a deltaic zone or littoral (in the intertidal area). Other amber outcrops are found in dysodile, lithographic limestone and coaly marls. The presence of amber in Lebanon has been documented several times since the beginning of the nineteenth century but it was not until the late 1960s that fossil insects were recorded in this material.

The lowermost Cretaceous amber from various localities in Lebanon represents the oldest amber with intensive macroscopic biological inclusions (curiously and for unknown reasons, to date only around 25 of the numerous Lower Cretaceous outcrops have yielded fossil inclusions). The most fascinating aspects of the Lebanese amber are the abundance and outstanding preservation of the biological inclusions, which help shed light on palaeobiodiversity and evolution during the very important period that witnessed the appearance of flowering plants and the subsequent co-evolution between angiosperms and insects. Lebanese amber contains a lot of extinct families (some of them are known only from Lebanon) and the records of the oldest representatives of many modern families of terrestrial arthropods. Most of the time Lebanese inclusions constitute the “missing links” between the prehistoric fauna and the modern one. Moreover, the study of Lebanese amber inclusions is to date the best (and maybe the only) way for determining North-East Gondwanan palaeodiversity and for reconstructing the palaeoenvironment as a wet and dense tropical forest.

Lebanese ambers are sometimes found preserved with the wood, leaves, and even female and male cones of the amber producing tree. As a result of morphological and geochemical study of this material several origins for the Lebanese amber have been proposed: Araucariaceae, Cheirolepidiaceae and Podocarpaceae. Examination of the epidermal structure suggests an additional botanical group with cycad affinities, or even a new fossil family. However, further research is needed before any reliable conclusions can be drawn.

## Non-biting midges (Diptera: Chironomidae) in Eocene ambers from East and South Asia

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With almost 6000 described species, non-biting midges (Diptera: Chironomidae) are among the most diverse and abundant aquatic insects in the world. Non-biting midges are widely used as indicators of ecological status in freshwaters, due to the close and specific association of the preimaginal stages with their habitat. The family has also left a rich fossil record dating back to the Triassic, with numerous modern genera known from the Paleogene. Chironomids are one of the most common taxa in amber, sometimes comprising up to 70% of all animal inclusions. Their abundance in amber, together with knowledge about ecological preferences of modern representatives, allows conclusions on palaeoenvironmental conditions. Chironomid faunas from East and South Asian Eocene amber outcrops were almost unknown until recently, which was significantly hampering our progress in understanding the structuration of freshwater ecosystems during the Eocene Temperature Optimum. Investigations of Eocene ambers from Sakhalin, Fushun and India have uncovered diverse chironomid faunas.

According to palaeobotanical data, Sakhalinian amber of the Russian Far East is of Middle Eocene age. Six species of non-biting midges were described from this outcrop, all of which belong to modern genera of Orthocladiinae. Modern representatives of these genera are associated with semi-terrestrial, terrestrial or shallow aquatic habitats, which together with palaeobotanical data implies that the Sakhalinian amber forest existed on a large warm-temperate swamp.

The chironomid fauna from Fushun amber (Early Eocene, China) was originally described using poor quality systematic descriptions and type depositories were not mentioned. Consequently, these names should be considered as *nomina dubia*. Our investigation of a small sample of Fushun chironomids revealed eight genera, seven of which belong to the subfamily Orthocladiinae and one to Chironominae. At least three genera and one species are shared with Sakhalinian amber.

Cambay amber from the Early Eocene of India has preserved a diverse and unique chironomid fauna. Thirty-three specimens could be assigned to seven modern genera. The Cambay amber chironomid fauna consists of a mixture of tropical or warm-temperate taxa, with some boreal or high-altitude mountainous taxa (subfamily Podonominae). The habitat requirements of modern representatives of the latter subfamily either indicate the presence of cold mountainous streams near the site of amber formation or a shift of ecological restrictions from the past to the present.

## **The ants (Hymenoptera: Formicidae) of early Eocene Indian amber**

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Today, ants are among the most ubiquitous and ecologically diverse arthropods in terrestrial environments worldwide, however, this is a relatively recent development. The earliest definitive ants from mid-Cretaceous ambers comprise less than 1% of all insect inclusions. The majority of these early ants belong to stem-group lineages distinct from their modern relatives and, curiously, despite exhibiting surprising diversity and evidence for social behavior as early as the Cenomanian, ant fossils do not appear in high abundance until the Eocene. Recently discovered fossil material from Gujarat, India, dated to ~52 Ma offers valuable insight into a key period of crown-group ant evolution and exhibits the highest pre-Miocene ant prevalence so far known in amber. Because Indian “Cambay” amber is dated to shortly after the tectonic collision of India into Asia, ending ~40 million years of isolation for the Indian subcontinent, there is potential for a highly endemic fauna. Moreover, as the deposit is dated to shortly after the Paleocene Eocene Thermal Maximum (PETM), the hottest period in Cenozoic Earth history and a proposed driver of ant diversification, these fossils may offer insight into the “rise of the ants” as they apparently increased in overall prevalence and diversity. The ant faunal composition of the deposit is discussed with respect to overall ant evolutionary history, endemism, and the role of fossils in reconstructing phylogenies.

## **Fidelity of preservation of fossil insects from the Lower Cretaceous Crato Formation of Brazil: truly exceptional preservation**

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The Crato Formation (Cretaceous, Latest Aptian/Early Albian) is a world-famous fossil insect Konservat-Lagerstätte that provides a rare glimpse into a Gondwanan terrestrial ecosystem during an important period for the co-evolution of insects and angiosperms. The formation yields an astonishingly diverse and beautifully preserved insect assemblage. Over the past two decades the vast majority of research on these fossils has focused on their systematics and morphology. Until recently (Barling *et al.*, 2015), little attention had been directed towards the preservation of these insects, preventing their preservational fidelity from being quantified and the mechanisms of preservation identified. Until these can be clarified, it is uncertain if there may be size, taxonomic, or other biases that could be clouding our view of the Crato Formation palaeoecosystem.

The quality of preservation, the preserving minerals, and the taphonomic pathways were examined, not only to reveal how astoundingly well preserved these fossils can be, but also to demonstrate the range of preservation styles and qualities present. A total of 117 specimens were studied using scanning electron microscopy and energy dispersive x-ray analyses to determine preservational textures, microscopic preservation, and replacement mineralogy. The primary texture of replication is that of 'pseudoframboid-like' aggregates of iron sulphides and iron hydroxides. These vary in aggregate diameter, grain size, and arrangement, but all share characteristics of pyrite framboid formation. It is likely that these textures are the result of failed/stalled pyrite framboid formation, and may represent a unique form of preservation. Additionally, systems of measuring and quantifying completeness and other taphonomic characters have been defined, and a taphonomic pathway has been modelled to explain the origin of these fossils, helping us to further understand this important palaeoecosystem.

Barling, N., Martill, D.M., Heads, S.W. & Gallien, F. 2015. High fidelity preservation of fossil insects from the Crato Formation (Lower Cretaceous) of Brazil. *Cretaceous Research*, 52: 605–622.

## Blattaria of the Green River Formation

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The Eocene Green River Formation of Colorado, Wyoming and Utah is the most important non-amber palaeontomological locality after the K/Pg. More than 150,000 fossil insect specimens have been recovered from the lacustrine sediments of the Colorado region (<http://www.entsoc.org/press-releases/cockroach-reappears-n-america-after-49-million-years>), representing the most numerous group of fossil organisms from that deposit. More than 300 species have been described (EDNA lists 187 fossil insect species [accessed 12 January 2016]), with many additional taxa still awaiting formal description. Compared to some other insect groups, Blattaria (families Diplopteridae, Ectobiidae, Blaberidae, Blattidae) are less numerous, but they are ecologically and evolutionarily probably the most important because of their excellent preservation (including preserved gut contents) and their assignment to extant genera with known ecologies. The Colorado part of the Green River Formation includes the localities of Denson, Donnel and Anvil Points, which has two facially different sub-localities: Anvil Point Labandeira and Anvil Point Kohls. The abundance of Blattaria species differs among these localities, but the species are mostly shared. They are represented by the genera *Blattella* Caudel, 1903; *Symploce* Hebard, 1916; *Allacta* Saussure & Zehntner, 1895; *Supella* Shelford, 1911; *Sigmella* Hebard, 1940; *Diploptera* Saussure, 1864; *Cariblattoides* Rehn & Hebard, 1927 (with *C. labandeirai* Vršanský *et al.*, 2011 – a common and advanced Eocene ectobiid genus, which indicates early radiation of most recent cockroach genera near the PETM) and *Ectobius* Stephens, 1835 (with *E. kohlsi* Vršanský *et al.*, 2014 – which suggests its local extinction followed by Recent re-introduction in the Americas (Vršanský *et al.*, 2011, 2012, 2013, 2014; Vršanský & Labandeira, in press)), being a cosmopolitan genus both during the Eocene and secondarily today.

Vršanský, P., Cifuentes-Ruiz, P., Vidlička, L., Čiampor, F. JR. & Vega, F.J. 2011. Afro-Asian cockroach from Chiapas amber and the lost Tertiary American entomofauna. *Geologica Carpathica*, 62: 463–475.

Vršanský, P., Vidlička, L., Čiampor, F. JR. & Marsh, F. 2012. Derived, still living cockroach genus *Cariblattoides* (Blattida: Blattellidae) from the Eocene sediments of Green River in Colorado, USA. *Insect Science*, 19: 143–152.

Vršanský, P., Vidlička, L., Barna, P., Bugdaeva, E. & Markevich, V. 2013. Paleocene origin of the cockroach families Blaberidae and Corydiidae: Evidence from Amur River region of Russia. *Zootaxa*, 3635: 117–126.

Vršanský, P., Oružinský, R., Barna, P., Vidlička, L. & Labandeira, C.C. 2014. Native *Ectobius* (Blattaria: Ectobiidae) from the Early Eocene Green River Formation of Colorado and its reintroduction to North America 49 million years later. *Annals of the Entomological Society of America*, 107: 28–36.

Vršanský, P. & Labandeira, C.C. in press. Early-derived Eocene cockroaches (Blattaria: Ectobiidae: Pseudophyllodromiinae, Blattellinae) from the Green River Formation, Colorado, U.S.A. *Proceedings of the Washington Entomological Society*.

## **New insects from the Jurassic Talbragar Fish Bed, Australia**

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Fieldwork at the Talbragar Fish Bed, over the period 2006–2015, has yielded at least nine orders of insects, the most abundant being Hemiptera and Coleoptera. Talbragar insect fossils tend to be small, but recently the wings of a large undescribed orthopteroid have been discovered. Ten insects and one spider species have been formally described since 2012 and others are currently under study. Particularly, the fossil Diptera and Coleoptera have enhanced our understanding of the trophic relationships in this freshwater lake palaeoecosystem and the interactions between these insects and the fringing terrestrial plants. The Talbragar site probably represents the junction of terrestrial and an oligotrophic shoreline habitat. The fossil site continues to yield further taxa with the potential to provide an opportunity for a reconstruction of this Jurassic palaeoecosystem. This presentation updates the 2012 reconstruction of the Talbragar palaeoecosystem and our knowledge of the diversity and composition of the entomofauna.

## Xiaheyan, the 2016 update

**Olivier Béthoux\*, Yingying Cui, Jun-Jie Gu, Qiang Yang, Ninon Robin, Ekaterina Sidorchuk, Sile Du, Steffen Trümper, Jörg W. Schneider, Yingnan Li, Pierre Guériaux & Dong Ren**

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Within the last couple of years new data have been gathered on the early Late Carboniferous Xiaheyan locality (China), known to yield the earliest insect fauna. The newly described insect taxa include two new species of Palaeodictyoptera (Calvertiellidae and Spilapteridae; *Xiaheyanella orta* and *Tythospilaptera wangae*, respectively), one being the smallest representative of the order; four species of Megasecoptera (*Brodioptera sinensis*, *Sinopalaeopteryx splendens*, *Sinopalaeopteryx olivieri* and *Namuroptera minuta*); and two new species of stem-Orthoptera (Archaeorthoptera; *Xixia huban* and *Protomiamia yangi*). It could be determined that the latter had a female-biased sexual size dimorphism, a pattern common among crown-Orthoptera but rarely documented in the fossil record. A specimen of a formerly described stem-Orthoptera species, viz. *Miamia maimai*, was recovered with a 800 µm long oribatid mite on it (*Carbolohmannia maimaiphilus*). The mite was investigated using phase contrast tomography. Specimen preservation and abundance distribution data derived from the fossil insect sample indicate that specimens from the corresponding layer were buried rapidly, indicating a *syn-vivo* association, considered phoretic. Incidentally, this discovery is the first pre-Cretaceous case of a fossil mite associated with another animal. A putative decapod crustacean is currently under investigation. In addition to the description of the arthropod fauna, sedimentology analyses were carried out. The 260 m. of the Tupo Formation, containing nine insect beds at Xiaheyan, were measured in cm-resolution. Fossil content and lithofacies patterns point to shallow marine to lagoonal deposits during a sea level fall. In those times the Xiaheyan area was situated in an inland sea at the southern margin of the North China block. The sea level fall was superimposed by sea level undulations of higher frequency, resulting in the alternating deposition of insect-bearing proximal siltstones and poorly fossiliferous distal claystones. Conodonts from abundant limestone concretions indicate an early Bashkirian age of the insect-yielding upper part of the Xiaheyan section. In addition, five ash horizons provide the chance for obtaining absolute ages. Future studies will concentrate on the description of additional insect taxa and in a refinement of the diversity and abundance data.

## **New palaeobiogeographical investigations on stoneflies (Plecoptera)**

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Dong Ren, Michel Laurin & Olivier Béthoux**

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The 16 recognised extant stonefly families of the hexapod order Plecoptera are characterised by a primarily disjunctive global distribution. As indicated by the names, the suborders Antartoperlaria and Arctoperlaria refer to the distributions in the Southern and Northern Hemisphere, respectively. With a few exceptions (e.g. the occurrence of Perlidae and Notonemouridae [Arctoperlaria] in the Southern Hemisphere), this distribution pattern makes the group suitable for historical biogeographical investigations. It has been proposed that the Arctoperlaria and Antartoperlaria diverged during the Jurassic period. The main impediments to resolving stimulating evolutionary questions are the problematic taxonomic assignment of fossil species and a weakly constrained phylogenetic framework. In recent years, we have produced a number of descriptions and revisions of Paleozoic and Mesozoic species of this order. This presentation summarises this recent progress, including a new investigation of the affinities of *Sinosharaperla zhaoi* and the description of the first fossil Pteronarcyidae (based on a series of more than ten specimens). The next steps of the project, including the description of amber material, and the elaboration of a timetree, will be outlined.

## **Geometric morphometrics of bee fossils (Hymenoptera: Anthophila) wing shape provide insights to bee evolution**

**Manuel Dehon\* & Denis Michez\***

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One of the main challenges in palaeontology is to integrate fossils in the taxonomy and phylogeny of extant clades. Robust statistic tools are quite rare to achieve this important task. Fossil taxonomy is still often based on the description of a few qualitative and subjective characters, mostly limited to the estimation of the author. Here we present a taxonomic revision we developed on bee fossils with new statistic tools. Bees are an interesting model because their ecology, diversity and most importantly their systematics are well known. Wing-shape analysis by geometric morphometrics procedures has proven to be a powerful tool for morphological discrimination of bee taxa at different taxonomical levels. Moreover, bee forewings are easy to analyse because of their flatness and because they represent a neutral character with enough variation to discriminate taxa at different levels. Previous studies showed the utility of wing shape analysis to assess taxonomic affinities between extinct and extant clades of bees. Bees are relatively rare in fossil deposits; nonetheless using this method, fossils of anthophorids, halictids, bumblebees and other clades have been revised or described, from deposits like the Eocene shale of the Green River Formation (USA), the Oligocene lacustrine beds of Céreste (France), the Late Miocene lacustrine beds of Cerdanya (Spain), the Florissant shale of Colorado (USA), the Miocene deposit of Oeningen (Germany) and the Eocene Baltic amber.

**This is a single abstract for two related talks in the same session**

## **Fossil spiders and ancient salt lakes**

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Fossil spiders are relatively abundant in lacustrine deposits. In addition to their palaeodiversity they have the potential to provide information about the palaeoenvironment. Fossil spiders from the Green River Formation of Colorado (Eocene) include specimens from the families Uloboridae, Hersiliidae, Selenopidae and Thomisidae that have recently been described. The Florissant Formation (Eocene) has a similarly diverse fauna with several families represented, including Lycosidae, Tetragnathidae, Thomisidae and Gnaphosidae. Few fossils from the Crato Formation (Cretaceous) have been formally described but include mygalomorphs, araneids, nephilids and an exquisite palpimanid. The diversity from these three deposits represents various life modes and habitats. Recently, it has been demonstrated that the leg flexure of spiders may serve as a proxy for the paleosalinity of ancient lakes. The typical pose of fossil spiders from the Crato Formation, for example, is legs tightly curled under the body, and is suggestive of hypersalinity. Fossil spiders from each of the three deposits were examined and compared to modern spiders drowned in varying salinities.

## Amber centipedes and their bearing on dating chilopod divergences

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Like many soil arthropod groups, Chilopoda has a fossil record informed by a few Palaeozoic Konservat-Lagerstätten (notably the Rhynie/Windyfield cherts, Gilboa and Mazon Creek), and phylogenetic work on fossils has focused on these taxa for their effects on inferring and dating ordinal-level divergences. The Mesozoic and Cenozoic have been less intensely investigated. Until the past decade, published taxonomic work on Chilopoda in amber mostly consisted of mid-19th Century descriptions from Baltic amber, these being species assigned to extant genera and in need of modern revision. Up to 2009, the Mesozoic record of centipedes consisted of a few holotypes of monotypic genera preserved in lithographic limestones from Germany and Brazil. Recent descriptions of Geophilomorpha from Late Cretaceous amber from western France and Burma (Myanmar) allowed assignment to extant families. In light of recent phylogenetic schemes based on combined morphological and molecular data, Cenomanian members of Schendylidae and Geophilidae constrain the divergence times of deep branches of Geophilomorpha. An extinct species of *Scolopocryptops* from Mexican amber provided the majority of morphological characters coded for extant taxa in a dataset dominated by molecular characters. A new species of the extant genus *Theatops* Newport, 1844, is presented from Baltic amber. This genus has a disjunct distribution in temperate North America, the Mediterranean and Sichuan, China, its record in Baltic amber consistent with the extant distribution being pruned by extinction. Morphological parsimony analysis nests the Eocene species within European–North America clades. The degree of completeness of its external morphological information permits its coding into more broadly sampled analyses of scolopendromorph phylogeny that also code for multi-locus sequence data, allowing for an empirical comparison of traditional node calibration and tip-dating (“total evidence”) approaches for estimating divergence times.

## The exceptional Late Triassic (Norian) assemblage from Solite Quarry, Virginia, USA

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The Virginia Solite Quarry, situated in the Dan River basin of the Newark Supergroup, preserves one of the few fossil assemblages that bears intact Triassic insects. This, together with the diverse flora and two very specialised tetrapods, makes it one of the most significant Triassic localities anywhere in the world. The insects are for the most part completely articulated and even some of the smallest specimens preserve exquisite anatomical detail such as microtrichiae. While this entomofauna is very diverse, it is especially notable for containing representatives of many modern orders and families, including four extant families of Diptera, the oldest belostomatid water bugs and the oldest thysanopteran (*sensu stricto*). Plant macrofossils lack cuticle as a result of the high thermal maturity of the sediments, yet the assemblage is still very diverse with bennettitaleans, sphenophytes, ginkgophytes, cheirolepidaceous conifers and dipteridaceous ferns among the more common elements. The floral assemblage also contains the intriguing wind dispersed seed, *Edenia*, and *Fraxinopsis*, a form more normally associated with Gondwanan localities. The most abundant tetrapods represent the Protorosauria, an archaic lineage comprising mostly marine, and often rather bizarrely long-necked taxa that did not survive beyond the Triassic–Jurassic boundary. There is considerable debate regarding the depositional environment, but evidence is presented to support deposition under relatively shallow conditions in a saline/alkaline lake.

## **Taphonomic studies of fossil insects from the new Kishenehn Formation Konservat-Lagerstätte**

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The Kishenehn Formation (46 Ma) in northwestern Montana is a new Konservat-Lagerstätte characterised by exceptional preservation of morphological detail, an abundance of insect fossils of very small size and the preservation of original component materials. The Kishenehn Formation entomofauna includes 15 different orders of insects, 60% of which are Diptera. The majority of the fossils appear to be fully articulated. Bias for preservation of tiny insects is documented by the presence of the only known compression fossils of fairy wasps (Hymenoptera: Mymaridae), specimens of the feather-winged beetles (Coleoptera: Ptiliidae) less than 1 mm in length and the smallest known proctotrupoid (Hymenoptera: Proctotrupidae), extant or extinct. The Kishenehn Formation is relatively rich in fossil mosquitoes, with over 50 specimens found to date. Additionally, more than 200 specimens of parasitic wasps of the subfamily Belytinae (Hymenoptera: Diapriidae) have been collected. Amongst these are at least 30 well-defined morphotypes. Such diversity, although still less than that found in extant ecological niches, is extremely unusual in the fossil record. Mass spectrometry (ToF-SIMS) has been used to detect the presence of haemoglobin-derived heme in the abdomen of a blood-engorged mosquito from the Kishenehn Formation and energy-dispersive X-ray spectroscopy has been used to detect the presence of zinc at the cutting edges of the mandibles of a rove beetle (Coleoptera: Staphylinidae). The insect fossils, present as distinct carbonaceous bodies of variable carbon content (60–97%), are preserved within varves composed of very fine eolian siliciclastic silt grains overlain with non-diatomaceous, possibly cyanobacteria-derived microbial mats which contain distinct traces of polyaromatic hydrocarbons; the mat layers define the bedding planes of the oil shale. The mats, approximately 10 µm in thickness when overlying the fossil, contain numerous siliciclastic grains, the long axes of which are aligned parallel to the fossil's surface. This layer is opaque when dry but nearly transparent when wet, allowing for the visualisation of the fossil. Unless removed, this layer prevents compositional analyses of the fossils. This layer is absent in the fossils of other North American Lagerstätten and may play a critical role in the unique preservation of the Kishenehn Formation fossils.

## **Crustaceans in Late Devonian continental ecosystems: insights from the Strud locality, Belgium**

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Arthropods were the first animals to colonise land, with myriapods and arachnids at least by the Silurian (443.4–419.2 Mya), and hexapods by the Early Devonian (~410 Mya). Much later at least four groups of crustaceans also literally ventured onto land, most probably independently. These were the isopods, amphipods, ostracods and decapods, whereas other groups such as copepods and branchiopods have colonised almost every terrestrial aquatic habitat. All faced a series of challenges, in particular gas exchange, desiccation, reproduction, osmoregulation and exposure to ultraviolet radiation, resulting in many morphological, physiological and ecological adaptations. Nonetheless, whether they reached land via salt or fresh water remains poorly documented, mainly because relevant localities are few. Here, I will present two assemblages of continental aquatic crustaceans recently described from the Late Famennian (Late Devonian, ~365 Mya) locality of Strud, which represents an exceptional source of information on early aquatic terrestrial ecosystems. Firstly, an assemblage of early decapod crustaceans has been recovered from fine shales representing a calm and confined floodplain habitat, indicating that decapods have been part of continental ecosystems at least since the Late Devonian. Secondly, fresh to brackish temporary pools, seasonally dried and flooded, yielded a modern-looking community of branchiopod crustaceans comprised of notostracans, anostracans and spinicaudatans. Insights into their reproductive strategy and life cycle show how these crustaceans adapted to invade the land successfully at the onset of the terrestrialisation process.

## **Bizarre dancing flies – the genus *Ragas* (Diptera: Empididae) in Eocene Baltic amber**

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Dancing flies of the genus *Ragas* within the empidid family are small Diptera not often found in collections. Worldwide, six species are known and in the fossil record the genus is also rarely reported. *Ragas* is defined by short spine-like setae on the postgena, fore coxa and trochanter and a recurved labrum at least in females. Adults are active in winter and found on tree trunks. A first fossil from Baltic amber described as *Ragas generosa* by Meunier (1908) was recognised in lacking the *Ragas*-typical characters and thus must be placed in another genus. A study of 19 *Ragas* inclusions from two private collections revealed a surprising diversity of species: *R. baltica*, *R. electrica*, *R. eocenica*, *R. succinea* and *R. ulrichi* were described. A recently discovered additional specimen shows a particular modification of the postgena which was previously unknown in the family Empididae. This unique species is named as *R. bizarra* based on its beak-like extension of the postgena. The function of the spinose genal extension is unclear. We hypothesise that in combination with the strongly recurved and sclerotised labrum it functioned as a tool for opening arthropod prey. The most frequently encountered fossil species within the genus is *R. ulrichi* (known from both males and females).

Sinclair, B.J. & Hoffeins, C. 2013. New fossil species of *Ragas* Walker (Diptera: Empididae) in Baltic amber (Tertiary, Eocene). *Bonn Zoological Bulletin*, 62(1): 92–99.

Hoffeins, C., Sinclair B.J. & Stark, A. 2015. Description of a further *Ragas* species (Diptera: Empididae) from Baltic amber (Tertiary, Eocene). *Studia dipterologica*, 21(2): 177–180.

## KEYNOTE TALK

# What everyone should know about British fossil insects

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The British Isles have a diverse geology for their size and insects as rock fossils have been described from the Lower Devonian, Upper Carboniferous, Upper Triassic, Lower–Upper Jurassic, Lower Cretaceous and Palaeogene. They occur in non-marine and marine sedimentary rocks, including chert, sideritic ironstone, siltstone, mudstone (sometimes phosphatic) and limestone, as impressions and even casts. Generally, older finds are from the north and west of Britain, and younger from the south and east, but there are exceptions. In addition, insect inclusions occur in Early Cretaceous Wealden amber and reworked Paleogene Baltic amber, and insects have also been studied as Quaternary subfossils.

Nineteen British sites were selected by the Geological Conservation Review to represent the British fossil insect record. These will be reviewed, along with some sites that were not selected. The initial selection of sites was primarily not species-based, so for the first time, 12 key British fossil insects will be presented for discussion, as well as some outstanding subfossils and important revisions. The selection will not be purely systematic.

Britain has a longish history of palaeoentomological investigation, often by keen individuals and collectors, usually male. The father of English palaeoentomology will be nominated – an educated Victorian vicar. Collecting and recording fossil insects, however, needs interpretation and the major works on British fossil insects will be reviewed; the secondary literature, however, must not be underestimated, especially considering its popularity. Displaying fossil insects, nevertheless, remains a challenge.

The British fossil record is biased towards England with Scotland proudly represented, but Wales, and especially Ireland, have been left somewhat lagging behind, despite possessing some excellent Carboniferous strata. This, and future prospects for British palaeoentomology, will be summed up. An appreciation of fossil insects, like much else, started in the industrial revolution but is now part of the fast-moving and international age of the computer. As ever, chance finds in the field can stimulate new research and simply need a discerning eye to recognise them. The careful amateur can contribute to filling gaps in our knowledge, as well as the professional palaeoentomologist, and it is a field in which new UK species are the norm and not the exception.

## Mantispidae (Neuroptera) and mantispid-like neuropterans from the Mesozoic

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It has been suggested that Mantispidae first evolved in Asia or Europe at the beginning of the Jurassic, or potentially earlier in the latest Triassic. There have been nine genera and 11 species of mantispid described from the Mesozoic. The first known species of Mantispidae in the fossil record is from the Lower Jurassic of Dobbertin, Germany. Other Jurassic mantispids are known from Daohugou, China, and Karatau, Kazakhstan. The Cretaceous has yielded one species of mantispid from the Lower Cretaceous of Baissa, Siberia, and three from the Yixian Formation, China. In the Upper Cretaceous, two species have been recorded from Kazakhstan and Burmese amber. The majority of taxa have been placed within the extinct subfamily Mesomantispinae, with the exceptions of *Liassochrysa* and *Promantispa* that have been placed in the extant subfamily Drepanicinae, and *Doratomantispa* that is considered as Mantispidae *incertae sedis*. New specimens have also been discovered, which are awaiting description. The aforementioned fossils are considered to be true mantispids, displaying diagnostic characters, both from wing venation and body morphology, which give strong evidence for their affinity. In addition to these, there are some Mesozoic fossils that show similar characters to Mantispidae, in their wing venation and body morphology, for example, the presence of raptorial forelegs, these have often been described or identified as Mantispidae. These mantispid-like fossils can usually be separated into two subfamilies that are currently placed in Berothidae: Mesithoninae and Paraberothinae. Mesithoninae species are found in the Jurassic of Asia, and the species of Paraberothinae are found exclusively in amber from the Cretaceous of Lebanon, Burma, France, New Jersey (USA) and Canada. Why are these taxa often identified as Mantispidae? How do these subfamilies differ from Mantispidae? Are these differences enough to confidently exclude them from Mantispidae? Answers to these questions will be discussed, as well as a review of the Mesozoic fossil record of Mantispidae.

## Sounds from the past: from fossil to song in Ensifera

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Ensifera (Orthoptera) were amongst the earliest terrestrial arthropods to develop acoustic communication; probably as early as the mid-Triassic. Extant male bush-crickets (Ensifera: Tettigoniidae) are known to produce loud courtship songs by tegminal stridulation, i.e. the rubbing together of specialised structures on the forewings, namely the file (a serrated vein) and the scraper (a plectrum-like, hardened region). The songs are further amplified by modified and specifically resonating wing cells and detected by other bush-crickets via pressure-sensitive tympanal organs located in the front tibiae. The general biomechanics and bioacoustics of this system are well understood in modern bush-crickets, where it was found that most species communicate with signals in the ultrasonic frequency range (20–150 kHz). However, earlier research provided evidence to suggest that the origins of tettigoniid courtship songs lie in audible, much lower frequency signals (<7 kHz). Here, we describe how detailed understanding of the anatomy and biophysical function of the auditory communication system in living bush-crickets and the use of modern imaging techniques, comparative methods and multiphysics modelling of the signal producing and receiving structures in fossils can help to gain insight into the evolution of singing in Ensifera. By incorporating results from experiments using laser Doppler vibrometry on ears and wings of extant species with 3D models, we can build finite element models recreating the bioacoustic properties of these structures. By applying the same models to 3D reconstructions of fossilised wings and ears, we will then be able to infer the resonances of these systems and thereby the likely frequency ranges used in acoustic communication by the extinct taxa. A more detailed understanding of the evolution of singing in ensiferans will enable us to shed light on changes in the sensory physiology and the palaeoecology of these insects and their predators through time.

## **New discoveries of Miocene arthropods from amber and diatomite deposits in New Zealand**

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The fossil history of pre-Quaternary terrestrial arthropods in New Zealand has been largely unknown, due to a paucity of fossil sites that preserve such delicate organisms. The discovery of arthropods at new Cenozoic localities over the past decade is providing an expanded perspective on the past diversity and biogeographic patterns of arthropods in New Zealand. In particular, finely laminated lacustrine diatomites at two Miocene maar-type fossil Lagerstätten in Otago, southern New Zealand, have yielded well preserved compression fossils of arthropods, along with diverse micro- and macrofloras representative of different rainforest palaeoecosystems in warm-temperate to subtropical climates. At the earliest Miocene Foulden Maar (Aquitanian; 23 Ma), the first insects (14 scale insects attached to an angiosperm leaf) were discovered in 2007. Since then, fossils of 18 insect families in eight orders have been identified, dominated in diversity and specimen numbers by members of the Isoptera, Coleoptera and Hymenoptera, but also including representatives of the Odonata, Plecoptera, Hemiptera, Diptera and Trichoptera. In addition to insects, four spiders were discovered at Foulden Maar. Preliminary palaeontological excavations at the early Miocene (Aquitanian or Burdigalian) Hindon Maar in 2014 have yielded numerous compression fossils of the insect orders Hemiptera, Coleoptera, Trichoptera and Hymenoptera, with weevils (Coleoptera: Curculionidae) the most diverse group. The new fauna from Hindon Maar is currently under study.

Recently, New Zealand amber has become a promising new palaeontological source for fossil arthropods. Amber is nearly ubiquitous in coal-bearing sedimentary sequences across New Zealand, from the late Cretaceous and throughout the Cenozoic. The ongoing search for amber inclusions has yielded a diverse array of arthropods in Miocene amber from three localities on South Island. Preserved as 3-dimensional inclusions, the amber fauna so far includes arachnids, such as pseudoscorpions, diverse mites and spiders, representatives of springtails, as well as insects in the orders Psocoptera, possibly Hemiptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera. Preservation of arthropods from both amber and diatomite allows an identification to lower taxonomic ranks, often the first fossil record for Australasia, or on a global scale.

The geological setting, taphonomical aspects and the paleodiversity of the arthropod-bearing diatomites and amber in New Zealand will be outlined, and commonalities and differences to the modern New Zealand arthropod fauna will be highlighted and discussed.

## Earwigs (Dermaptera) from the Mesozoic of England and Australia, described from isolated elytra

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Earwigs are rare in the fossil record, with the oldest described species *Brevicula gradus* Whalley, 1985, from the Lower Lias (Lower Jurassic) of England. We examined previously unstudied and hitherto unrecognised earwig specimens, consisting predominantly of isolated elytra, from the Late Triassic to the Early Cretaceous of England and Australia, most of which are in the collection of the Natural History Museum, London. As a result, new taxa have been discovered and are being described. *Phanerogramma heeri* (Giebel, 1856) was named more than 150 years ago and there has been much confusion over its correct taxonomic placement. Originally it was thought to be either a homopteran or blattodean and was subsequently redescribed and placed within Coleoptera by Cockerell (1915), so it has had quite a turbulent history. Only now has its correct identity been established, based on a number of specimens from different localities.

Cockerell, T.D.A. 1915. British Fossil Insects. *Proceedings of the United States National Museum*, 49: 469–499.

Giebel, C.G. 1856. *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere. Die Insecten und Spinnen der Vorwelt*. F. U. Brockhaus, Leipzig.

Whalley, P.E.S. 1985. The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. *Bulletin of the British Museum (Natural History), Geology Series*, 39(3): 107–188.

## Mesozoic evolution of green lacewings (Neuroptera: Chrysopidae)

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Today, the Chrysopidae is the second largest family of Neuroptera, comprising about 1200 species. The first green lacewings appear in the fossil record in the latest Middle Jurassic. The earliest record of Chrysopidae has been reported from the Daohugou locality, China (Khramov *et al.*, 2015). Green lacewings are rather abundant in the Middle Jurassic–Early Cretaceous localities following their first appearance.

Almost all Mesozoic green lacewings belong to the extinct subfamily Limaiinae, except for a couple of rare genera, whose subfamily affiliation has not been established. The cosmopolitan genus *Mesypochrysa* Martynov, 1927 and very closely allied genera, which are likely to be synonyms (Khramov *et al.*, 2015), make up the majority of Mesozoic Limaiinae (>90% of specimens). *Mesypochrysa* represents the most abundant and widespread taxon of all Mesozoic lacewings. Seventeen species of *Mesypochrysa* have been described to date. Apart from the Asian region, this genus has been reported from the Early Cretaceous Durlston Formation (England) and the Crato Formation (Brazil). The only other well-established genus of Mesozoic Limaiinae is *Baisochrysa* Makarkin, 1997, which was also widely distributed throughout Asia in the Middle Jurassic–Early Cretaceous. However, in contrast to *Mesypochrysa*, *Baisochrysa* is known from very few specimens.

The Upper Cretaceous record of Chrysopidae is scarce, with the single, poorly preserved specimen of *Cretachrysa* Makarkin, 1994 described from the Cenomanian of the Far East (Russia), which probably belongs to Limaiinae. The larvae of Mesozoic green lacewings are almost unknown. Only two Mesozoic chrysopoid larvae have been described: *Hallucinochrysa* Perez-de la Fuente *et al.*, 2012 from Albian Spanish amber and a first instar larva from Campanian Canadian amber. Some chrysopoid larvae appear to be present in Early Cretaceous Burmese and Lebanese ambers.

Limaiinae survived into the early Eocene as a minor part of the green lacewing assemblage, when they were probably exterminated by ants, which became much more numerous during that period. The larvae of Limaiinae could have lacked defense mechanisms, like trash-carrying behavior and high maneuverability, which are needed for feeding on aphids and other Sternorrhyncha protected by ants. It may be a reason why this predominantly Mesozoic lineage became replaced by the recent subfamilies of Chrysopidae.

Khramov, A.V., Liu, Q., Zhang, H.C. & Jarzembowski, E.A. 2015. Early green lacewings (Insecta: Neuroptera: Chrysopidae) from the Jurassic of China and Kazakhstan. *Papers in Palaeontology*, DOI: 10.1002/spp2.1024.

## On the constancy of the subfamily Cupedinae (Coleoptera: Cupedidae) in time: explanation and significance

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The generalised structural pattern seems to be most stable among members of the subfamily Cupedinae compared to any other archostematan subfamily represented by more than ten fossil members. Fossil specimens studied so far suggest that the structural cupedine type or cupedine morphotype evolved at a very early stage in the evolutionary development of the family, which originated close from the phylogenetic root of Archostemata. The *Priacma*-type of aedeagus is plesiomorphic for both the family and probably the order in general. The Middle/Late Triassic *Kirghizocupes* shares many structural characters with modern groups. The distinguishing characters of *Priacma* can preliminarily be recognised as apomorphic. However, the plesiomorphic aedeagus in *Priacma* supports an inherited continuity of its structural peculiarities from the ancestor of the Holometabola. Changes in food plants in the Mesozoic seem not to be reflected in structural features of the family. The ecology and bionomy of its fossil and Recent members were, and probably still are, more dependant on the structure of wood tissues, also on the fungal and microbial compositions associated with wood rather than the systematic position of food trees. Data on the Cenozoic pre-Pleistocene faunas of cupedines are still scant and many species already collected and deposited in scientific collections are still awaiting formal study. The difference in the male genitalia of *Priacma* and *Gracilicupes*, on one hand, and those of other genera with known male genitalia, on the other hand, seems to support the viewpoint that these lineages must be rather old. The combination of plesiotypic and apotypic characters available in the extant members of this group does not correspond to the sequence of diversifications. Hypotheses of relationships based on formal structural analysis of characters fail to correspond to the patterns which can be observed in the historical development of archostematans. The existence of *Priacma serrata* among the Recent members of the subfamily makes it possible to trace very old structural features of the family, suborder and order. Such studies permit the generation of hypotheses regarding the early diversifications of the order, particularly the appearance of the male aedeagi characteristic of each coleopterous suborder.

## A preliminary classification of the Mesozoic family Parandrexidae (Coleoptera)

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Two genera of the extinct beetle family Parandrexidae are known from the Jurassic of eastern Siberia and north-eastern China, as well as from the Cretaceous of Spain. The species are considered floricolous, with distinct sexual dimorphism. The systematic position of the parandrexids remains unclear: in the original description, *Parandrexis* Martynov, 1926 was classified within Cerambycidae, while later authors speculated upon its relationship to Boganiidae and Cleroidea, or suggested an intermediate state between basal Cucujoidea and Phytophaga. By courtesy of Huang D.-Y., the author was given the opportunity to study about 30 well preserved parandrexid fossils in the Nanjing Institute of Geology and Palaeontology, China. They originated from Inner Mongolia, China (Jiulongshan Formation, Middle Jurassic, approximately 165 Ma) and constitute some of the earliest known fossils of this beetle family. Apart from descriptive taxonomy, this communication constitutes a further attempt to clarify the systematic position of Parandrexidae. The original dataset (366 beetle genera, 515 morphological characters of adults and larvae) of Lawrence *et al.* (2011) was used, but in a considerably adapted and modified format. About 200 genera of cucujiform beetles were selected together with some 20 outgroups from other Polyphagan families. After unambiguous optimisation in WinClada 1.00.08, more than 200 morphological characters were retained. Some of these were modified and certain characters added. TNT 1.1 was used for parsimony analysis, employing traditional search strategy (or heuristic analysis). Characters were unweighted and treated as unordered; all were switched as non-additive. The majority rule consensus technique was applied. In the first step, extant taxa were analysed and the tree was rooted with a hypothetical ancestor. The character matrix was then recounted by TNT with the same parameters, together with the identified characters of parandrexids, in order to establish their approximate positions. Preliminary results of the analysis show well-defined superfamilies of Cucujiformia and, surprisingly, place Parandrexidae once more within a clade of phytophagan families.

Lawrence, J.F., Slipinski, A. Seago, A.E., Thayer, M.K., Newton, A.F. & Marvaldi, A.E. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici (Warszawa)*, 61(1): 1–217.

## **Diptera and Mecoptera from a little known locality in Germany (Jurassic, Lower Toarcian)**

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The locality “Große Kley” is located in a part of Wolfsburg, Lower Saxony in Germany and is dated as Jurassic, Lower Toarcian (182.7–174.1 Ma). Twelve specimens of Diptera and Mecoptera that were found during house building activities in the 1980s were investigated for the present study. The fossil material is unfortunately poorly preserved, although some are good enough for taxonomic purposes. Three specimens of Mecoptera from the family Orthophlebiidae and nine representatives of Diptera from the following families were identified: Limoniidae, Eoptychopteridae and Anisopodidae. The fossil fauna of Wolfsburg is similar to those from other Lower Jurassic sites in Germany, described by Handlirsch (1939), Bode (1953) and Ansoerge (1996).

- Ansoerge, J. 1996. Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Paläontologische Abhandlung*, 2: 1–132.
- Bode, A. 1953. Die Insektenfauna des ostniedersächsischen oberen Lias. *Palaeontographica A*, 103: 1–375.
- Handlirsch, A. 1939. Neue Untersuchungen über die fossilen Insekten. 11. Teil. *Annalen des Naturhistorischen Museum Wien*, 49: 1–240.

## New immatures of Palaeodictyoptera from the Late Carboniferous of Poland

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Palaeodictyoptera are among the most specialised herbivorous groups of the Pterygota and one species, *Delitzschala bitterfeldensis* (Spilapteridae) from the Early Namurian of Germany, was for a long time considered to be the oldest record of winged insects. The nymphs have been reported from the Carboniferous deposits in Europe, North America and Russia by a number of authors (e.g. Rolfe, 1967; Carpenter & Richardson, 1971; Sharov, 1973; Kukalová-Peck, 1978; Sinitshenkova, 1979; and others). Wootton (1972) provided precise reconstructions of two onisciform immature palaeodictyopterans including their wing pads. They were named as *Rochdalia parkeri* and *Idioptilus onisciformis*, both originating from the Coal Measures of the UK. According to his results the prothoracic wings were capable of movement and these nymphs did not show adaptations for an aquatic lifestyle. Our findings of several new palaeodictyopteran nymphs in the Early Pennsylvanian deposits of the Upper Silesian Coal Basin in Poland, as well as re-examination of the Wootton's specimens, enabled us to provide further details on their morphology.

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## The significance of fossil material in understanding the homology of Mecoptera wing venation

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The order Mecoptera appeared in the Permian, but the Lower Cretaceous witnessed the greatest radiation of scorpionflies. Recently, the majority of scorpionflies have been grouped into two families: Bittacidae and Panorpidae. Seven additional families are species poor and are often represented mainly by relict species, like *Austromerope poultoni* (Meropeidae) or *Notiothauma reedi* (Eomeropidae). Mecoptera is a group of a special significance for understanding the evolution and phylogenetic relationships within and among several of the largest and currently most important insect orders, such as Lepidoptera, Trichoptera, Diptera and Siphonaptera. However, the unstable taxonomic system, numerous unsolved phylogenetic problems and unstable wing venation nomenclature of Mecoptera make the understanding of homology of individual veins difficult to interpret, thus hindering discussions on the phylogeny of these insects. Unfortunately, the nomenclature of wing venation (which has never been satisfactory) has become increasingly complicated as a result of successive taxonomists. Following our intensive investigation of fossil evidence, we conclude that the main goals and problems to be solved concerning Mecoptera wing venation nomenclature can be considered as follows:

- The homology and nomenclature of veins in costal (C) and subcostal (Sc) sectors.
- The nomenclature and homology of the radial sector (Rs), with special attention to its lower branch, which is considered by some researchers as homologous with medial veins.
- The nomenclature of medial veins (Ms).
- The nomenclature of the basal part venation, so-called vein  $M_5$  and route of  $Cu_2$ .

The stabilisation and standardisation of the terminology of veins would, in our opinion, facilitate drawing robust conclusions concerning the evolution and relationships of Mecoptera. In this presentation we try to find answers for at least some of the problems that require clarification.

## **Mantodea and Blattaria (Insecta) from the Aptian Crato Formation, Northeast Brazil**

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The Crato Formation is situated in the north central part of the Chapada do Araripe, a large plateau in north-eastern Brazil. The limestones from this location are famous for their wealth of fossils, including flora (gymnosperm and angiosperm), invertebrates, e.g. Chilopoda, Arachnida, Crustacea and Insecta and the vertebrate fauna including fish, anurans, turtles, lizards, crocodiles, pterosaurs and birds. More than 300 insect species have been described. All fossils originated from the Nova Olinda Member, with an age of ~120 Ma (Aptian). Cockroaches, mantises and termites represent a traditionally monophyletic Dictyoptera, originating in the Late Carboniferous and abundant throughout the entire Paleozoic. Mantodea are very rare in the fossil record – 28 fossil species have been reported since the earliest occurrence of mantoids in the Upper Jurassic. Three species with primitive characters have been reported from the Crato Formation. About 26% of arthropods in the Crato Formation are cockroaches. Although abundant, the species diversity is generally low, with only a dozen species reported and with thousands of specimens representing just three dominant species. The Crato dictyopteran faunal assemblage is similar to those of the Cretaceous localities of Mongolia, namely Chaeteessidae, Ectobiidae, Blattulidae and Umenocoleidae.

## Phylogeny of Mesopsychidae (Mecoptera) and origin of the proboscis in early Mecoptera

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Within Mecoptera, Mesopsychidae and three other families: Aneuretopsychidae, Pseudopolycentropodidae and Nedubroviidae, form a major clade of basal Mecoptera, the Aneuretopsychina, which have elongate, siphonate proboscides, and likely fed on pollination drops of gymnosperms. Phylogenetic relationships among Mesopsychidae and other mecopteran-related families, including extinct basal panorpoids, extinct basal mecopterans and extant mecopterans have been reported. However, the phylogeny of genera within Mesopsychidae and the origin of the long siphonate proboscis in early Mecoptera have not been studied formally, attributable to the limited number of well preserved fossils. Recently, based on data from two newly erected species and previously described representative species, we selected a suite of unique characters and carried out phylogenetic analyses to shed light on the taxonomy, classification and phylogeny of the genera within Mesopsychidae. We also applied geometric morphometric analyses to supplement the phylogenetic analyses. Four important findings are presented:

- Phylogenetic results support that Mesopsychidae is a monophyletic group, and the systematic positions of the two new species are confirmed.
- Based on our phylogenetic analyses and geometric morphometric analyses, we suggest to revise the taxonomy of some species of *Mesopsyche*.
- It is suggested that the long-proboscid condition might have independently originated four or five times within the early Mecoptera.
- It is hypothesised that repeated rounds of suppression of *ext* and *hth* genes could explain initial stages of the proboscis origin among the early Mecoptera.

Future discovery of well preserved material and studies and examinations of mouthparts of these fossil specimens will augment our understanding of the origin of early Mecoptera and their siphonate proboscides.

## Systematics of Mesozoic Apocrita (Hymenoptera) from China

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The Lower Cretaceous Yixian Formation and the Middle Jurassic Jiulongshan Formation, both located in northeastern China, have yielded many well preserved apocritan fossils. Based on morphologic characters of these apocritans, we have conducted taxonomic studies and, in some cases, phylogenetic analyses to provide insights of their evolutionary trends, origination and dispersal, and potential roles in the palaeoecosystems. Up to date, we have described 49 new species in 17 new genera and eight families: Anomopterellidae, Ephialtitidae, Evaniidae, Heloridae, Mesoserphidae, Pelecinidae, Praeaulacidae and Scolebythidae. Three cases of key findings will be presented:

- Based on the research of the broad articulation between the propodeum and metasoma in basal Ephialtitidae, we suggested three separate pathways of the transformation of the “wasp waist” in three different derived lineages leading from Ephialtitidae to: (i) Kuafuidae and further to the remaining Apocrita, (ii) Stephanidae, and (iii) Evanioidea.
- According to phylogenetic analyses and the temporal and spatial distribution of pelecinids, the most parsimonious hypothesis is that the basal species initially originated in northeastern China and spread to central and eastern Asia, and then dispersed to the Americas.
- In Evaniidae, except for three genera from the Cenozoic, all thirteen other genera are from the Cretaceous, suggesting that Evaniidae most likely originated in the Late Jurassic or near the Jurassic–Cretaceous boundary, and radiated in the Early Cretaceous.

These findings from the Middle Jurassic to the Early Cretaceous of northeastern China have enhanced our knowledge of Apocrita and provided a foundation for future studies with new fossil (including amber) specimens.

## **New data on the age of the Lower Cretaceous amber of Lebanon**

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Lebanon is famous for its numerous amber outcrops (more than 450 localities) occurring in different geological layers, ranging from the Late Jurassic (Kimmeridgian) to Albian. Most of the outcrops are stratigraphically Lower Cretaceous, among which around 25 are intensively fossiliferous. Several ages have been attributed to those fossiliferous ambers (sometimes Neocomian, sometimes Lower Aptian) according to several workers and based on geological facies and lithostratigraphy. This way of dating is regarded today as facies-driven and poorly constrained. In the upper part of the “Sandstone of Lebanon”, i.e. beneath the recently created regional stage: the Jezzian (an Unconformity Bounded Unit), we identified three discrete intervals characterised by their richness in amber with biological inclusions, mostly insects. The upper interval is located between the lower Jezzian unconformity and the “Mrejatt bed”, and dated Late Barremian, the middle interval is located between the “Mrejatt bed” and a pisolitic interval, and dated Early Barremian; the lower amber level is located below the pisolitic interval and dated Early Barremian or (possibly) older. The entomofaunal composition and associations of the amber-bearing deposits in the three levels are very similar, suggesting that the amber and its inclusions (from the three levels) are most likely of the same age, though the amber-bearing deposits can obviously not be given the same age. It is suggested that the amber of at least the two higher intervals, has been reworked from possibly the lower interval or before. Moreover, the amber found at those levels have shipworm perforations on their surfaces, indicating that the resin was already hardened when deposited in its final bed. The polymerisation process of the resin into copal or amber is believed to be chronophagous. Accordingly, the age of the fossiliferous amber from the “Sandstones of Lebanon” could be at youngest Early Barremian or even older.

## **On the systematic position of a highly derived Amphiesmenoptera insect from Burmese amber (Insecta: Amphiesmenoptera)**

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Amphiesmenoptera combine the orders Trichoptera and Lepidoptera. Dating analyses based on molecular chronograms across many Lepidoptera groups yielded different results for the early divergence in Lepidoptera spanning a period from 215 Ma (late Triassic) to 160 Ma (late Jurassic). Also, the origin or time of the basal split of both orders cannot be determined with a better precision from the fossil record. The descriptions of Mesozoic fossils are almost always based on wing venation, a character insufficient to discriminate between Trichoptera and Lepidoptera. The oldest Lepidoptera species are supposed to be *Archaeolepis mane* Whalley, 1985 from the Lower Lias of Dorset (England) and two species from the Upper Lias of Grimmen (NE Germany), which were tentatively assigned to Micropterigidae. The assignment of these Early Jurassic species to Lepidoptera is based solely on the observation of wing scales. In the absence of any other distinguishing characters the presence of scales is regarded as the principal trait that defines Lepidoptera and separates the group from remaining Amphiesmenoptera, including Trichoptera. We follow this view here, and consider a small amphiesmenopteran insect from Burmese amber with wing scales as a fossil representative of Lepidoptera. With an age of ~100 Ma the Burmese amber is of Early Cretaceous origin (Albian). At that time, the evolution of the Lepidoptera had been under way for 55 Ma and the extant family Micropterigidae already existed. The Micropterigidae, together with extant Agathiphagidae and Heterobathmiidae are the basalmost groups of Lepidoptera (= Aglossata). Their systematic position is based on a number of apomorphies and groundplan characters. In contrast to the rest of the Lepidoptera, the adult moths retained functional mandibles and an undifferentiated maxilla.

The specimen from Burmese amber is relatively well preserved and allows the examination of important character complexes. The insect is described in detail, and photos and line drawings are provided for wing venation, head, mouthparts, legs and abdomen. All characters shared with primitive Lepidoptera are symplesiomorphies or groundplan traits of Amphiesmenoptera. In contrast, the Burmese fossil has a number of remarkable autapomorphies giving it an appearance that deviates strongly from Lepidoptera and Trichoptera. The species, representing a family of its own, is provisionally placed at the base of the Lepidoptera phylogeny together with the Aglossata. An alternative placement, outside the Lepidoptera, would imply an independent and multiple evolution of wing scales in stem-group Amphiesmenoptera.

KEYNOTE TALK  
**Amber research in the 21<sup>st</sup> century:  
trends and perspectives**

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Within the last few decades technological advances such as the internet and new imaging techniques (e.g. computed tomography and synchrotron scanning) have revolutionized how we do research in the 21st century. High quality publications resulting from international, interdisciplinary collaborations are now commonplace, though there is still much scope for improvement in certain branches of amber palaeobiology. This talk reviews trends in amber research over the past decade or so and highlights areas that warrant more focused research. Topics covered include important new Cenozoic and Mesozoic amber deposits, advances in imaging technologies, quantitative palaeoecology, molecular palaeobiology, and climate change/biogeography.

## **Aphid–*Buchnera*–ant symbiosis, or why are aphids rare in the tropics and very rare further south?**

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The Cainophyte tropical fauna of aphids was depleted because of the low heat tolerance of *Buchnera* and the associated switch of aphids to obligatory parthenogenesis at high average annual temperatures. Cretaceous aphids were affected more than other insects by the extinction event at the Mesozoic–Cenozoic boundary. Their extinction was simultaneous with the establishment of symbiosis between the surviving aphidoids and Formicinae or Dolichoderinae, which was accompanied by the rise and expansion of all three groups.

## African fossiliferous amber: a review

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Amber has only rarely been found in Africa and the few known occurrences are mostly devoid of organic inclusions. The first fossiliferous African amber was reported a few years ago from Ethiopia, and was considered to be early Late Cretaceous in age (Cenomanian, ~93–95 Ma). However, recent investigation of additional amber material and associated sediment questions the previously assumed age and provides compelling evidence that Ethiopian amber is Cenozoic, likely Miocene. Support for this dating is based on both new and revised palynological and palaeontomological data. Insect fossils mostly belong to extant families and genera. A particular reference to ants (Hymenoptera: Formicidae) is made here, with the report of 51 individuals assignable to new extinct species of Dolichoderinae (e.g. *Technomyrmex*), Formicinae, Myrmicinae (e.g. *Melissotarsus*, *Carebara*), Ponerinae and Pseudomyrmecinae (e.g. *Tetraponera*). Chemical analysis indicates that Ethiopian amber belongs to the Class Ic ambers typical of Fabaceae (although the earliest record of a Class Ic amber dates back to the Carboniferous) and was presumably produced by the genus *Hymenaea*, similar to East African Pleistocene copals and Neotropical Miocene ambers. Although much younger than previously suggested, fossils in Ethiopian amber remain highly relevant as Miocene insects are exceedingly rare in Africa.

The recent discovery of a new deposit of fossiliferous amber is also reported here, from the Early Cretaceous (Aptian, 113–117 Ma) of Congo-Brazzaville. Chemically, Congolese amber belongs to the Class Ib typical of conifers, and the family Cheirolepidiaceae is assumed to be the plant source. Amber nodules are dark red in colour, with large pieces reaching up to 12 cm. The search for organismic inclusions using conventional optical techniques is limited by the opacity of the amber, but diverse arthropods and plant remains have already been found in few more translucent pieces. A large survey using synchrotron imaging will be necessary to evaluate the overall biodiversity of Congolese amber, the only fossiliferous amber from the Cretaceous of Africa to date.

## **Corbiculate bees from the Middle Eocene of Río Pichileufú, Patagonia, Argentina**

**Julián F. Petrulevičius\* & Ari Iglesias**

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Middle Eocene bees are quite common in the Northern Hemisphere, and include the corbiculates of the Baltic amber, Messel and Eckfeld Maars (Germany) and the Parachute Creek Member of the Green River Formation (USA). As a result of persistent research on Patagonian localities, principally from Eocene ages, a couple of bees were recovered from a Middle Eocene (48 Ma) locality of Río Pichileufú, Río Negro province, Argentina. One of the bees has a conspicuous corbicula in the metatibia and 6–7 comb rows on the inner surface of a wide and elongated metabasitarsus. In addition, pollen clusters of monoporate (probable Poaceae) and tricolpate pollen grains are preserved on the abdomen. The previously known localities with fossil corbiculate bees in North America and Northern Europe share with Río Pichileufú, an early Lutetian age and a high palaeolatitude. The present discovery of eusocial bees in the Southern Hemisphere, together with the known distributions in the Northern Hemisphere, suggest a bihemispheric distribution in high latitudes for the clade Corbiculata during the middle Eocene.

## Palaeodictyopteroidea: new finds, morphology and development of wings

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Palaeodictyopteroidea are a specialised group of Paleozoic insects well known for the possession of unique rostrum-like piercing-sucking mouthparts and remarkable diversity in Carboniferous and Permian palaeoecosystems. However, the excessive adaptations of this group were probably the main reason why its members did not survive the Permian–Triassic mass extinction. Recently discovered new material of *Brodioptera sinensis* from Early Pennsylvanian deposits in Xiaheyan (Ningxia Autonomous region, China) documented by a large series of specimens, enhanced our knowledge on the intraspecific variability of megasecopteran wing venation. *B. sinensis* uncovers the detailed morphology of the haustellate mouthparts with conspicuous elongated stylets and male and female external copulatory organs that were previously unknown in Brodiopteridae or were poorly preserved. The female genitalia comprise an endophytic ovipositor with apical parts of the first and second valvulae bearing oblique ridges, and the male styliger plate has long two-segmented forceps.

Discovery of a palaeodictyopteran nymph *Bizarrea obscura* and a new adult specimen of *Homaloneura cf. dabasinskasi* in the Pennsylvanian ironstone nodules of Mazon Creek enlighten the morphology of immatures in Spilapteridae. Both taxa share a particularly unique division of the abdominal segments by two transverse sulci and apically pointed laterotergites. Nevertheless, an alternative hypothesis for the placement within Homiopteridae based on the size of the wing pads is also considered. Our comparative study of the morphology of abdominal segments revealed the presence of subcircular sclerotised structures beneath the nymphal laterotergites I–VII, ?VIII. These structures are well delimited and lack any emerging filaments. Instead the morphology is that of abdominal spiracles, indicative of a terrestrial or semiaquatic habitat for these immatures. Furthermore, our re-examination of the enigmatic Vogesonymphidae (Protereismatina), known from the Middle Triassic of Grès à Voltzia in France, confirms the presence of homologous structures, also interpreted as spiracles. Thus, our discovery supports the parallel coexistence of ancestrally terrestrial or semi-terrestrial lineages of Ephemeroidea in early Mesozoic ecosystems.

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## KEYNOTE TALK

**The Palaeozoic terrestrial arthropods of Scotland**

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Scotland is remarkable for yielding a high diversity of different terrestrial arthropods from the Silurian, Devonian and Carboniferous periods, often from particular times when they are unknown elsewhere in the world. The most notable discoveries include *Pneumodesmus newmani* Wilson & Anderson, 2004 – a millipede (Diplopoda) from the mid-Silurian of Stonehaven, Aberdeenshire, which is the earliest known fully terrestrial animal, as demonstrated by the presence of spiracles. This specimen suggests that other contemporary diplopods were also terrestrial. The Rhynie and Windyfield Cherts from the Early Devonian (Lochkovian) of Rhynie, Aberdeenshire, are remarkable for preserving the earliest known terrestrial ecosystem in the world, consisting of plant stems in situ, preserved at the cellular level, along with a diverse arthropod fauna including the earliest known hexapods (*Rhyniella praecursor* Hirst & Maulik, 1926, *Rhyniognatha hirsti* Tillyard, 1928 and *Leverhulmia mariae* Anderson & Trewin, 2003 – see Fayers & Trewin [2005]), along with trigonotarbid, acarine and opilionid arachnids, and a scutigermorph centipede (Chilopoda). Scotland has also yielded a diverse Early Carboniferous (Visean) diplopod, scorpion and opilionid fauna from East Kirkton, West Lothian. A recently discovered slightly older (Tournaisian) diplopod and scorpion fauna from Chirnside and Burnmouth, Berwickshire, along with numerous amphibian, plant and other invertebrate remains have filled ‘Romer’s Gap’ and demonstrate that this perceived gap was due to a lack of suitable non-marine deposits of that age rather than a dearth of terrestrial life due to low oxygen levels. Finds from the Late Carboniferous are much rarer than from other parts of the UK due to most of the Westphalian C and D deposits having been subjected to deep weathering, which removed the organic components and thus the deposits were not exploited for coal.

Fayers, S.R. & Trewin, N.H. 2005. A hexapod from the Early Devonian Windyfield Chert, Rhynie, Scotland. *Palaeontology*, 48: 1117–1130.

## Towards a new picture of the ‘Baltic amber forest’

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The Eocene Baltic amber deposit constitutes the largest accumulation of any fossil resin worldwide and it is particularly well known for the great diversity of arthropod inclusions it contains. However, the botanical origin of Baltic amber and the floristic composition of its source vegetation are still controversial, with conflicting evidence from chemical analyses of the amber and study of the botanical inclusions. To gain new palaeoecological insights we chose those amber inclusions of vascular plants that provide information about habitat structure and climate by comparing the inclusions to fossil analogous taxa and their nearest living relatives.

Our investigation of amber inclusions from historic collections and from recently discovered amber pieces revealed the presence of a range of extant and extinct conifer genera. Conifer inclusions encompass a variety of Cupressaceae (*Calocedrus* sp., *Taxodium* sp. and *Quasisequoia couttsiae*), one representative of the Geinitziaceae (*Cupressospermum saxonicum*), several Pinaceae (*Abies* sp., *Cathaya* sp., *Nothotsuga protogaea*, *Pinus* div. sp. and *Pseudolarix* sp.) and cladodes of Sciadopityaceae (*Sciadopitys* cf. *tertiaria*). Ecologically relevant angiosperms recovered so far comprise members of the Cyperaceae with affinities to *Rhynchospora* sp. and Poaceae, as well as representatives of the dwarf mistletoes *Arceuthobium* sp. (Viscaceae), and the first fossil record of the carnivorous plant family Roridulaceae.

These new findings hint to distinct source ecosystems: coastal swamps, back swamps and riparian forests, as well as mixed-mesophytic conifer–angiosperm forests with meadows and open areas. Based on the comparison of the climatic requirements and distributions of extant and fossil analogues of the amber inclusions, a warm-temperate humid climate is assumed. Our results challenge previous hypotheses about Baltic amber deriving from Lower Eocene tropical or subtropical forests.

## The use of fungi and lichens in the reconstruction of the 'Baltic amber forest'

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Fungal inclusions are common in amber from many deposits around the world. However, in most cases only sterile mycelia are preserved without any reproductive structures. As in extant fungi, taxonomic treatment of such specimens is hampered, and consequently relatively few amber-preserved fungal fossils have been assigned to extant lineages, so far.

Recent screening of Baltic amber pieces revealed that remains of corticolous fungi and lichens are more abundant than previously thought, and seem to be more overlooked than rare. We evaluated such amber fossils of Ascomycota both systematically and ecologically, and identified several taxa that can provide reliable information about vegetation structure and climate of the Baltic amber source area.

Calicioid fungi, a polyphyletic group within the Ascomycota, can be highly specific to certain forest types and climatic conditions, and the extant forms exhibit high selectivity in their microhabitat preferences. Furthermore, their abundance and diversity in modern forest ecosystems is climate and habitat dependent. As the group has a wide extant distribution and it dates back at least to the Eocene it can provide valuable information about forest conditions, past and present. The assemblage of calicioid fungi from Baltic amber most closely resembles those found in modern transitional mixed conifer forests along a transect across major temperate to warm-temperate forest types. Moderate humidity and semi-open forests with open-edge habitats are required to accommodate the diversity of these fungi from Eocene Baltic amber.

The lichen communities from Baltic amber reveal tremendous changes in the European lichen flora since the Eocene and include taxa that are today predominantly found in warm-temperate to temperate biomes. Some abundant Eocene taxa, including *Anzia* species, are today restricted to Northern and Southern Hemisphere relict areas. Many lichen taxa from Baltic amber possess special structures related to water supply and aeration of the thallus that we interpret as adaptations to relatively humid conditions.

**The oldest palpimanid spider (Araneae: Palpimanidae),  
from the Crato Fossil-Lagerstätte,  
Cretaceous of Brazil**

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Palpimanidae is a small family (16 genera, 139 species) of nocturnal, ground-dwelling spiders which occur mainly in tropical and subtropical regions of the world, except Australia. They are characterised by an extremely thick cuticle on all parts of the body except the opisthosoma (even here, there are commonly sclerotised scuta) and enlarged front legs. By this means, they stalk and capture other spiders as prey, and are armoured against retaliatory bites. Spiders from the Cretaceous Crato Fossil-Lagerstätte of Brazil are relatively numerous but, hitherto, few have been described. Here, we present a single specimen of a palpimanid from this locality. It is the oldest member of the family and the first Mesozoic record; the previously known oldest, and only known fossil occurrence of Palpimanidae, are three juvenile specimens of the extant genus *Otiothops* MacLeay, 1839. Nevertheless, the superfamily Palpimanoidea has representatives dating back to the Jurassic period, so the existence of the nominate family in the early Cretaceous is not unexpected. The excellent, three-dimensional preservation of this specimen, together with synchrotron CT-scanning technique, used for the first time on a matrix-preserved fossil spider, we have been able accurately to place this specimen in the extant subfamily Palpimaninae.

## **Associations of insects with plants, other insects and vertebrates in two mid-Mesozoic ecosystems of Northeast China**

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The Lower Cretaceous Yixian and Middle Jurassic Jiulongshan Formations of northeast China have yielded well preserved fossil plants, insects and vertebrates which have provided a significant amount of palaeoecological data for demonstrating the ubiquity of autecologic relationships. We present nine categories of biotic associations involving seven orders of insects that interacted with coexisting plants, other insects and vertebrates.

There are four examples of associations with plants: (1) The pollination mutualism was demonstrated by three families of pollinating Mecoptera that evolved convergent long-proboscid siphonate mouthparts for consumption of pollination drops from tubules or channels in gymnosperm ovulate organs; (2) Mimesis or camouflage was present in two lacewing taxa (Neuroptera) that imitated co-occurring pinnate gymnosperm pinnules; (3) Similarly, a scorpionfly (Mecoptera) involved mimicry of an entire, co-occurring ginkgo leaf, presumably providing mutual protection to the plant model and the insect mimic; (4) Considerable insect damage occurred on a variety of plants involving galls by beetles (Coleoptera) and stylate punctures and margin feeding, probably by Hemiptera and Orthoptera, respectively, among others, on vascular-plant tissues.

There are three instances of associations with other insects: (1) Parasitoidy was implied by ovipositors of apocritan wasps such as Ephialtitidae and Pelecinidae (Hymenoptera); (2) Male–male competition and sexual display were represented by two genera of Mecoptera with exaggerated male organs; (3) Reproduction was highlighted by a pair of copulating froghoppers (Hemiptera), hitherto the earliest record of copulating insects *in flagrante delicto*.

Last, we report two cases of associations with vertebrates: (1) Integumental blood feeding was established by ectoparasites, such as early and transitional fleas (Siphonaptera) that possessed long beaks consisting of robust, outwardly directed, serrated stylets involved in piercing thick vertebrate integument and imbibing host blood and possibly lymph; (2) Two taxa of the earliest known blood-feeding true bugs (Hemiptera) were discovered from the use of geochemical methods for determining their diets and a combination of morphological and taphonomic data.

These intricate associations provide an expanded understanding of the ecologic role and evolutionary developments that insects had with other organisms in mid-Mesozoic ecosystems.

## Mapping the diversity of names: trying to clear up the nomenclature of French Oligocene Bibionidae (Diptera)

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Bibionid flies are very abundant among insect fossils from the Oligocene of France, and a large number of species have been named from this period during the 19th and (first half of the) 20th centuries. Many of the taxa were based on type specimens which show very few diagnostically relevant characters, and characters used to distinguish taxa are often of taphonomic origin and hence not systematically relevant. This has led to many species being described repeatedly. We have attempted to revise the material of French Oligocene bibionids, with the aim of producing a workable and reliable key to the species. This has proved difficult since the types of many previously described species are lost or unrecognizable. We have found about 95 specific names given to French Oligocene bibionids, in contrast we were able to recognise just 29 plausible species from the material, three of which were previously undescribed. Since bibionid flies are very abundant in the 'Tertiary' fossil record and the different genera have fairly distinctive climate preferences, this group has some potential as a proxy in reconstructions of past climates. However, we found that a large fraction of the nominal species have been placed in the wrong genus, making the previously published information useless for such purposes. It is difficult to draw a non-arbitrary line between the genera *Penthetria* and *Plecia* in the fossil faunas. We discuss the various problems encountered when trying to sort out the unrealistic diversity of names for the French Oligocene bibionids.

## **Sticky traps and resin vs amber: an actualistic approach in Mexican and Malagasy forests**

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Amber is fossil resin that functioned as a trap, preserving ancient organisms with great fidelity even from the distant past. It represents a window into past biodiversity and ethology. Using artificial tree trunk sticky traps and natural resin emissions from the trees as amber analogues, we can study the taphonomy of Recent tree trunk associated faunas and compare these with the assemblages preserved in Cenozoic ambers. We compared selected arthropod groups collected with sticky traps and resin in Recent forests in Mexico and Madagascar having *Hymenaea* trees with fossil faunas associated to *H. mexicana*/*H. allendis*, and *H. protera* (supposedly the Miocene Mexican and Dominican amber producers, respectively). The main aims were to review key questions about taphonomic biases and filters of the processes of fossilisation based on representative taxa in amber and to produce well-documented general, palaeoecological interpretations of the global amber fossil record.

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## What “*Orthophlebiidae*” really means: preliminary results of a revision of the family *Orthophlebiidae* (Insecta: Mecoptera)

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The family Orthophlebiidae was described by Handlirsch in 1906 and besides the family *Permochoristidae*, was one of the two largest extinct families of the order Mecoptera. The number of genera and species within this family fluctuates due to a very unstable and changing taxonomic system. However, an estimated 190 species have been described from all regions of the world. The unclear taxonomic position of this family and its very weak and unclear diagnosis result in constant shifts within the Mecoptera phylogenetic system and it is considered to be either polyphyletic (“*Orthophlebiidae*”) or monophyletic (*Orthophlebiidae*). The lack of a comprehensive analysis of orthophlebiids results in the inclusion of numerous newly described taxa of doubtful taxonomic position, often without any necessary justification, to this systematically ill-defined group. This increases the existing chaos in the taxonomy of Mecoptera. Thus, in our opinion the group of species “*Orthophlebiidae*” form a center of attention in taxonomy and phylogeny of the modern lineages of Mecoptera. The taxonomic revision and redefinition of this controversial family will prevent future misinterpretation and help to clarify its phylogenetic relationships. Based on the holotypes from the German collections of Handlirsch and Bode, the English collection of Tillyard and the Russian collections of Martynov, Martynova, Sukatsheva and Novokshonov, in addition to new material from England and China, we restudied the species included in Orthophlebiidae. Here we present the preliminary results of this taxonomic investigation.

## **Palaeobiogeography and palaeoecology of Diptera from Early Eocene Indian amber**

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A highly fossiliferous amber deposit from the Early Eocene of India provides the opportunity to investigate India's geological history and get insight into a terrestrial ecosystem in tropical latitudes at the beginning of the Early Eocene Climatic Optimum. As in many other types of amber the Diptera are the most common and diverse inclusions in Cambay amber from India. Investigation of selected dipteran groups revealed relationships to fossil taxa from contemporaneous Fushun amber (Ceratopogonidae) and amber from the Baltic region (Ceratopogonidae, Lygistorrhinidae), indicating that the Indian subcontinent was not highly isolated at the time of the amber formation. In addition, some Cambay amber Ceratopogonidae have modern representatives, which today have distribution patterns ranging from ubiquitous to endemic to the Australian and Oriental Region. The latter group includes the first fossil of the genus *Camptopterohelea*. Synchrotron micro-computed tomography has revealed a pocket like structure on the wings, which was previously unknown in fossil or modern Ceratopogonidae. Its morphological resemblance to scent organs of certain Lepidoptera implies a pheromone related function. The fossil might represent one of the rare cases in palaeontological research where evidence for behavioural traits can be provided.

## Indicative value of Ceratopogonidae (Diptera) in biostratigraphy, identification of ambers and ecological reconstructions

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Biting midges (Diptera: Ceratopogonidae) are a relatively well-studied, large family of nematocerous flies inhabiting a wide range of aquatic, semiaquatic and terrestrial habitats, with almost 6300 extant species grouped in more than 110 genera and four subfamilies. The phylogenetic history of the family probably dates back to the Jurassic, although the oldest fossil records are from the Lower Cretaceous (140 Ma). This family includes numerous fossils from the Lower Cretaceous to the Miocene, comprising almost 280 species (4.3% of the family) in 48 genera (25 extant, 23 extinct). Fossil biting midges have been described mainly from amber inclusions. They show well preserved morphological details allowing them to be studied with a taxonomic equivalency to extant forms. The morphological criteria used in the identification of fossil genera and species are identical to those used in studies of the extant fauna and, as a result, the potential indicative value of fossils is reliable. Two relictual extant genera (*Leptoconops* and *Austroconops*) reported from Lower Cretaceous Lebanese amber are at least 135 million-years-old. The latter genus is a typical living fossil. In Oligocene–Miocene deposits no strictly fossil genera have been reported. The ceratopogonid genera indicative for the Lower Cretaceous are *Lebanoculicoides* and *Archiculicoides*, for the Upper Cretaceous include *Protoculicoides*, *Brachycretacea* and *Peronehelea*, and for the Eocene are *Gedanohalea*, *Eohalea* and *Mantohalea*. Biting midges preserved in Baltic amber from Ukraine, Bitterfeld and the Gulf of Gdansk indicate that they inhabited similar palaeoenvironments in the same palaeogeographic region. Some taxa are indicative for forests (*Forcipomyia*), seashore environments (*Leptoconops*), boreal (*Ceratopogon*) or tropical palaeoecosystems (*Baeodasymyia*, *Leptoconops*, subgenus *Phytohelea* of *Forcipomyia*).

## Unity, diversity and conformity of bugs (Hemiptera)

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True bugs, order Hemiptera, are an incredibly diverse and successful group, with nearly 300 extant and extinct families known (they represent one of the Big Five insect orders), inhabiting all terrestrial and some marine habitats. The order has a long and complicated evolutionary and taxonomic history. Since the Carboniferous their evolutionary history has incorporated many originations and extinctions, ecological shifts and revolutionary changes. Since the time of Linnaeus, the views on their scope and classification have varied. The recent opinion of Hemiptera comprising six suborders seems to be corroborated. However, the monophyly and relationships between the subunits are still the subject of debate. The first division of ancient Hemiptera took place in the Carboniferous – sternorrhynchan lineage vs. euhemipteran lineage. Euhemiptera are believed to be monophyletic, the monophyly of sternorrhynchans is disputable. This is not only based on the fossil record and its interpretation, but also the different evolutionary strategies, range of adaptations and heterogeneity presented by the Hemiptera. Firstly, global events (climatic, abiotic) influenced the history of the hemipterans in different ways. Secondly, biotic changes, such as host availabilities, host shifts and adaptations have shaped the evolutionary scenarios of the bugs. Thirdly, long-term interaction with various internal symbionts and external partners, have carved their marks on the evolutionary traits of the group.

Viewed from one angle, the Hemiptera can be treated as a uniform, monophyletic group, presenting number of autapomorphies, recognisable in both extinct and recent forms. However, the other side of the coin is rather blurred. The very early stages of Hemiptera evolution remain virtually unknown. A number of questions concerning the formation and specialisation of the rostrum remain unanswered. The head capsule structure needs to be reinterpreted. The wing structure, venation pattern (including a homologous nomenclature) still need to be elaborated. The genital structures and the homology of these elements are still disputable. The behaviour and other biological features, such as sound production, chemical communication, wax production and use, need attention. The endosymbiotic interactions and their influence on food-adaptations and evolutionary processes are still far from understood. The mutualistic interactions with other organisms is another challenging field of research. Some of these questions and problems can be at least partly answered with fossils. The uniformity of the Hemiptera in some features, juxtaposed by the enormous diversity in others, high adaptability to various conditions, and developmental plasticity are all phenomena that are recorded in fossils. The evolvability of the Hemiptera and their potential for great diversification, make the study on this group frustrating on one hand, but fascinating on the other.

KEYNOTE TALK

**Chinese amber: progress and prospects**

**Bo Wang**

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Amber is not frequently found in China, and only some scarce records have been presented to date. We recently reported on the Fushun amber biota (50–53 Ma) from northeastern China, which fills a large biogeographic gap in Eurasia. Fushun amber is derived from cupressaceous trees as determined by gas chromatography-mass spectrometry, infrared spectroscopy and paleobotanical observations. Twenty-two orders and more than 80 families of arthropods have been reported so far, ranking it among the most diverse amber biotas. Some insect taxa have close phylogenetic affinities to those from coeval European ambers, demonstrating a biotic interchange between the eastern and western margins of the Eurasian landmass during the early Paleogene.

Within the last five years, several new fossil localities have been found, such as the Eocene Nima amber in Tibet, Yanji amber in northeastern China and the Miocene Zhangpu amber in southeastern China. So far, more than 3000 amber pieces have been collected from the Zhangpu amber mine, and each piece commonly contains some insects. The Zhangpu amber biota will provide novel insights into the evolution of Asian tropical rainforests and intercontinental faunal interchange driven by the mid-Miocene climatic warming.

## The first discovery of fossil Orthoptera in the Jiuquan Basin and its palaeogeographic significance

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In the Jiuquan Basin of Gansu Province, northwestern China, the Lower Cretaceous Xinminpu (Xinminbao) Group consists of the Chijinpu (Chijinbao), the Xiagou and the Zhonggou formations in ascending order. Abundant insect fossils have been discovered in these strata since 1947 when the giant mayfly *Ephemeropsis trisetalis* Eichwald was discovered in the Jiuquan Basin. Typical components of the Jehol Biota have been reported from this basin, including *Coptoclava longipoda*, *E. trisetalis* and *Lycoptera*. Although these strata have been studied for a long time, their age is still in dispute. Recently, we found a fossil Orthoptera, *Parahagla sibirica* Sharov, 1968, from the Chjinbao Formation in the Jiuquan Basin, representing the first discovery of fossil Orthoptera from this locality. The diagnosis of the species has been revised based on the new specimen. To date, more than ten specimens assigned to *P. sibirica* have been found in the Lower Cretaceous of Siberia and North China, based on which we discuss its palaeogeographic and stratigraphic distributions. Two possible migration paths of the species are indicated as follows: (1) This species initially appeared in northern Hebei and western Liaoning, China at latest in the earliest Aptian, and further migrated northwestwards to Transbaikalia and westwards to Gansu Province soon after (early–middle Aptian). (2) Alternatively, it originally occurred in Transbaikalia earlier than the Aptian and further migrated southwards to northern China during the Aptian.

## **Iceland: a special island in the North Atlantic**

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Islands improve our understanding of the ecology and evolution of communities in general and have been model systems of choice for biologists ever since Wallace and Darwin. As such, Iceland is the only known terrestrial place in the subarctic North Atlantic providing a continuous sedimentary and plant fossil record for the past 15 million years. While the basic framework of this pattern has been well established during the last couple of years, less attention has been paid to the abundant insect traces on leaves. Here, we assessed the diversity and frequency of insect herbivory on nearly 4500 fossil angiosperm leaves and leaflets from six plant-bearing sedimentary formations exposed at several localities. In total, we documented 49 damage types (DTs) representing seven functional feeding groups (FFGs). The FFGs comprise external foliage feeding (hole, margin and surface feeding), piercing and sucking, oviposition, galling, and mining on 42 plant hosts, occurring with a frequency of 4.9–24.1% of total herbivory.

By combining analyses of environmental factors, species interactions, ecology, biogeography and the geological history, we could demonstrate how patterns of herbivory have changed over time, and establish likely climatic envelopes that profoundly influenced levels of insect-mediated damage diversity and frequency. In addition, higher structural complexity, particularly the establishment of extended herb layer communities seems to positively influence the structure of insect communities in the Icelandic palaeoforests.

## Innovations and disparity in Eocene insects

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Eocene insects can showcase the high potential of innovations and of disparity in insects. Some examples of Eocene bugs (Heteroptera) and lacewings (Neuroptera) demonstrate that the morphological diversity among these insect groups was formerly more much complex than previously known.

In one example, lace bugs (Tingidae) from Green River (USA) have antennae with an extremely enlarged apical segment situated on a long antennal stalk. Such strongly enlarged last antennal segments do not occur in extant lace bugs. However, similarly enlarged antennal segments are known today from leaf-footed bugs (Coreidae), where they possibly play a role in male–male competition or as a long-distance attractant for females. These apically enlarged antennae are an example of convergent evolution in lace bugs and leaf-footed bugs (Wappler *et al.*, 2015). Another example for exaggerated morphological features can be found in stink bugs (Pentatomidae) from Green River and Messel (Germany). These stink bugs exhibit a peculiar morphology in possessing very spiny humeral angles of the pronotum and also spines on other parts of the body. A similar morphology is rare among extant pentatomids, and the phylogenetic relationships are still under investigation. A possible function of this extreme morphology may be defense against predators, as spines and protuberances of the body complicate predator handling (Wedmann *et al.*, in prep).

Baltic amber inclusions of rare neuropteran larvae probably belonging to the Berothidae were found to possess unique morphological characters, e.g. unusual segment numbers in the antennae and labial palps. These larvae were impossible to place in any of the known extant groups. A complicating factor was that the larvae of several extant subgroups of Berothidae are currently unknown, and so the fossils may well be the first record of one of these extant groups. From the different morphologies of the berothid larvae from Baltic amber we were able to deduce that both termitophilous and non-termitophilous lifestyles were present in the Eocene (Wedmann *et al.*, 2013).

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## **The diversification and systematics of Mesozoic Auchenorrhyncha (Hemiptera) from China**

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The Lower Cretaceous Yixian Formation and the Middle Jurassic Jiulongshan Formation from northeastern China, and the early Miocene Garang Formation from the northeastern Tibetan Plateau, have yielded many well preserved insect fossils. We conducted morphological studies and phylogenetic analyses to provide insights into their evolutionary trends, origination and dispersal. To date, we have described many new species assigned to the families Palaeontinidae, Tettigarctidae, Procercopidae, Sinoalidae, Erlangshanidae, Fulgoridiidae and Cixiidae. Our principal findings and their significance are as follows:

- A new hairy species of Tettigarctidae provides evidence that tettigarctids with long dense hairs had appeared by the latest Middle Jurassic.
- A new species of Cixiidae was described, representing the first fossil insect from Qinghai Province, and providing potential information on the climatic condition of Zeku in the Early Miocene.
- A fossilised pair of copulating froghoppers indicates that genitalic symmetry and mating position in froghoppers have remained static for more than 165 million years.
- The intra-specific and individual variations of Palaeontinidae and numerous other insect fossils probably indicate long-lasting ecological stresses and a competitive environment in the Middle Jurassic to Early Cretaceous palaeoecosystems.

These findings from the Middle Jurassic to the Early Miocene of China have enhanced our knowledge of Auchenorrhyncha and provided the foundation for future studies of new fossil (rock and amber) specimens.

## Improving phylogenetic resolution in rove beetle systematics via rigorous study of fossils

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With more than 60,000 described species, rove beetles (Coleoptera: Staphylinidae) are an outstanding example of mega-diversity. With the short elytra leaving their abdomen exposed and flexible, they are well adapted to cryptic microhabitats in nearly all possible terrestrial habitats. The family is divided into four groups of subfamilies that supposedly represent monophyletic lineages. The largest of them, the Staphylinine-group, consists of nine subfamilies, and includes Steninae, one of the most striking examples of the evolutionary mega radiation.

Steninae comprise more than 2700 species organised in two extant genera, the mega-diverse *Stenus* Latreille, 1797 and much less species-rich *Dianous* Leach, 1819. With ~2500 described species, *Stenus* is among the most diverse genera of organisms but is also fairly conservative in its morphology. Due to lacking robust phylogenetic study, nothing is known about how, when and why Steninae radiated to become the mega-diverse group we see today. Usually Steninae has been considered to be closely related to the subfamily Euaesthetinae, but their placement within the Staphylinine-group still remains controversial. However, neither morphology has ever been combined with molecular data in a phylogenetic analysis, nor has the fossil record been used for such inference. The latter, however, is crucial since the combination of phylogenetic signals preserved in recent species with palaeontological data is the most effective way to explore the history of a given organismal group, especially deep divergencies. So far, only two species of Mesozoic *Stenus* have been described, and all other known fossils of Steninae come from the Cenozoic deposits (Cai *et al.*, 2014). Although not very abundant, all these fossils are of great significance for understanding the origin and early diversification of this lineage.

Here, we present a new extinct genus of Steninae notably different from all extant members of this subfamily. The studied material consists of 15 specimens from one piece of Burmese amber (Late Cretaceous, earliest Cenomanian) that belong to at least two extinct species. Our new finding is discussed in the context of a possible scenario for the early evolution of Steninae prior to their modern radiation, and in terms of the possible sister-group relationships of this subfamily within the Staphylinine-group.

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## Insights into the origin and evolution of the long-proboscid scorpionfly family Aneuretopsyhidae (Mecoptera) based on new Mesozoic and Palaeozoic records

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The extinct, mainly Jurassic–Cretaceous family Aneuretopsyhidae Rasnitsyn & Kozlov, 1990 is a small, compact group of highly specialised insects, comprising seven described species in two genera. They are a part of the major clade of basal Mecoptera, the Aneuretopsyhina, which are characterised by having elongate, siphonate proboscides, and apparently fed on pollination drops of gymnosperms. Aneuretopsyhidae have a set of unique morphological features and strikingly differ from all other Mecoptera in appearance, resembling moths or cicadas. The wing structure and venation of Mesozoic aneuretopsyhids are highly modified. The structure of the anal area in the forewing is unique in having specific anal loops that are possibly functionally related to wing folding. The homology of their constituent veins, however, is unclear. These loops appear to be an apomorphic feature of the entire family, although sometimes they are hardly discernable when the wings are folded over the body in the completely preserved specimens, and therefore are missed in descriptions.

The new finds represented by well preserved forewings from the Lower Cretaceous of Russia and Mongolia and the Jurassic of Karatau reveal some evolutionary trends in venation patterns of aneuretopsyhids and indicate a high diversity of the group in the Mesozoic. Furthermore, an isolated wing referable to Aneuretopsyhidae was found in the transitional Permian–Triassic deposits of European Russia (the Nedubrovo beds). Its venation corresponds to the general venation scheme of Aneuretopsyhidae, with several shared synapomorphies. Another, even older (Late Permian) representative, *Neudolbenus* Bashkuev, 2013, was described previously in the Permochoristidae; it is reinterpreted here as a basal aneuretopsyhid and assigned to a new subfamily. *Neudolbenus* has an unmodified venation and demonstrates some plesiomorphic characters, such as a six-branched M of permochoristid type and the undeveloped, albeit outlined, loop in the anal area, formed by the oblique crossvein  $a_1$ – $a_2$ . In the Nedubrovo specimen, there are two anal loops, also formed by crossveins, but more expressed than in *Neudolbenus*. These loops look similar to, and are possibly homologous with, the anal loops of Mesozoic aneuretopsyhids, and therefore allow a better understanding of evolution of the wing venation in this family. The new finds shed light on the origin and phylogeny of Aneuretopsyhidae by linking them to one of the Late Permian permochoristid lineages, with *Neudolbenus* as an intermediate form.

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## **Is amber altered by microCT or confocal microscopy studies? A preliminary assessment using optical microscopy, FTIR and Raman spectroscopy**

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Amber represents an invaluable ‘time capsule’ preserving fossil inclusions in three-dimensions. Many institutions, however, restrict the analysis of important inclusions using state-of-the-art imaging methodologies yielding high quality three-dimensional reconstructions, including micro-computed-tomography ( $\mu$ CT) and confocal microscopy. This is because it is presumed the techniques have the potential to physio-chemically alter the amber matrix, but the short-term and/or long-term effects of these analytical methodologies are unknown. In this study, the chemical characterisation of a number of samples of different types of amber was carried out using Raman and FTIR spectroscopy, prior to and after exposure to X-rays in a  $\mu$ CT scanner, and to laser illumination using confocal microscopy. Subtle depolymerisation and oxidation chemical changes were observed by FTIR on some of the samples analysed, appearing to be similar to a photo-ageing mechanism. Additional exposure to synchrotron X-rays was carried out on a few sub-samples. Hard synchrotron X-rays imparted a visible discoloration to irradiated amber and copal samples.

**Fossil Ceratopogonidae (Diptera): best understood family of fossil insects**

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The Ceratopogonidae (biting midges) are a diverse, worldwide group with 6,256 named, valid extant species. The basal lineages and many of the derived ones are understood cladistically and this provides the backbone of a well established phylogeny. The fossil record is well represented, particularly in ambers of every age – from Dominican amber (~25 Ma) to Lebanese amber (121 Ma). The oldest fossil is a compression fossil of a wing at 142 Ma. There are 285 fossil species named, based on thousands of specimens present in the ambers. There is a remarkable congruence between the ages of the fossils and their position in the phylogeny, with the oldest fossils representing only the oldest lineages (two extant, several extinct) and graduating to the youngest, which represent a wide array of only extant genera. Based on its sister group relationship with Simuliidae + Thaumaleidae, the Ceratopogonidae should extend back to at least 176 Ma.

## Terrestrial isopods: progress in their fossil record

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Currently, terrestrial isopods (Crustacea: Oniscidea) represent a large part of the mesofauna and primary decomposers in soil. For a long time, terrestrial isopods were believed to be a recent group, their fossil record being quite scarce and, until recently, restricted to the Cenozoic. However, several terrestrial isopods have been recently reported in Cretaceous ambers. The first to be formerly described – *Myanmariscus deboiseae* Broly, Maillet & Ross, 2015, is of late Early Cretaceous age (Albian) and is preserved in Burmese amber from Myanmar. This specimen belongs to the *Synocheta* Legrand, 1946 and its assignment to the family *Styloniscidae* Vandel, 1952 is discussed in regards to the biogeographical distribution of Recent species of Oniscidea. A second piece of Burmese amber, currently under study, contains a specimen probably belonging to the *Tylidae* Milne-Edwards, 1840 and to the genus *Tylos* Audouin, 1826, a genus currently composed of supralittoral endemic species. There is also a third Burmese amber specimen that was recently acquired by the National Museum of Scotland, and yet to be studied, that contains four individuals. These Burmese specimens, along with other, as yet undescribed, Cretaceous amber records from Western Europe (Charente Maritime, France; Álava, Spain) indicate that Oniscidea were already highly diversified by the Cretaceous. Furthermore, the progressive discovery of a rich Mesozoic fossil record considerably improves our knowledge of the evolutionary history of this remarkable group of terrestrial crustaceans.

Broly, P., Maillet, S. & Ross, A.J. 2015. The first terrestrial isopod (Crustacea: Isopoda: Oniscidea) from Cretaceous Burmese amber of Myanmar. *Cretaceous Research*, 55: 220–228.

## Wax and wane of Baltic amber Achilidae (Hemiptera: Fulgoromorpha)

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The Achilidae family of planthoppers (Hemiptera: Fulgoromorpha) appear in the fossil record in the early Cretaceous (*Acixiites* Hamilton, 1990; *Niryasaburnia* Szwedo, 2004). Currently, the family comprises three subfamilies: Achilixinae, Bebaiotinae and Achilinae, the last including 11 Recent tribes: Myconini, Rhotanini, Mycarini, Amphignomini, Plectoderini, Achilini, Achillini, Ilvini, Sevini, Apatesonini and Tropiphlepsini. The taxic diversity of Achilidae is often expressed by a single or just a few species representing particular tribes. For many of the tribes, the material available in collections is poor, often with just one or two specimens of a single sex. The biological data for the species are very scarce.

The early descriptions of fossils from Baltic amber, from the classical Germar & Berendt (1856) work present several undoubted Achilidae placed in non-achilid genera (Szwedo *et al.*, 2004; Emeljanov & Shcherbakov, 2009). Subsequently, the achilids were described by Cockerell (as cixiid) and by Usinger (1939). The extinct tribes Ptychoptilini (Emeljanov, 1990 – *Ptychoptilum*; Szwedo & Stroinski, 2001 – *Ptychogroehnia*) and Waghilidini (Szwedo, 2006 – *Waghilde*) were described later. Lefebvre *et al.* (2007) added a monotypic genus *Angustachilus* Lefebvre, Bourgoin & Nel, 2007. Emeljanov & Shcherbakov (2009) added three more genera: *Paratesum*, *Protomenocria*, *Psycheona* and discussed Achilidae fossils from Baltic amber.

Surprisingly, the vast majority of the fossils from the Baltic amber are to be placed in the tribe Achilini, in a modern fauna represented by the subtribes Elidipterina (11 modern genera), Achilina (four modern genera) and Cixidiina (a single Recent genus). The last subtribe comprises also the extinct *Protepiptera*, the remaining genera are not ascribed to subtribes.

The former studies on taxic diversity and morphological disparity of Baltic amber Achilidae revealed a number of unique forms, not present among recent Achilidae (Ptychoptilini, Waghilidini), nor ascribable to Recent Achilini (which are not particularly diverse). Achilidae seems to be a relict in the modern fauna, and their taxic diversity is the result of a long evolutionary history. This hypothesis could be tested with detailed studies of the inclusions of Eocene Baltic amber, the probable time of the Achilidae heyday.

No room to include the full reference citations, please contact the author for full details.

## **A new 3D imaging method for micropaleontology in ambers and entomology using basic light source: the Optical Coherence Tomography (FF-OCT)**

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3D methods are gaining importance in the reconstruction of palaeontological objects for illustration in both scientific and popular realms. The availability of various methods, mainly techniques using X-rays, has enabled a very rapid development of powerful tools in the study of fossils. These include synchrotron facilities and CT scanners of different size and power.

However, some tomographic methods using basic light (optical tomographies), developed for biological samples and in vivo studies, may also be used for some paleontological samples, such as inclusions in amber or small arthropod specimens. Here we present several case studies on the use of Full-Field Optical Coherence Tomography (FF-OCT), as applied to fossils preserved in amber. The method is based on low coherence interferometry using basic light. The OCT microscope used was developed in a physics institute specialising in medical imaging, and demonstrates the possibility of using such devices to image certain inclusions in amber, complementary to X-ray tomography methods or as an alternative in some specific cases. This method is also suitable for small biological objects, such as small to very small insects.

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## **Cercopoidea (Hemiptera: Cicadomorpha) from the Cretaceous of China and Myanmar**

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The Cercopoidea Leach, 1815, known as froghoppers (adults) or spittlebugs (nymphs), is one of the most speciose superfamilies of Cicadomorpha, with nearly 3000 described species attributed to five modern families (Machaerotidae Stål, 1866; Clastopteridae Dohrn, 1859; Cercopidae Leach, 1815; Epipygidae Hamilton, 2001; Aphrophoridae Amyot & Serville, 1843) and three extinct families (Cercopionidae Hamilton, 1990; Sinoalidae Wang & Szwedo, 2012; Procercopidae Handlirsch, 1906) from the Mesozoic. This insect group has been systematically neglected and so its biodiversity and high-level evolutionary relationships remain poorly understood. Recently, some studies based on fossil records and molecular data focused on the early evolution of Cercopoidea and the origin of its modern groups. However, the results of these studies were astonishingly contradictory, and so instead of resolving problems, these studies add further confusion to the topic. For example, morphological characters in the available fossil record suggest that the earliest Cercopoidea appeared in the Early Jurassic, represented by the family Procercopidae, and the ancestral group of modern families diverged from Procercopidae since the mid-Cretaceous, whereas the divergence time estimation based on molecular data suggests that the separation of the modern Machaerotidae from the stem Cercopoidea occurred between 197 and 216 Ma (latest Triassic–earliest Jurassic). The contradiction might be caused by the overestimation of divergence time analysis inferred by molecular data, but that the fragmentary fossil record of Cercopoidea (most known fossils are tegmina and/or wing impressions) leading to underestimation cannot be completely excluded. Here, some new cercopoids from the Cretaceous of China and Myanmar are reported. Many well preserved Mesozoic cercopoids collected from northeastern China have provided new insights into the early evolutionary history of Cercopoidea, but the classification of some taxa is problematic. On the basis of new fossils from the Early Cretaceous Jehol biota, the taxonomy of certain cercopoid groups from China is revised and the early evolution of Cercopoidea and the origin of its modern groups are discussed. In addition, some highly diversified cercopoids with well preserved body structures in mid-Cretaceous ambers (~99 Ma) from northern Myanmar also add new information on the diversity and evolutionary history of early cercopoids. The new fossil data reported herein suggest that the ancestral group of modern families likely diverged in the Cretaceous and confirm that the divergence time of Cercopoidea inferred from the molecular analysis seems to be overestimated.

## **A new Courceyan (Lower Carboniferous) eumalacostracan crustacean from the Forest of Dean**

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In 1982 the carapaces of an unknown Carboniferous crustacean were presented to the Natural History Museum. It was originally thought that these may represent a new species of *Tealliocaris*. Further, better preserved, material has since been collected from the Great Doward in the Forest of Dean which allows a better comparison with other Carboniferous crustaceans. Although there are similarities with other Carboniferous eumalacostracan crustaceans, there are also some significant differences in the shape of the carapace and the ornamentation of the carapace and pleon. The broad, squat telson is more akin to *Pseudogalatea*, but the length of the pleon and the lack of elongated sharp postero-lateral angles to the carapace is more like that of *Tealliocaris*. The lack of an enlarged third pleomere is one feature that differentiates it from *Tealliocaris*, however, PCA on 12 landmarks of the carapace indicate that this new crustacean is quite distinct from both *Tealliocaris* and *Pseudogalatea* and represents a new genus and species of Lower Carboniferous eumalacostracan which has been named *Schramocaris* in honour of the palaeocarcinologist: Prof. Fred R. Schram. Comparisons with other fossil crustaceans from around the world also suggest that this new crustacean is morphologically similar to *Chaocaris*, *Tylocaris*, *Fujianocaris*, *Pseudogalatea* and *Tealliocaris*. Similar crustaceans from the Borders of Scotland and New Brunswick, Canada, may also belong to this genus.

## **Rapid recovery of plant–insect associations in Patagonia after the Cretaceous–Paleogene mass extinction**

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Study of the end-Cretaceous mass extinction has been heavily regionally biased towards the western USA. Recently, a growing body of evidence, especially from Patagonia, Argentina, suggests that extinction and recovery dynamics may have been very different in Gondwana. Low pollen extinction across the Cretaceous–Paleogene (K–Pg) boundary, the survival of many vertebrate and typically mid-Mesozoic gymnosperm lineages into the Paleocene, and the discovery of diverse early Paleocene macrofloras have led to the hypothesis that Patagonia provided a refugium for biodiversity during the global catastrophe. Plants and associated insect herbivores provide the foundation for most terrestrial food webs. To test whether Patagonia provided a refuge for associational diversity, we compared insect damage on latest Cretaceous and early Paleocene fossil floras from coastal deposits in Chubut Province, Patagonia to previously studied insect damage from the western USA, which decreased significantly at the K–Pg boundary. We compared ~850 leaf fossils from the latest Maastrichtian (67–66 Ma) Lefipán Formation in northwestern Chubut to ~2750 fossil leaves from three Danian time intervals, including localities that correlate to palaeomagnetic chrons C29n and C28n in the Salamanca Formation and C27n in the overlying Peñas Coloradas Formation. We found that insect damage types (DTs) on both the Cretaceous and Paleocene floras (50 Cretaceous and 61 Paleocene DTs) were more diverse than in the western USA (49 Cretaceous and 44 early Paleocene DTs from much larger sample sizes). Also, comparisons of sampling-standardised DT diversity in Patagonia revealed a lower K–Pg decrease than what has previously been observed in North America during the same interval. In addition, damage diversity, including overall and specialised DT diversity, increased through the three early Paleocene time intervals. We also analysed the morphology of Patagonian leaf mines to determine if any leaf miners crossed the K–Pg boundary. Our preliminary results do not suggest any clear boundary-crossing leaf mines, even on surviving plant species, similar to the pattern observed in the western USA. Instead, there are many new leaf mine associations that first appear at the early Paleocene localities, providing further evidence for a faster recovery of insect herbivore diversity in Patagonia compared to the western USA. These results, combined with earlier work, support an emerging hypothesis that southern latitudes suffered significant extinctions, but recovered much more quickly from the global environmental disaster after the end-Cretaceous impact.

## Review of the peculiar subfamily Psallopinae (Hemiptera: Heteroptera; Miridae)

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The extinct members of the Psallopinae are important for classifying and understanding the relationships between the closely related mirid groups Isometopinae, Psallopinae and Cylapinae. These subfamilies are considered to be the most primitive sister groups among mirids, while their taxonomic composition, geographical distribution, and life history are still poorly known. Extant Psallopinae live on tree trunks and bark. The proximity of Psallopinae and Cylapinae is also distinctly demonstrated by Wolski & Henry (2015) who reevaluated the position of the extant genus *Isometocoris* within the Psallopinae as well as the status of the subfamily. They provided evidence for transferring *Isometocoris* to the subfamily Cylapinae and even proposed to reduce Psallopinae to a tribe within Cylapinae. Their first suggestion is accepted, but we disagreed with reduction of Psallopinae to a tribe within Cylapinae since the tribal rank of Psallopinae and especially inclusion of it into Cylapinae requires a deeper analysis (Herczek & Popov, 2015). An autapomorphy of Psallopinae is the strong dorso-ventral development of the eyes reaching the gula and usually smoothly blending into the curvature of the head. They also differ from all Cylapinae in then number of meta-femoral trichobotria, clearly distinguishing Psallopinae from Cylapinae. In addition, *Cylapopsallops* has its own characters differing from other psallopinous genera, such as semiglobular eyes, quite strongly elongated (three times as long as wide), their large size (5.3 mm), and a very long rostrum reaching at least the middle of the abdomen are more distinctive for Cylapinae.

The smallest relict subfamily Psallopinae contains only one recent genus: *Psallops* (17 species) inhabiting tropical and subtropical regions. These species have been described from Old World tropics, subtropics, and warm temperate regions: Micronesia (Guam, Marian and Caroline Islands), Saudi Arabia, Nigeria, Ghana, Congo, Singapore, South Africa, Japan, China, Taiwan and Thailand.

The first fossil psallopinous bug, *Isometopsallus schuhi* Herczek & Popov was described from the Eocene Baltic amber in 1992. In recent years the number of known fossil Psallopinae (exclusively from Baltic amber) has increased considerably and currently they are represented by the following taxa: *Isometopsallops schuhii* Herczek & Popov, 1992; *Epigonomiris skalskii* Herczek & Popov, 1998; *Cylapopsallops kerzhnerii* Popov & Herczek, 2006; *Epigonopsallops groehnii* Herczek & Popov, 2007, *Psallops eocenicus* and *P. bitterfeldi* Herczek & Popov, 2015; *P. niedzwiedzkii* Herczek & Popov, 2016 and *P. linnavuorii* Herczek & Popov, 2016 (all from Baltic amber); *Psallops popovi* Herczek, 2011 (Dominican amber) and also *Isometopsallops prokopi* Vernoux, Garrouste & Nel, 2010. Among them, *Isometopsallops prokopi* is the oldest known psallopinous Miridae from the Lowermost Eocene French (Oise) amber.

**First representative of the genus *Helius* Lepeletier & Serville,  
1828 (Diptera: Limoniidae) from Cretaceous  
Álava amber (Spain)**

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The oldest representatives of the genus *Helius* (Diptera: Limoniidae) are known from the Early Cretaceous. Hitherto, four species of the genus *Helius* have been described from this period, but none of them from Álava amber, Spain. Two were described from the central Lebanon Early Cretaceous outcrop of Hammana-Mdeyrij, two others are known from the Late Cretaceous: Cenomanian of Myanmar (Tanai village) and Turonian of Botswana. A wide spectrum of species of the genus *Helius* occur in the Eocene. Three are known from the Oligocene of Germany – Rott am Siebengebirge, USA – North Montana and three from the Miocene of Russia, Caucasus, Stavropol. Here, we present a new species, representing the first representative of the genus *Helius* from the Lower Cretaceous Álava amber.

The fossil record offers the opportunity to trace directions of evolution of different groups. It is debated whether adaptive radiations are marked by the initial expansion of taxonomic diversity or of morphological disparity (the range of anatomical form). The genus *Helius* exemplifies the value of both indicators of success. It belongs to one of the largest and oldest dipteran families (Limoniidae) and appears in the fossil record as a one of the oldest representatives of the subfamily Limoniinae. The appearance of *Helius* is concordant with the Cretaceous rapid adaptive radiation of angiosperm plants. Hence, contemporaneous radiations of terrestrial plants, radiations of plant-feeding and plant pollinating insects can be studied and compared. These crane flies probably developed an elongated rostrum to consume nectar and pollen from diversifying flowers. The Early Cretaceous fossil record includes a wide spectrum of disparate *Helius*, e.g. species with a comparatively elongated (only 0.25 times longer than head) rostrum, like *Helius lebanensis* Kania, Krzemiński & Azar, 2013; those with a very elongated rostrum are exemplified by *Helius ewa* Krzemiński, Kania & Azar, 2014 – both were described from Lower Cretaceous Lebanese amber. The newly discovered specimen from Álava amber belongs to the group of taxa with a moderately elongated rostrum. So, the Cretaceous times witnessed the differentiated Limoniidae morphotypes, taxa with varying degrees of rostrum elongation.

**Palaeo-forensics: what fossil puparia (Diptera: Calliphoridae: *Protophormia terraenovae*) can tell us about the taphonomic history of Upper Pleistocene mammals from Hesse (Germany)**

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Cranial fragments of four Pleistocene mammalian individuals were recovered from the fluviatile deposits of the ancient Rhine near Darmstadt (Hesse, Germany). Fossil puparia were discovered inside the pneumatized cavities of *Mammuthus primigenius* (Blumenbach, 1799) (1), *Megaloceros giganteus* (Blumenbach, 1799) (9) and *Bison priscus* Bojanus, 1827 (19) from Groß-Rohrheim and *Mammuthus primigenius* (Blumenbach, 1799) (94) from Geinsheim, and could be identified as remains of the blow fly species *Protophormia terraenovae* (Robineau-Desvoidy, 1830). The baseline data for an interpretation and reconstruction of the taphonomic history of the mammals derive from actual observations of blow flies in the field of modern forensic entomology. The mammals died near the ancient River Rhine and lay there for a certain time on dry ground or were located by or in shallow water accessible to necrophagic insects. Fertile blow flies deposited eggs at natural body orifices and open wounds (if they existed). The first instars hatched, fed on soft and relatively moist tissue and passed all larval stages until they started to pupate. After pupation most of the fully developed blow flies emerged. Given that their life cycle is highly temperature dependent, a mean ambient temperature of at least 15–16°C is assumed during the development of the blow flies. At fluctuating temperatures with mean values of 15–16°C a laytime for the mammal carcasses of 24 to 32 days is quite possible. Shortly after the emergence of the blow flies, the vertebrate remains were submerged and transported by running water until they were embedded. Most of the blow flies inside the skull cavities of *Megaloceros giganteus* died inside their puparia, maybe as a consequence of freezing, drowning or smothering.

## **Evaluating the influence of resin chemistry on preservation in amber**

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Insect fossils in amber and resin occur from the Triassic to Recent and are a particularly important and unique palaeobiological resource. Amber is best known for preserving exceptionally life-like fossils, complete down to even the most minute detail, but there is a wide-spectrum of preservation quality in amber. The best preservation includes external cuticle as well as internal organs and tissues, but many amber sites only preserve cuticle or hollow moulds, and most amber sites have no fossils at all. The taphonomic processes that control this range of preservation are essentially unknown, but they likely include a number of variables. In order to determine if resin chemistry may be an important variable controlling preservation in amber, a literature review was conducted to assess previous hypotheses about the role of resin chemistry on preservation and to determine how the preservation of fossil inclusions varies within and between different chemical classes of resin. Taphonomic experiments have shown that the general chemistry of resin is necessary for preservation in amber; compared to a control fly decaying in air, a fly sealed in inert wax decayed more quickly, but a fly decaying in maple syrup (more chemically similar to resin) decayed more slowly. In the fossil record, inclusions have not been reported from some of the major chemical categories of amber (in two different classification schemes these are Group E or Classes 3, 4 and 5). However, these categories of amber are rare, and do not polymerise well. All of the four most common chemical classes of amber (Groups A–D and Classes Ia–c and II), have sites without fossil inclusions, sites with poorly preserved fossil inclusions, and sites with well preserved fossil inclusions. More specifically, there are examples where one piece of amber includes multiple inclusions, some with and some without preserved internal organs. In conclusion, resin chemistry may have a general influence (in conjunction with other variables) on whether or not there are fossil inclusions in amber. However, other variables are likely to have a stronger influence on the quality of preservation of the inclusions.

## **Insect herbivory on angiosperm leaves in Zealandia: evidence from the early Miocene Hindon Maar Fossil-Lagerstätte**

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Plants and insects are the most important components of terrestrial ecosystems and insect herbivory is the most important form of food consumption. The herbivory pattern observed in the fossil record offers an opportunity for testing macro-evolutionary dynamics of plant–insect interactions. Much work on the diversity and palaeoecology of such interactions has been conducted on leaves of the Northern Hemisphere. Our study presents the first results for such associations between plants and insects for fossil leaves of the Miocene Hindon Maar, Central Otago, New Zealand. A total of 584 fossil angiosperm leaves belonging to 24 morphotypes were examined for the presence or absence of insect damage types (DTs). 73% showed 821 occurrences of some kind of herbivore activity and 87 different damage types were recorded. In comparison to other fossil localities using the same methodologies, the Hindon leaves show a higher abundance of insect damage and a higher diversity of damage types. The maar lake was initially surrounded by a rich and diverse vegetation with an angiosperm dominance of Myrtaceae and the endemic *Nothofagus* (southern beech). Furthermore, leaves of the *Nothofagus* exhibit a more diverse and much higher percentage of damage than a comparable dataset of leaves from the Antarctic Peninsula.

## Miocene ants (Hymenoptera: Formicidae) of Russia and adjacent territories

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There are several Miocene localities known to date in Russia (and adjacent territories), which occupies a large territory of Eurasia. We have collections from the localities of the Crimea (Kerch), Buryatia (Ust-Dzhilinda), East Sayan Mountains (Ourika valley), Russian Far East (Amgu, Velikaya Kema) and the Caucasus. The ant assemblage is a very informative characteristic of the biocenosis. Groups forming the ant assemblage were initially classified as herpetobionts, hortobionts and dendrobionts (foraging on the earth surface, in the herb layer and on trees, respectively), being accompanied later with stratobionts (foraging within leaf litter) and geobionts (foraging in soil). Studying the ratio of dendrobionts, geobionts and other groups gives a picture of biocenosis' features. We attempted to reconstruct Oligocene–Miocene changes using our description of the available fossil ant assemblages. Our findings showed a resemblance between ant assemblages of Russia and Europe in some aspects. For example, there is a case, known as Wheeler's dilemma, concerning the former co-existence of ant genera, which are currently restricted either to the Holarctic or the tropics. These are *Formica* and *Lasius*, with extant species in temperate Eurasia, and *Oecophylla* and Myrmeciinae, with extant species known exclusively in tropics. The comparison of ant assemblages from the Miocene with more recent assemblages reveals climatic and biotic changes. We observed not only temporal differences, but geographic ones as well. Analysis of similarities and differences in the composition of ant assemblages permits discussion on the existence of diverse communities within the geological periods. Ant assemblages of the Russian Far East are more similar to the Chinese and the European ones than to their North American counterparts. The temporal trend (from Eocene to Miocene) is characterised by an increase in the proportion of Myrmecinae and a decrease in the proportion of "professional" dendrobionts – Dolichoderine. The presence of thermophilic *Oecophylla*, Myrmeciinae in Miocene deposits revealed, in our opinion, the lesser influence of climatic factors (compared with biotic factors) on the changes in communities.

## **Palaeobiology of beetles (Insecta: Coleoptera) from western European Cretaceous ambers**

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The whole assemblage of beetles in the Cretaceous ambers of Western Europe (Spain and France) is surveyed for the first time. Spanish amber (upper Albian) has 149 specimens of 30 families, while French amber (upper Albian–Santonian) has 65 specimens of 16 families. Only five families are shared by both ambers, thus totalling 41 different families identified, mainly of Polyphaga. This low number of shared families is surprising considering the temporal and palaeogeographic proximity of both areas. Thirteen of the families have their oldest known representatives in these ambers; in some cases they represent the only record for the entire Mesozoic, or even the entire fossil record. Based on the ecology of modern taxa, most of the families identified are saproxylic or detritivorous; wood borers are almost absent. Therefore, beetle attacks could not have influenced the release of large amounts of resin in these Cretaceous forests of gymnosperms; this release was influenced by other causes such as wildfires, storms or some other biological effect. Some beetle families identified in these ambers may act today as pollinators of angiosperm flowers. The study of these groups of beetles may help us understand insect–flowering plant coevolution.

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## Springtails (Hexapoda: Collembola) from Early Cretaceous Spanish amber

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Springtails (Hexapoda: Entognatha: Collembola) are a primitive lineage of conspicuous and ecologically varied hexapods, that comprise one of three groups in the clade Entognatha, and sister group to the hyper-diverse insects. The fossil record of springtails is scant and largely biased towards preservation in amber with its high fidelity. With a few exceptions, this bias generally restricts their geological occurrence to the Cretaceous and later, as it is from this period and onward that prolific ambers with bioinclusions are known. The extinct collembolan diversity from Early Cretaceous Spanish amber is reassessed owing to new and improved preparations of those previously reported specimens as well as the discovery of much new material. We have documented a total of more than 102 specimens preserved in Albian-aged amber from the Peñacerrada I outcrop, Burgos Province, northern Spain, which constitute the earliest amber fauna of springtails yet described. This review reveals a modest species diversity but one of considerable phylogenetic breadth in representation. All specimens identified belong to two orders: the elongate forms of the Entomobryomorpha and the more globular-bodied Symphypleona. Among the Entomobryomorpha, the family Isotomidae, with three new species described, appears numerically dominant regarding the total Spanish collembolan fauna. Although less abundant, a diverse fauna of Symphypleona, with five new genera and species described, was classified in at least three families (Sminthuridae, Katiannidae, Sminthuridae: Sphyrothecinae and Sminthuridae: Sminthurinae?). These discoveries include the first Mesozoic records of the Sminthuridae and Sphyrothecinae. Interestingly, many of the described forms are remarkably similar to their extant relatives, emphasizing the antiquity of the group as a whole as well as likely long-term niche conservatism. Based on morphological characters associated with specific habitat preferences and biological traits, some specialised reproductive strategies have been investigated for these fossil springtails.

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**New member of the family Tanyderidae (Diptera)  
from Eocene Baltic amber**

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Tanyderidae Osten-Sacken, 1879 is a small family of Diptera including only 38 extant and 27 fossil species. More than half of all described species in this family are distributed in the temperate zone of the Northern or Southern Hemisphere, others occur either in the subtropical or tropical zone. The family is characterised by having the highest number of plesiomorphic features of the entire order. Adults are small (6 mm body length) to large (30 mm length), with patterned wings and frail, elongate legs. Inclusions of Tanyderidae in Baltic amber are very rare, with only three species described to date. Following analysis of new fossil material (three specimens: two males and one female) from Eocene Baltic amber an additional new genus and species have been identified.

## **Terrestrial environment inferred from the insects from a Triassic marine Lagerstätte**

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Monte San Giorgio (split by the Italy/Switzerland border) is one of the most renowned among the Middle Triassic sites in the world, since it concentrates several marine vertebrate levels in a small area of approximately 20 km<sup>2</sup>. The Swiss side of Monte San Giorgio was included in the UNESCO World Heritage List in 2003, joined by the Italian side in 2010, for the global significance of their fossil marine faunas. The Monte San Giorgio basin is located at the western termination of the South-Alpine domain situated on a passive continental margin open to the tropical western Neo-Tethys, which was progressively submerged by a long-term transgression from the east. Its location resulted in a peculiar sedimentary succession, showing the onset, at least temporarily, of severe dysoxic to anoxic bottom water conditions. Due to the characteristics of its vertebrate fossil record, mainly fishes and marine reptiles, it has traditionally been described as a shallow lagoon, adjacent to a carbonate platform, at a certain distance from emerged land. More recently, the collection of fossil insects from two of the fossiliferous levels, and particularly from the Lower Kalkschieferzone (KSZ; 239.51 ± 0.15 Ma), confirms the close proximity of emerged land. The insect fauna described here was collected during fieldwork carried out between 1997 and 2003 in the Lower KSZ at Val Mara near Meride (CH). The excavations led to the collection of 19 specimens, both adult and larvae. They preserved the external exoskeleton and, in the phosphatised specimens, soft tissues as structures of the central nervous system and muscular bundles. Even though some specimens are still under study, the representatives of seven different orders have been identified so far, indicating an unexpectedly high biodiversity. The insect fossil assemblage of Monte San Giorgio includes terrestrial groups with phytophagous, detritivorous and predatory habits as representatives of Archaeognatha, Coleoptera and Hemiptera, as well as larvae and adults of aquatic groups (Ephemeroptera and Plecoptera), which required permanent freshwater pools or small streams for their development. The entomofauna of the Kalkschieferzone, including terrestrial and aquatic taxa, provides evidence for a complex environment and suggests the presence of stable freshwater basins, as well as emerged land where diverse habitats were established, close to the depositional environment.

## **A slice of Devonian life: the Rhynie and Windyfield cherts**

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The Rhynie and Windyfield cherts from Rhynie, Aberdeenshire, Scotland are world-famous because they contain exceptionally well preserved fossils of some of the earliest plants and animals to colonise habitats on land. They are fine-grained, silica-rich deposits formed between 400 and 412 million years ago, early in the Devonian period. The area was volcanic, with mineralised waters flowing from hot springs into a range of environments similar to those of Yellowstone (USA) today. On cooling, the waters coated and permeated with silica the tissues of plants and invertebrates living nearby, preserving them in exquisite detail. Since 1916 palaeontologists have described seven species of higher plants and seven distinct groups of land-living and freshwater arthropods, such as arachnids, a springtail, an insect, crustaceans, mites and myriapods.

Finding such small organisms in what is now a very hard rock presents practical difficulties. The simplest technique is to cut thin slices with a rock-cutting saw and examine them in reflected light under a binocular microscope. The slices can be further thinned to make them translucent for examination in transmitted light. As a volunteer with National Museums Scotland, I use these methods to find good examples, particularly of the animals, to add to the museum collections. Here I show photomicrographs of some of my best finds. They include trigonotarbid (extinct arachnids) with mouth-parts and book-lungs visible; crustacean larvae; mites; a univalve crustacean; a possible nematode worm; and fine details of higher plants, algae and fungi.

**A new species of *Microphorites* Hennig, 1971 (Diptera:  
Dolichopodidae s. lat.) in Paleogene amber from  
eastern Moravia (Czech Republic)**

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We report a new species of the extinct genus *Microphorites* Hennig, 1971 (Dolichopodidae s. lat.: Microphorinae) based on a Paleogene amber inclusion found in the Studlov locality in eastern Moravia (Czech Republic). *Microphorites* sp. n., described from a single female has the typical wing venation of the genus, i.e. three radial veins, crossvein r-m, crossvein bm-cu complete, cell dm, two medial veins and vein CuA<sub>1</sub>. It differs from the other species of *Microphorites* by the long antenna, with a prolonged and laterally compressed first flagellomere and the presence of a pterostigma at the fusion of the first radial vein and the costa. Our new fossil is compared with all other species of *Microphorites*, as well as fossil and extant species of *Microphor* Macquart, 1827. In addition, the age and source plant of Študlov amber is debated based on recently performed geochemical analyses.

## Evolution of aphid wing structure: a result of multiple convergence

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With ~5000 species worldwide, aphids (Hemiptera: Sternorrhyncha, Aphidomorpha sensu Heie & Wegierek, 2009) represent one of the most biologically interesting groups, due to the exceptional complexity of their life cycles, considerable variability in biological traits, and the mutualistic association with the endosymbiotic bacteria *Buchnera*. They are also a rare example of insects that are much more diverse in the temperate climate of the Northern Hemisphere than in the tropics and Southern Hemisphere. All these could make them an ideal model group to test different evolutionary hypotheses, but to do so, a robust phylogeny of the group is needed. Even though aphids attract so much attention, their classification at the higher taxonomic level is still not fully resolved. A general impediment for phylogeny reconstruction and building a natural classification of aphids is the paucity of morphological synapomorphies for higher-level lineages and difficulty in determining whether a certain feature is an ancestral (plesiomorphy) or derived (apomorphy) state. One of the most valuable sources of morphological information is the fossil record, which helps to assess character polarity and patterns that determined aphid evolution.

The Triassic and Jurassic aphids are rather scarce, and a significant abundance of their fossils begins from the Early Cretaceous. Interestingly, most of the groups known from this time were also reported from the previous period, but none of them survived until the Cenozoic (Heie & Wegierek, 2011). Although not very numerous, the Mesozoic fossils can provide very important data on the body construction at the early stages of aphid evolution.

Here, we analysed wing structure and venation among Mesozoic groups of aphids. We can conclude that a heavy, flattened body, with well developed prothorax and wide abdomen has triggered the elongation of the forewings. They become relatively narrow, which in turn results in a wide spacing of the cubital veins, reduction of  $M_1$  branch, and elongation of the pterostigma. Such a construction of the forewings led to the reduction of hind wing venation, which retains only the common stem of cubital veins while individual branches are reduced, or in the most advanced case, they are reduced into a special structure, the so-called hamulohalters. Our results show that any clear intermediate stages could be recognised, and it seems that the similar wings structure is a result of convergence that happened several times during aphid evolution.

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Heie, O. & Wegierek, P. 2011. A list of fossil aphids (Hemiptera, Sternorrhyncha, Aphidomorpha). *Monographs of the Upper Silesian Museum*, 6: 1–82.

## **First caddisflies (Trichoptera) in Lower Cretaceous Lebanese amber**

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Lebanese amber contains a diverse biota from the Lower Cretaceous and more than 100 families of arthropods have been reported from its deposits. Among these fossil insects, caddisflies are very scarce as inclusions. Some few fragments indicate caddisflies, but very few inclusions permit clear descriptions of new species. Here, we describe the first two Trichoptera species from this amber, which belong to Dipseudopsidae and Ecnomidae. Hitherto, the oldest fossil species of Dipseudopsidae was known from the Upper Cretaceous amber of New Jersey and Ecnomidae from the Eocene Baltic amber.

## The Tanytarsini (Diptera: Chironomidae) in Eocene ambers

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The Tanytarsini Zavřel, 1917 is a species-rich extant tribe within the large family Chironomidae, with the oldest known representatives found in Eocene resins: Baltic amber, including that collected in the Rovno region (40–45 Ma), Cambay amber from India (50–52 Ma) and Fushun amber from China (50–53 Ma).

In contrast to the extant fauna, Eocene Tanytarsini are rare and so far known only from 17 species of eight genera, including five extant (*Caladomyia* Säwedal, 1981; *Rheotanytarsus* Thienemann & Bause, 1913; *Stempellina* Thienemann & Bause, 1913; *Stempellinella* Brundin, 1947; *Tanytarsus* van der Wulp, 1874) and three extinct genera (*Archistempellina* Gilka & Zakrzewska, 2013; *Corneliola* Gilka & Zakrzewska, 2013; *Eonandeva* Gilka & Zakrzewska, 2015) – all described from Baltic amber. At least two further genera are represented by specimens found in Fushun and Cambay ambers (authors' forthcoming data), thus altogether ten genera with nearly 25 species of Eocene Tanytarsini are known to the authors. Most of them belong to extant subtribes (Tanytarsina Zavřel, 1917 and Zavreliina Sæther, 1977), whereas the subtribal placement of four extinct genera has not been determined definitively.

The examined specimens were obtained from several collections: the Museum of Amber Inclusions, University of Gdańsk, Poland; the private collection of amber inclusions of Christel and Hans Werner Hoffeins, Germany; the I.I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine; the Steinmann Institute, University of Bonn, Germany; the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences and the American Museum of Natural History, New York, USA.

## Some new records of Late Carboniferous (Pennsylvanian: Westphalian) dragonflies (Odonatoptera: Meganisoptera) from Piesberg near Osnabrück, Germany

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The active large quarry within Piesberg N Osnabrück, Lower Saxony, Germany, has been an important Late Carboniferous (Pennsylvanian: Westphalian C/D) fossil locality for a long time. It is mainly known for its rich and exceptionally preserved flora but, as yet, has been rather less known for its fauna. There have been found non-marine (limnic) animals, e.g. Bivalvia (*Anthraconauta*), Xiphosura (*Euproops*), and Vertebrata (scales of Palaeoniscidae and egg capsules of Chondrichthyes). Of particular significance are terrestrial Arthropoda like Arachnida (*Eoscorpius*, *Aphantomartus*), Arthropleurida (*Arthropleura*), and Insecta, which have been collected during the last three decades. The insects are mainly preserved as wings. Among the insects there are about 20 specimens of Odonatoptera: Meganisoptera, of which only *Erasipterella piesbergensis* Brauckmann, 1983 and *Piesbergtupus hielscheri* Zessin, 2006 have already been named. All the other specimens are undescribed and are documented here for the first time. One of them consists of four wings and other body parts. Thus, the Piesberg Fossil-Lagerstätte is one of the most important localities for Carboniferous Odonatoptera in Europe. Some of the photographs show the Piesberg quarry as it developed during the last few years. A description of the fossils is in preparation by the authors.

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