



# Programme and Abstracts

3<sup>RD</sup> INTERNATIONAL CONGRESS OF PALAEOENTOMOLOGY  
with  
2<sup>ND</sup> INTERNATIONAL MEETING ON PALAEOARTHROPODOLOGY  
and  
2<sup>ND</sup> WORLD CONGRESS ON AMBER AND ITS INCLUSIONS

7<sup>th</sup> to 11<sup>th</sup> February 2005

Pretoria  
SOUTH AFRICA



# **Fossils X 3**

## **Programme and Abstracts**

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**Pretoria**  
**SOUTH AFRICA**

***Organising Committee:***

**Chairperson:** Denis Brothers (brothers@ukzn.ac.za)

**Venue and Accommodation:** John Anderson (anderson@nbi.ac.za)

**Programme and Abstracts:** Denis Brothers, Mike Mostovski (mmostovski@nmsa.org.za)

**Others:** Alex Rasnitsyn, Dany Azar, Conrad Labandeira, Julián Petrulevičius

***Sponsorships and other assistance:***

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UNIVERSITY OF KWAZULU-NATAL

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**NOTE: This publication is not intended to form part of the permanent scientific record; it is therefore not a valid publication for the purposes of biological nomenclature.**



## PROGRAMME (\* = presenter)

<b>Sunday 6 February</b>	
14:00 – 18:00	Registration (Hotel 224)
18:00 – 20:00	Welcoming cocktails (Hotel 224)
<b>Monday 7 February</b>	
08:00 – 09:00	Registration (SANBI)
09:00 – 09:15	Welcome and opening .
<b>Session 7.1 – Chairperson: Denis Brothers</b>	
09:15 – 10:00	Rubidge, B.S. – Palaeontology in South Africa.
10:00 – 11:00	*Engel, M.S. & Grimaldi, D. – Evolutionary implications of insect radiations and extinctions in the Cretaceous. (KEYNOTE)
11:00 – 11:20	TEA
<b>Session 7.2: Insect Phylogeny &amp; Systematics 1 – Chairperson: Mike Mostovski</b>	
11:20 – 11:50	Rasnitsyn, A.P. – History of the orders of winged insects. (KEYNOTE)
11:50 – 12:10	Toms, R.B. – Rooting the insect phylogenetic tree: independent adaptations to terrestrial life.
12:10 – 12:30	Shcherbakov, D.E. – Martynov and Handlirsch <i>versus</i> Rasnitsyn: are Palaeoptera primitive?
12:30 – 12:50	Zessin, W. – Remarkable steps of the origin of Odonata.
12:50 – 13:10	*Arillo, A. & Engel, M.S. – A third rock crawler in Baltic amber, with note on the Mantophasmatodea (Notoptera).
13:10 – 14:00	LUNCH and POSTERS
<b>Session 7.3: Insect Phylogeny &amp; Systematics 2 – Chairperson: Alex Rasnitsyn</b>	
14:00 – 14:20	Heads, S.W. – The phasmid wing-recurrence debate: a palaeobiological perspective.
14:20 – 14:40	*Wappler, T. & Gröning, E. – Antiquity of lice.
14:40 – 15:00	*Azar, D., Hajar, L. & Indary, C. – A new Mesozoic fossil family of Psocoptera (Insecta: Psocoptera: Psocomorpha).
15:00 – 15:20	Popov, Yu.A. – History of true bugs (Heteroptera).
15:20 – 15:40	Emeljanov, A.F. & *Shcherbakov, D.E. – Planthoppers: from the Permian to Cenozoic.
15:40 – 16:00	Szwedo, J. – Fossil Achilidae and their significance for the phylogeny and classification of the group (Hemiptera: Fulgoromorpha).
16:00 – 16:20	TEA
<b>Session 7.4: Insect Phylogeny &amp; Systematics 3 – Chairperson: David Grimaldi</b>	
16:20 – 16:40	Szwedo, J. – Lower Cretaceous Fulgoromorpha (Hemiptera): their diversity and disparity.
16:40 – 17:00	Vilhelmsen, L.B. – The old wasp and the tree: estimating the size and age of the common ancestor of Orussidae (Hymenoptera).
17:00 – 17:20	*Rasnitsyn, A.P. & Brothers, D.J. – Extending ancestry: two new hymenopteran fossils from the mid-Cretaceous of southern Africa (Hymenoptera: ?Jurapriidae, Evanidae).
17:20 – 17:40	Brothers, D.J. – A new family of chrysidoid Hymenoptera from New Jersey Cretaceous amber.
17:40 – 18:00	*Petrulevičius, J.F., Huang, D-Y. & Ren, D. – A new hangingfly (Insecta: Mecoptera: Bittacidae) from the Middle Jurassic of Inner Mongolia, China.



**PROGRAMME** (\* = presenter)

<b>Tuesday 8 February</b>	
<b>Session 8.1: Insect Phylogeny &amp; Systematics 4 – Chairperson: Dmitri Shcherbakov</b>	
08:40 – 09:00	*Blagoderov, V., Grimaldi, D. & Fraser, N. – Diverse Diptera from the Late Triassic of Virginia (USA) and the early radiation of the Diptera.
09:00 – 09:20	Veltz, I., *Azar, D. & Nel, A. – New chironomid flies from the Early Cretaceous Lebanese amber (Diptera: Chironomidae).
09:20 – 09:40	Grund, M. – Chironomids in Dominican amber: a fossil tropical fauna.
09:40 – 10:00	*Arillo, A. & Hippa, H. – A new genus and species of sciaroid fly from Lower Cretaceous amber of Spain (Diptera: Sciaroidea).
10:00 – 10:20	*Azar, D., Adaymé, C. & Jreich, N. – The discovery of a new Cretaceous species of <i>Paleopsychoda</i> Azar et al. 1999 from Taimyr amber (Diptera: Psychodidae: Psychodinae).
10:20 – 10:40	Dikow, T. – Leptogastrinae in the fossil record (Insecta: Diptera: Asilidae) – evaluation of minimum age, biogeographical implications and morphological characteristics.
10:40 – 11:00	TEA
<b>Session 8.2: Other Arthropods – Chairperson: Julián Petrulevičius</b>	
11:00 – 11:40	Penney, D. – Completeness and bias versus adequacy of the spider fossil record. (KEYNOTE)
11:40 – 12:20	Selden, P.A. – Fossils and phylogeny of spiders.
12:20 – 13:00	Kraus, O., *Brauckmann, C.A. & Gröning, E. – Extinct Late Palaeozoic Arthropleurida and extant relatives (Diplopoda, Penicillata): relationship, functional morphology and ecological aspects.
13:00 – 13:20	Pinto, I.D. – New data on <i>Pygocephalus</i> Huxley, 1857 and the correlate genera of the Pygocephalomorpha Order.
13:20 – 14:00	LUNCH and POSTERS
<b>Session 8.3: Assemblages 1 – Chairperson: Conrad Labandeira</b>	
14:00 – 14:20	Jarzembowski, E.A. – Insect/other-animal interactions in the Late Carboniferous.
14:20 – 14:40	*Petrulevičius, J.F., Sallenave, S.A. & Nel, A. – Ambush-predator guild of backswimmers in the Cretaceous of Argentina.
14:40 – 15:00	*Krassilov, V.A. & Rasnitsyn, A.P. – Pollen eaters and pollen morphology in Paleozoic and Mesozoic plants.
15:00 – 15:20	*Andrade-Morraye, M. de & Genise, J.F. – An association of fossil larval tubes and head capsules of Chironomidae (Diptera) from the Jurassic (Callovian-Oxfordian) Cañadon Asfalto Formation, Patagonia, Argentina.
15:20 – 15:40	*Wedmann, S. & Richter, G. – Aquatic life in a Tertiary lake ecosystem.
15:40 – 16:00	TEA
<b>Session 8.4: Assemblages 2 – Chairperson: Ed Jarzembowski</b>	
16:00 – 16:20	Soriano, C. & Delclòs, X. – Palaeoentomological associations in Lower Cretaceous lacustrine deposits from Spain: Las Hoyas and El Montsec fossil sites.
16:20 – 16:40	*Beckemeyer, R.J. & Hall, J. – The Lower Permian fossil-insect beds of Kansas and Oklahoma, USA.
16:40 – 17:00	Beattie, R.G. – A palaeoenvironmental and palaeoecological reconstruction of the Upper Permian insect beds at Belmont, New South Wales, Australia.
17:00 – 17:20	Ponomarenko, A.G. & *Shcherbakov, D.E. – Insects about the Permian/Triassic boundary.
17:20 – 17:40	*Azar, D., Ziadé, K. & Gèze, R. – Fossil-insect outcrops in Lebanon.
17:40 – 18:00	POSTERS
<b>Wednesday 9 February</b>	
09:00 – 17:00	Excursions



## PROGRAMME (\* = presenter)

Thursday 10 February	
<b>Session 10.1: Biodiversity – Chairperson: Jorge Genise</b>	
08:40 – 09:00	Anderson, J.M. – The insect contribution to the elucidation of Gondwana biodiversity trends.
09:00 – 09:20	Rust, J. – Diversity changes in fossil insects from middle and northern Europe during the Paleogene.
09:20 – 09:40	Archibald, S.B. – A diverse new Eocene Mecoptera (Scorpionflies, Hangingflies) fauna from the Okanagan Highlands (British Columbia, Canada and Washington State, USA).
09:40 – 10:00	*Martins-Neto, R.G., Gallego, O.F. & Brauckmann, C.A. – A review of South American Palaeozoic entomofauna with description of three new genera, two new species and four new combinations, from Bajo De Véliz locality (Upper Carboniferous, Argentina).
10:00 – 10:20	Anderson, J.M. – Towards a monograph on the insects of the Late Triassic Molteno Formation, South Africa.
10:20 – 10:40	Grachev, V.G. & *Mostovski, M.B. – Aptian (mid-Lower Cretaceous) weevils (Coleoptera: Curculionioidea) of Asia and Brazil: a comparison.
10:40 – 11:00	TEA
<b>Session 10.2: Miscellaneous – Chairperson: Jes Rust</b>	
11:00 – 11:20	Wappler, T. – Outstanding fossil insects from the Middle Eocene Eckfeld maar.
11:20 – 11:40	Martins-Neto, R.G. – The Santana Formation palaeoentomofauna reviewed: Polyneoptera (Isoptera, Blattoptera, Dermaptera, Orthoptera) with description of six new species, one new genus and one new combination.
11:40 – 12:00	Ansorge, J. – Mass occurrence of <i>Oryctes nasicornis</i> (Linné, 1758) (Coleoptera: Scarabaeidae: Dynastinae) in wasted tanbark in the medieval town hall of Stralsund (Germany, Mecklenburg-Vorpommern) – an example for archaeoentomological studies.
12:00 – 12:20	Beckemeyer, R.J. – Three-dimensional geometry of the wing of <i>Megatypus schucherti</i> Tillyard (Odonatoptera: Meganeuridae).
12:20 – 12:40	Mitchell, A.A. & *Jarzembowski, E.A. – The EDNA fossil-insect database – the first 20,000 species.
12:40 – 13:30	LUNCH and POSTERS
<b>Session 10.3: Taphonomy and Trace Fossils – Chairperson: Val Krassilov</b>	
13:30 – 14:00	Delclòs, X. – Fossil-insect taphonomy: their preservation in carbonate rocks. (KEYNOTE)
14:00 – 14:20	*Petrulevičius, J.F. – Palaeobiology and taphonomy of amber and its inclusions: theoretical framework of their historical relationships.
14:20 – 14:40	Hasiotis, S.T. – Preservation of ichnofossils and body fossils in continental environments: understanding the depositional conditions, soil-forming processes and the taphonomic filter.
14:40 – 15:00	*Petrulevičius, J.F., Deploëg, G. & Nel, A. – Taphonomy of the Paris amber and its inclusions, early Eocene of France.
15:00 – 15:30	Genise, J.F. – The palaeontological significance of insect trace fossils in palaeosols. (KEYNOTE)
15:30 – 15:50	TEA
<b>Session 10.4: Trace fossils – Chairperson: Xavier Delclòs</b>	
15:50 – 16:10	Hasiotis, S.T. – Insect trace fossils – their use as proxies for biodiversity, and indicators of palaeoenvironment, palaeoecology, palaeohydrology and palaeoclimate.
16:10 – 16:30	*Labandeira, C.C., Anderson, J.M. & Dilcher, D.L. – The early history of leaf mining on gymnospermous and angiospermous floras.
16:30 – 16:50	Krassilov, V.A. – Galls and mines on fossil leaves from the Late Cretaceous of southern Negev, Israel.
16:50 – 17:10	*Bordy, E.M., Bumby, A.J., Catuneanu, O. & Eriksson, P.G. – Exceptional trace fossils from the Lower Jurassic, main Karoo Basin, southern Africa: termite nests vs. ???
17:10 – 17:30	Pickford, M. – Arthropod bioconstructions from the Miocene of Namibia and their palaeoclimatic implications.
<b>Session 10.5: AGM and Dinner</b>	
17:40 – 19:00	International Palaeoentomological Society AGM – Rasnitsyn, A.P. (President)
19:00 – 22:00	Congress Dinner (at Congress venue)



**PROGRAMME** (\* = presenter)

Friday 11 February	
<b>Session 11.1: Amber – Chairperson: Dany Azar</b>	
08:40 – 09:10	Perkovsky, E.E., Rasnitsyn, A.P., Eskov, K.Yu. & Vlaskin, A.P. – A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples.
09:10 – 09:30	Solórzano Kraemer, M.M. – Arthropods in Mexican amber.
09:30 – 09:50	Prokop, J. & Nel, A. – Fossil resin with biological inclusions in early Paleogene deposits from the Bile Karpaty Mountains in eastern Moravia (Czech Republic).
09:50 – 10:10	Perrichot, V. – The underestimated importance of the Cretaceous amber of France.
10:10 – 10:30	*Arillo, A. & Nel, A. – The first Baltic amber dysagrionine damselfly (Odonata: Zygoptera: Thaumtoneuridae: Dysagrioninae).
10:30 – 11:00	TEA and POSTERS
11:00 – 13:00	visits to SANBI
13:00 – 13:40	LUNCH
13:40 – 18:00	visits to BPI/SANBI

**POSTERS** (\* = in attendance)

**Insect Phylogeny & Systematics**

1. \*Andrade-Morrays, M. de, Pinheiro, J. & Nel, A. – Preliminary notes on the record of Protanisoptera (Insecta: Odonoptera) in Itu varvite, Itararé Subgroup (Permo-Carboniferous), Paraná Basin, Brazil.
2. Vršanský, P. & \*Ansorge, J. – Lower Toarcian (Lower Jurassic) cockroaches (Insecta: Blattodea) of Germany and England.
3. Nel, A., \*Delclòs, X., Béthoux, O. & \*Azar, D. – *Chresmoda*, an enigmatic Mesozoic insect that is finally placed.
4. \*Martins-Neto, R.G. & \*Szwedo, J. – New data on Fulgoromorpha (Hemiptera) from Lower Cretaceous Santana Formation, Brazil.
5. \*Ren, D. – New ommatids from the Late Jurassic of western Liaoning, China (Coleoptera: Archostemata).
6. \*Soriano, C., \*Ponomarenko, A.G. & \*Delclòs, X. – New cupedids (Coleoptera: Cupedidae) from the Lower Cretaceous of Spain.
7. \*Krzemiński, W. – Bittacidae (Mecoptera) from the Baltic amber revised (Upper Eocene).
8. \*Krzemiński, W. & Krzemińska, E. – The oldest Diptera and their importance to the phylogeny of the order.
9. Hauser, M. & Irwin, M. Fossil Therevidae (Diptera, Asiloidea) - How the past can change our view of the present. (in absentia)
10. \*Perrichot, V. & Nel, A. – Hymenopteran inclusions from the Cretaceous amber of France.
11. \*Kolyada, V.A. & \*Mostovski, M.B. – Revision of proctotrupid parasitic wasps (Hymenoptera: Proctotrupidae) described by Ch.T. Brues from the Baltic amber.



### Other Arthropods

12. \*Hasiotis, S.T. – 300-million-year trace-fossil record of terrestrial and freshwater burrowing crayfish from North America.
13. \*Leggitt, V.L. – Cladocerans (Branchiopoda: Anomopoda) from the Miocene Barstow Formation: Mojave Desert, California.
14. Menon, F., \*Penney, D., \*Selden, P.A. & Martill, D. – A scolopendromorph centipede from the Cretaceous Crato Formation of Brazil.
15. \*Penney, D. – Hispaniolan spiders: extinct and extant compared.
16. \*Selden, P.A., Corronca, J.A. & Hünicken, M.A. – The true identity of the supposed giant fossil spider *Megarachne*.

### Assemblages

17. \*Adami-Rodrigues, K., Iannuzzi, R. & \*Pinto, I.D. – Permian plant-insect interactions in a Gondwana flora of southern Brazil.
18. \*Beattie, R.G. – A palaeoenvironmental and palaeoecological reconstruction of the Upper Permian insect beds at Belmont, New South Wales, Australia.
19. \*Delclòs, X., Martín-Closas, C. & \*Soriano, C. – The aquatic Lower Cretaceous ecosystem of Las Hoyas (Spain): ecological interactions.
20. Peñalver Mollá, E. & \*Grimaldi, D. – An exceptional biocenosis in Miocene Dominican amber (Diptera: Phlebotominae; Vertebrata: Mammalia).

### Biodiversity

21. \*Grimaldi, D., Fraser, N. & \*Blagoderov, V. – A diverse insect fauna from the Late Triassic of Virginia, USA: summary and new findings.

### Miscellaneous

22. \*Rasnitsyn, A.P., Lukashevich, E.D. & \*Mostovski, M.B. – Centenary of Boris B. Rohdendorf and 125th birthday of Andrey V. Martynov.
23. \*Zessin, W. – Pictures of the German Carboniferous localities Hagen-Vorhalle and Ploetz.

### Amber

24. \*Azar, D. – Lebanese amber: “an exceptional trip into the past”.
25. \*Delclòs, X., Peñalver Mollá, E., \*Ariño, A., Ortuño, V., López Del Valle, R. & \*Soriano, C. – Spanish Mesozoic amber localities.
26. \*Hoffeins, C. & \*Hoffeins, H.W. – Frequency of inclusions in Baltic and Bitterfeld amber from unselected material, with special reference to the order Diptera.
27. \*Wappler, T. – The age of Baltic amber: could Eckfeld resolve this problem?



## ABSTRACTS OF PAPERS

(\* = presenter)

### **The insect contribution to the elucidation of Gondwana biodiversity trends**

John M. Anderson

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In a volume in preparation entitled "Gondwana Alive: biodiversity trends and the evolving terrestrial biosphere", we attempt a comprehensive overview of the insect faunas from the Gondwana supercontinent and its dispersed continental fragments. These faunas (productive 'formations') are few enough - 72 at the latest count - and the collections limited enough - normally in the 100s of specimens - to render this a feasible exercise. Fossil floras, reflecting the scaffolding of the ecosystem, are considerably more frequently encountered and the collections more numerate, and are hence impossible to cover equally fully at this time. The tetrapod vertebrates, the third of the three major preserved components of the evolving terrestrial biosphere, are known through perhaps twice as many faunas as the insects, but far fewer individuals, and the statistical data are a level more elusive to gather.

The insect faunas are spread, in part, fairly evenly across the Gondwana continents (South America 18 'formations', Africa 18, India 3, Antarctica 3 and Australasia 19) and stratigraphically from the Late Palaeozoic to Pleistocene (aside from the Carboniferous and Jurassic with only 3 faunas each). Sampling potential and quality of individual faunas, however, remains very uneven: 11 of the 72 are represented by Lagerstätten or key formations, 16 are of intermediate status, and the majority 45 are currently known only through reconnaissance sampling.

As far as the data allow (and a great deal more sampling and taxonomic work is needed), we aim to plot diversity trends for Gondwana stage by stage, and analyse the measure to which the graph parallels or diverges from similar plots for the plants and tetrapods. A second way of looking at insect diversity through time is via a selection of the best-sampled and -studied individual localities. The top 17 such locality-faunas for the Permian, Triassic and Cretaceous suggest that insect diversity (at all levels from species to order) shows a measure of constancy.

As for our Late Triassic Molteno insect fauna, this initiative has been devised as a consortium-project involving many colleagues. A good number of those attending our 'Fossils X3' event have already contributed extensively to the volume. Others are invited to participate. The planned schedule is to have the book largely completed by October 2005, to workshop it at the "Gondwana 12" congress in Argentina (6-11 Nov., 2005), and to publish - as a partnership between SANBI (Strelitzia) and other organisations - in the first half of 2006.

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### **Towards a monograph on the insects of the Late Triassic Molteno Formation, South Africa**

John M. Anderson

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The Molteno is a uniquely engaging flagship formation. It is the clearest window known to what appears to be the most explosive of all plant radiations; it represents the "heyday" of gymnosperm diversity following the end-Permian extinction; it possibly reflects the world's hottest terrestrial hotspot; it hints at new pathways of evolution during explosive radiation; it points to diversity highs in mid-latitudes during hothouse intervals; and its habitats and communities portray the dawn of the extant world.

The formation was deposited on an intracontinental fluvial plain, a simple biome with seven primary habitats (ecozones) from horsetail marsh to riparian forest. From the 100 taphocoenoses (assemblages) sampled it has yielded 57 genera and 206 species of plant, half pteridophytes, half gymnosperms. Among the gymnosperms, a



good majority of the the 23 orders is mono-familial and a similarly high proportion of the 32 families is mono-generic. We are clearly sampling the tip of the iceberg.

What is the nature of the of the Molteno insect fauna in this fecund Late Triassic world? Currently we have some 2,300 individuals from 43 of the plant assemblages. A provisional taxonomic sorting reveals around 335 species (117 genera, 18 orders), with the Coleoptera most diverse (161 species), the Homoptera second (69 species) and the Odonata third (22 species), whilst the Blattodea are most abundant (ca 1000 individuals). These are the observed data. Statistical extrapolations suggest a preserved fauna of 7,740 species and an existed fauna of 20,000 species in the Molteno floodplain - a diversity akin to that of equivalent biomes in today's world.

We have the full collection housed at SANBI (Pretoria) where it is curated by locality followed by order and down to species. The diversity noted reflects our provisional taxonomy and classification. The potential for further sampling is indeed great and will be undertaken. A first skeletal draft of a manuscript on the fauna is in place. The principal purpose of the current presentation is to invite our colleagues attending this conference to participate in preparing a full taxonomic monograph on the Molteno fauna - to be published (as part of our SANBI Strelitzia series) before end-2008. This will pair with a second Molteno volume being concurrently prepared by Conrad Labandeira on the rich and diverse evidence of plant-insect associations.

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### **An association of fossil larval tubes and head capsules of Chironomidae (Diptera) from the Jurassic (Callovian-Oxfordian) Cañadon Asfalto Formation, Patagonia, Argentina**

Monica de Andrade-Morrays<sup>1\*</sup> and Jorge F. Genise<sup>2</sup>

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There are few records of invertebrate trace fossils preserving their producers. Accordingly, it has usually been supposed that palaeoichnology could contribute little to the understanding of the evolutionary history of modern taxa, which in turn resulted in a lack of integration between the ichnofossil and the body fossil record. However, complex trace fossils can be attributed reliably to modern taxa, and some producers may unusually be preserved with their traces in particular environments as presented herein. The sample comes from a locality near Cerro Córdor (Chubut, Argentina) belonging to a lacustrine facies of the Jurassic (Callovian-Oxfordian) Cañadon Asfalto Formation. The slab shows tube-like, fusiform structures, compatible with chironomid tubes, preserved as convex epirelief, and oriented parallel to the bedding plan. They range in length from 8 mm to 20 mm, and in width from 3 mm to 5 mm. Their granulometry and mineralogy is distinct from both its fillings and matrix. Grain sizes suggest that a re-crystallization process took place inside the tube. The matrix is composed of a thin layer of small-grain-size siltite-argillite, with deposition of calcium carbonate. Tubes were built with fine-clay material, and later filled up with rich calcium carbonate solution during the taphonomic process, which allowed calcite crystallization inside. The recognition by Scanning Electron Microscopy of mandibles, mentum teeth, basal segments of antennae, and fragments of Chironomidae head capsules in the structures, confirmed their previous identification as chironomid tubes.

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### **Mass occurrence of *Oryctes nasicornis* (Linné, 1758) (Coleoptera: Scarabaeidae: Dynastinae) in wasted tanbark in the medieval town hall of Stralsund (Germany, Mecklenburg-Vorpommern) – an example for archaeoentomological studies**

J. Ansorge

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The unicorn beetle *Oryctes nasicornis* (Linné, 1758) is one of the largest and one of the most prominent European beetles. Males possess a remarkable horn on the head. *Oryctes nasicornis* is the only representative



of the subfamily Dynastinae in Europe. Besides the British islands, the beetle lives all over Europe including south Scandinavia, however preferring a Mediterranean climate. After up to three years of larval development, pupation follows in tennis-ball-sized pupation chambers generated from wood or bark particles. The oldest fossil of *O. nasicornis* was recorded in the Upper Pliocene (1.8 Ma) of Willershausen (Lower Saxony, Germany). After the Pleistocene Ice age the beetles resettled the northern part of Europe during the re-spreading of oaks in the Atlantikum, ca. 9200 years BP. Originally larvae developed in rotting oaks, but in Middle Europe *O. nasicornis* lived mainly in the surroundings of oak-bark-based tanneries until the decline of this industry at the beginning of the 20<sup>th</sup> century. Generally it was accepted that these beetles changed their place of development at the beginning of the 17<sup>th</sup> century. During archaeological excavations in the town hall of Stralsund (Mecklenburg-Vorpommern, Germany), *O. nasicornis* was recorded in large quantities in wasted tan (milled oak bark), which was used shortly after 1385 AD as filling material on the vaulting of the first floor. This medieval record indicates that the synanthropoid unicorn beetle appeared much earlier than previously believed in the surroundings of tanneries. During the early settlement of Germans in Mecklenburg and Pomerania in the 13<sup>th</sup> century many oak woods in the surroundings of newly founded cities were uprooted and the unicorn beetle lost his natural habitat. At the same time oak-bark-based tanneries produced large amounts of leather, where *O. nasicornis* found perfect living conditions in the rotting oak-bark waste.

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### **A diverse new Eocene Mecoptera (Scorpionflies, Hangingflies) fauna from the Okanagan Highlands (British Columbia, Canada and Washington State, USA)**

S. Bruce Archibald

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The insect order Mecoptera was unknown in the North American Paleogene entomofauna west of Florissant, Colorado, until recently, when a single specimen was reported from the Early Eocene Okanagan Highlands locality at Quilchena, BC, Canada. Since that time, a large and diverse assemblage of this order has been discovered throughout the Okanagan Highlands, a series of Early to early Middle Eocene fossil deposits in southern British Columbia, Canada and northeastern Washington State, USA. These now represent the most diverse Cenozoic family-level fossil record of the order. Genera are present that were previously known only from the Paleogene of Denmark and Pacific coastal Russia. This assemblage is comprised of at least seven families, including the extant Panorpidae, Bittacidae, and Eomeropidae, as well as the extinct Dinopanorpidae, Holcorpidae and Cimbrophlebiidae, and a new family. Dinopanorpidae, previously known from a single hindwing, is represented in the Okanagan Highlands by six new species of a new genus, and is now known from complete specimens. A new species of the morphologically bizarre genus *Holcorpa* is now found at the Early Eocene McAbee locality in British Columbia, previously known only from the Late Eocene of Florissant, Colorado.

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### **A third rock crawler in Baltic amber, with note on the Mantophasmatodea (Notoptera)**

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A third species of rock crawler (Mantophasmatodea) is described and figured from middle Eocene (Lutetian) Baltic amber. A revised key to the fossil species, all in Baltic amber, is provided. The phylogenetic position of the Mantophasmatodea is briefly discussed and their affinity to the Grylloblattodea stressed. As has been previously suggested (e.g., Engel & Grimaldi, 2004; Grimaldi & Engel, 2005), it may be best to consider the Mantophasmatodea and Grylloblattodea as members (suborders) of a single order, for which Crampton's name Notoptera would be most appropriate.



## A new genus and species of sciaroid fly from Lower Cretaceous amber of Spain (Diptera: Sciaroidea)

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Cretaceous amber from Alava (northern Spain) has yielded a great diversity of Diptera. Among around 600 fossil flies we have found two interesting specimens of Sciaroidea.

In these fossils the eyes are dichoptic, the ocelli are closely set on small tubercles, the scutum has the setosity in stripes, the tibiae have the vestiture evenly distributed, not in rows, the tibial spurs are well developed, and the wing membrane and all the longitudinal veins including Sc are setose. Further, the wing venation is strongly basalized with Rs near the wing base, CUA1 and CuA2 are separate, without a common stem, and reaching near the base of wing, and C is strongly shortened as e.g. in some Cecidomyiidae (Lestremiinae). In our preliminary cladistic analysis including members of all family rank taxa of Sciaroidea, recent and fossil, the taxon appears as the sistergroup of (*Ohakunea* + *Colonomyia*). These two recent genera have their main distribution in the southern hemisphere and still lack an established family assignment.

One of the specimens, specimen MCNA 8649, has a very interesting syninclusion (sensu Koteja); attached to the fly there is a small wasp belonging to the fossil family Stigmaphronidae, believed to be parasites.

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## The first Baltic amber dysagrionine damselfly (Odonata: Zygoptera: Thaumtoneuridae: Dysagrioninae)

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The Thaumtoneuridae: Dysagrioninae (Odonata: Zygoptera) is a fossil damselfly subfamily rare in the fossil record. Only five genera are known to date:

*Congqingia* Zhang, 1992 is from the Late Jurassic Laiyang Formation (Shandong Province, China). The other Dysagrioninae are Paleogene. More precisely, *Phenacolestes* Cockerell, 1908 is known from the Late Eocene–Early Oligocene of Florissant (Colorado, USA), *Dysagrion* Scudder, 1879 from the Eocene of the Green River (Wyoming, USA), *Primorilestes* Nel *et al.*, 2004 from the Early Oligocene of Primorye Territory, Russia, and *Petrolestes* Cockerell, 1927 from the Eocene of Colorado, USA.

The only European record of this subfamily is the “Dysagrioninae gen. indet. *jutlandica* (Henriksen, 1922)” known from the Danish Paleocene-Eocene and revised by Rust (1999).

For the first time a dysagrionine damselfly has been found in Eocene Baltic amber. It represents a new genus and species.

The *Petrolestini* (*Congqingia* and *Petrolestes*) differ from the new genus in the absence of secondary antenodal cross-veins, distal of Ax<sub>2</sub>, between C and ScP, and in the base of IR<sub>2</sub> in a more basal position.

The new genus differs from *Primorilestes* in the presence of secondary antenodal cross-veins between C and ScP, the absence of secondary antenodal cross-veins between ScP and RA, the narrower cubital area with four rows of cells between CuA and the posterior wing margin, instead of six (Nel *et al.*, 2004). Nevertheless, they have nearly the same organization of the areas between the branches of RP, MA, MP and CuA, and long and narrow petioles.



The new genus shares with the Dysagrionini (*Dysagrion* and *Phenacolestes*) the presence of two secondary antenodal cross-veins between C and ScP, distal of Ax2, the broad cubito-anal area, and the base of IR2 below the nodus. It differs from *Dysagrion* in its distinctly longer petioles, longer and narrower discoidal cells, presence of three (instead of one) rows of cells in the postdiscoidal area distal of the nodus level, MA distally not zigzagged, and the area between MP and CuA distally greatly broadened. The new genus is more similar to *Phenacolestes* in the elongate petiole, elongate discoidal cell, and the distally broadened postdiscoidal area. But they differ in the presence of only one row of cells in the postdiscoidal area opposite the nodus in *Phenacolestes*, instead of two in the new genus, and in the presence of only two rows of cells between MP and CuA near the apex of CuA in *Phenacolestes*, instead of 3-4.

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### The discovery of a new Cretaceous species of *Paleopsychoda* Azar *et al.* 1999 from Taimyr amber (Diptera: Psychodidae: Psychodinae)

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The genus *Paleopsychoda* Azar *et al.* 1999 includes three described species, *P. solignaci* Azar *et al.* 1999, *P. jacquelinea* Azar *et al.* 1999 and *P. inexpectata* Azar and Nel 2002, from the Lebanese lower Cretaceous amber. This extinct genus was probably a blood feeder, judging from the developed and phlebotomid-like mouthparts.

The discovery of a new species of *Paleopsychoda* in the Albian/Cenomanian Taimyr amber indicates that this genus survived at least 25 to 35 My and provides very interesting information on the wide distribution of this genus during the Cretaceous. The studied material comes from the locality of Zhdanikha, region of Khatanga, Taimyr, Siberia, Russia. The fossil resin was collected in the middle of the Begichev formation which is equivalent to the middle Cretaceous period (Albian to lowermost Cenomanian) and is represented by fluvial and deltaic sands with traces of wood containing lignite and amber.

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### A new Mesozoic fossil family of Psocoptera (Insecta: Psocoptera: Psocomorpha)

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A new genus and two included species are described from the Early Cretaceous amber of Lebanon and from the Jurassic limestone of Karatau, Kazakhstan. They are placed in the suborder Psocomorpha, in a new Mesozoic extinct family. This new family shares a lot of characters with Mesopsocidae within Psocomorpha. In addition, some characters are shared with Manicopsocidae (some wing-venation characters) and others are shared with members of the suborders Troctomorpha and Trogiomorpha (like Troctomorpha, pleisiomorphic flagellomeres with secondary annulations; presence of two anal veins; bifurcation of M in the hindwing into M1 and M2, this character shared with many members of Troctomorpha and Trogiomorpha).

Our new family must be placed very basally in the Psocomorpha. A phylogenetic analysis and a cladistic redefinition of the currently admitted major subdivisions of Psocomorpha are needed in order to determine the history and scenarios of evolution within this suborder. The discovery of these fossils increases our knowledge on the palaeobiodiversity of psocids and provides very interesting information on the wide distribution of this extinct new family during the Mesozoic period.



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## Fossil-insect outcrops in Lebanon

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Lebanon is well endowed in palaeontology, with its fossil-fish outcrops and numerous Mesozoic amber deposits. We have recently discovered more than 200 amber deposits ranging in age from Late Jurassic to Cenomanian. To date, only 13 Lower-Cretaceous amber outcrops have yielded material with fossil insects. Amber outcrops with fossil insects are:

*Northern Lebanon:* El-Dabsheh (Caza Akkar); Bsharreh (Caza Bsharreh); Tannourine (Caza El-Batroun).

*Central Lebanon:* Ouata El-Jaouz (Caza Kesserouan); Kfar Selouan; Trashish and Mdeyrij-Hammana (all Caza Baabda); Ain Dara (two localities) and Ain Zhalta (Caza Esh-Shouf).

*Southern Lebanon:* Roum-Azour-Homsiyeh and Jouar Ess-Sous (both Caza Jezzine).

*Beqaa Valley:* Esh-Sheaybeh (Caza Baalbeck).

In addition to fossil insects in amber, we found four more outcrops of fossil insects in the Lower-Cretaceous limestone of Qahmez (Caza Kesserouan), the Cenomanian lithographic limestone of Nammoura (Caza Kesseroun), and in the Lowermost Cretaceous dysodil of Bkassine and Snyia (both Caza Jezzine).

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## A palaeoenvironmental and palaeoecological reconstruction of the Upper Permian insect beds at Belmont, New South Wales, Australia

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The entomofauna of the Tatarian insect beds at Belmont, north of Sydney, was described many years ago by Tillyard, Consett-Davis, Evans and Riek. A new collection has produced some undescribed species, particularly beetles, and new exposure of outcrop. The depositional environment consisted of a series of very shallow, temporarily non-flowing freshwater pools along a gravel river-channel system within a regional coal swamp. A volcanic event produced a volcanic-ash dump, causing a “snapshot” kill of insects, validating possible interpretation of percentages of insect fossils in ecological modeling. The pool community included Conchostraca, *Permosyne* water beetles and extremely rare insect larvae. Swamp banks adjacent to the water courses had a producer base of *Glossopteris*-dominated flora, and *Phyllothea*, with an insect-dominated, first-level consumer community of phloem-feeding Homoptera and palinivorous? Mecoptera. A leaf-litter and bark-dwelling community consisted of Protelytroptera, Psocoptera and archostemate beetles. Neuroptera, and extremely rare Trichoptera, Diptera and the ancestors of the Orthoptera were also present in small numbers. No chelicerates, tetrapods or other potential top predators have been found in this, or proximal, facies. The top insect predators were Odonata. Adult Neuroptera fossils strongly suggest the local presence of their larvae as predators of the Homoptera. Disruptive color patterns in some of the insects may indicate predator-prey relationships. Of interest also is the identification of a number of *Glossopteris* leaves with chewed margins. If these observations are correct, they would represent the earliest record of phytophagous ichnofossils in Australia.



### Three-dimensional geometry of the wing of *Megatypus schucherti* Tillyard (Odonoptera: Meganeuridae)

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Wings of palaeopterous insects are often characterized by fluting or corrugation wherein the longitudinal veins are alternately convex or concave, thus providing structural stiffening to the wing membrane. Of the extant insects, the Odonata are perhaps the best examples of this type of wing construction. Corrugated surfaces are also often preserved in the fossil wings of Palaeozoic Odonoptera. Particularly well-preserved hind wings of a large (195 mm wing length) Permian meganeurid (*Megatypus schucherti* Tillyard, from the Elmo, Kansas fossil beds) were measured and the three-dimensional relief quantitatively characterized. Although some flattening of the wing surface obviously occurred during preservation of the fossils, a comparison with the relief of the wing of an extant dragonfly shows that the corrugation relief, when non-dimensionalized by the local wing chord, is roughly comparable. These preliminary results indicate that an allometric study of the variation of corrugation geometry with wing size in extant and fossil Odonoptera should be undertaken.

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### The Lower Permian fossil-insect beds of Kansas and Oklahoma, USA.

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The Lower Permian Wellington Formation fossil beds of mid-continent North America are known best for the famous Elmo, Kansas locality discovered by E. H. Sellards in the early 1900's. The Elmo site has produced tens of thousands of specimens from which more than 150 species of insects have been described. Equally productive and more widespread geographically, but less well known, are the Midco, Oklahoma beds located some 270 km to the south of Elmo. The Midco beds have also yielded tens of thousands of specimens, but the material has been less well studied, and to date only half as many species have been identified from the Oklahoma localities. Although little research had been done on the sites or their entomological fauna since the last published work of F. M. Carpenter, renewed attention has been given to both the geology and palaeontology of the Wellington Formation in recent years by workers in the region. The history of the Wellington Formation Permian insect beds is recounted and the insect faunal composition (just under 200 species) is briefly reviewed.

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### Diverse Diptera from the Late Triassic of Virginia (USA) and the early radiation of the Diptera

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The Cow Branch Formation (Carnian-Norian: Late Triassic) in southern Virginia, USA, contains a well preserved assemblage of aquatic and terrestrial insects, including the most diverse biota of early Diptera known thus far, and the only significant Triassic entomofauna from North America. Preservation of the flies consists of fully articulated specimens composed of two-dimensional films of silvery alumina silicates on fine, black shale,



which has preserved such fine details as microtrichia. The Cow Branch Formation lies in a southern basin that formed in a series of Triassic rift lakes along the coastal plain of northeastern North America. We report the following Diptera taxa from this deposit: a new genus and two new species of Limoniidae (Tipuloidea); a new genus and species of an unusual fly possibly near Psychodidae; two species (undescribed) in the Culicomorpha, perhaps similar to *Aenne* (Chironomidae); a new species of *Yala* (Procramptonomyiidae); a new genus and species of Protorhynchidae (Bibionomorpha); a new species possibly related to *Crosaphis* (Anisopodoidea); three new species and a new genus in the Paraxymyiidae (Bibionomorpha). There is also a new genus and two new species that are possible stem groups to Brachycera based on wing venation, but the antennae do not have the differentiated flagellomeres of true Brachycera. Lastly, there is a culicomorphan, which unfortunately lacks wings, that possesses a long rostrum, and which may be the earliest record of a hematophagous insect in the fossil record. The appearance of the major infraorders of Diptera by 220 mya, and of stem-group Diptera in the Late Permian, indicates an origin of the two-winged flies perhaps in the earliest Triassic. Dipteran abundance is plotted throughout the fossil record; it increases geometrically from about 1% or less of all insects in the mid to Late Triassic to 20-30% in the Early Jurassic, and asymptotes at 30-40% from the Late Jurassic through the Cenozoic. The rapid proliferation of Diptera 220-200 mya is probably due to a rapid diversification within each of the major infraorders at this time.

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### Exceptional trace fossils from the Lower Jurassic, main Karoo Basin, southern Africa: termite nests vs. ???

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Large, complex ichnofossils occur *in situ* and generally in the same stratigraphic horizon in several localities within the rocks of the Lower Jurassic Clarens Formation (Karoo Supergroup) throughout southern Africa (Zimbabwe, South Africa, Lesotho). The formation, which is well known for its large-scale aeolian dunes and associated sedimentary rocks, also contains sedimentary sequences indicative of wetter periods. In addition, the same formation produced *inter alia* several dinosaurian body and trace fossils and petrified wood with well developed growth rings, again suggesting seasonally wetter, relatively vegetated environments. Furthermore, the formation also hosts a whole array of trace fossils, some of which consist of an intricate system of distinct burrows (e.g., tunnels, shafts and galleries) as well as larger cavities (e.g., chambers). The high morphological complexity of these trace fossils is believed to have most probably resulted from the cooperative work of several individuals, and therefore points to eusocial behavior in Early Jurassic times. Currently, there are five distinct architectural groups recognized, and their classification is based on size, wall thickness, orientation, and presence of internal cavities. A number of these trace fossils have no modern counterparts, but many of them are comparable to structures constructed by extant termites; thus it was proposed that these trace fossils are the consequence of the eusocial behaviour either of some unknown Early Jurassic social group of organisms, or, more possibly, species of now-extinct ancient termites. Either way, this hypothesis is at odds with the traditional view of Cretaceous co-radiation of social insects and plants, and more in line with similar ichnofossil findings from the Triassic and Jurassic rock record of North America.



## A new family of chrysidoid Hymenoptera from New Jersey Cretaceous amber

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Two conspecific specimens of aculeate wasps found in Late Cretaceous amber from New Jersey (USA) cannot unambiguously be assigned to any known family. Features of the wing venation, mesosoma and mandibles indicate that they clearly belong in the Chryridoidea. The wing venation is more complete than in any other member of the superfamily, but does not show the development of RS2 (as found in Plumariidae), sometimes considered to be primitive. The antennae have sparse long erect setae similar to those found elsewhere only in Plumariidae, and the pronotum is similar to that in Plumariidae and Scolebythidae. Cladistic analyses of the fossil in various combinations with the genera of Plumariidae, with groundplans for the families of Chryridoidea and with the families of Aculeata, and using different character sets as appropriate, produced trees of similar length, with the fossil as the basalmost taxon in Chryridoidea, the basal taxon within Plumariidae or as a taxon originating immediately after Plumariidae (and so sister to all other chrysidoids). The last topology (Plumariidae + (fossil + (Scolebythidae + (Bethyidae + Chrysididae) + (Sclerogibbidae + (Embolemidae + Dryinidae)))) was most often the most parsimonious and therefore preferred. It is thus proposed that the fossil taxon be recognised as a new family.

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## Fossil-insect taphonomy: their preservation in carbonate rocks

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Insects are usually considered as soft-bodied terrestrial invertebrates with few possibilities of becoming fossilized. However, insects may remain in oxygenated aquatic media, without disarticulation, for more than one year on quiet bottoms, and in anoxic environments for the same time without decaying or disarticulation. Insects are rarely fossilised because their tissues are non-biomineralized and prone to decay, but when conditions are suitable for preservation, a lot of individuals are found.

Some insect groups have higher preservation potential due to their hardened sclerotization; plane structures, such as wings, also have higher preservation potential due to their rapid burial and slow degradation. Insects with a wider range of sizes are recorded in carbonates in comparison to amber. In carbonate rocks, insects related with aquatic or adjacent environments are mainly found, whereas in amber, insects are related with wooded environments.

Before being fossilized in aquatic ecosystems, insects need to surpass several barriers: predators, water surface tension, chemical composition of water (conditioned eutrophy/oligotrophy), currents, clines, etc. Floating time due to water surface tension varies even within the same insect taxon, and with the presence or absence of a pilose body. Biological (fungal and algae developments, insect wingspan, etc.), physical (water temperature, raining periods, etc.) and chemical (oligotrophy/eutrophy) agents control carcass articulation and sinking.

Rapid burial favours exceptional insect preservation, prevents scavengers, and promotes anaerobic conditions that inhibit necrophages. Low rates of decay are indispensable to allow authigenic minerals to form quickly enough to preserve the most labile soft-tissues.

Taphonomic processes that rule taphonomic bias and organism preservation in carbonate rocks usually favour insect preservation in two dimensions; complete three-dimensional insect preservation is rare. In carbonate rocks, fossil insects are usually preserved as organic remains of the original cuticle, or as a mould where the cuticle has been lost during fossil diagenesis. The most ancient insect cuticle with chitin and protein has been found in Oligocene deposits.

Insects are preserved in carbonate rocks in six major ways that usually represent particular environmental conditions and genesis: a) as an organic film remain, product of the original cuticle, usually not preserved, b)



preserved in an authigenic mineral, c) as a mould of the insect exoskeleton, d) as a cast, replicate in a secondary mineral, e) in a travertine, f) in a concretion.

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## Leptogastrinae in the fossil record (Insecta: Diptera: Asilidae) – evaluation of minimum age, biogeographical implications and morphological characteristics

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Fossil species play an important role in phylogenetic research projects as they serve as the only definitive evidence to hypothesise the minimum age of a taxon. However, fossils are often difficult to assign to a clade based on the few morphological details preserved or the morphological divergence of extant clades from stem-lineage members. The fossil species of Leptogastrinae (Diptera: Asilidae, robber flies) are reviewed, based on all available material and in light of the aforementioned difficulties when dealing with past and recent lineages. The two oldest fossil species of Asilidae are Cretaceous in origin, from the Santana Formation in Brazil (110 Million years ago) and from New Jersey Amber (94-90 Million years ago). Both species can be unambiguously assigned to the Asilidae, but the relationships to recent taxa are difficult to hypothesise because no comprehensive morphological phylogenetic hypothesis for Asilidae exists. The unnamed species from New Jersey Amber was postulated to belong to the Leptogastrinae and a re-examination supports this hypothesis, which provides a minimum age for this taxon. Newly available fossil specimens, primarily preserved in Dominican Amber (approximately 30 Million years ago), of species of Leptogastrinae are presented. These undescribed species are important as they exhibit combinations of character states unknown in extant species or provide insight into the historical biogeography of the Leptogastrinae. The three formerly described species of *Leptogaster* Meigen, 1803 from Oligocene and Miocene deposits (Florissant of Colorado, USA; Radoboj, Croatia; central and south-central France) will be reviewed and their generic combinations will be re-evaluated.

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## Planthoppers: from the Permian to Cenozoic

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Fulgoroidea is the oldest extant hemipteran superfamily. This lineage is traceable back from Cixiidae (Late Jurassic–Recent) via Jurassic Fulgoridiidae to Surijokocixiidae (Late Permian–Triassic). Putative ancestors of these latter, Permian Coleoscytoidea show such planthopper features as claval Y-vein, small postclypeus, lateral ocelli close to eyes (plesiomorphies), short basal cell in forewings, and disc of mesonotum separated (by furrows).

Surijokocixiids developed carinae on the head and pronotum and also on the mesonotum (first, two laterally along the furrows, then, two submedian and one median). They had the venation cixiid-like (rarely polymerized) and a wide precostal area (sometimes with crossveins) in the forewings. Fulgoridiids were like cixiids, with a pentacarinat mesonotum and incipient extravenal pterostigma, but with a deeper CuA fork.

Metatarsal pectens are setigerous or (1st or both) asetigerous in cixiids and achilids, whereas the metatibial pecten is always asetigerous. However, the latter could likewise be either setigerous or asetigerous in Early Cretaceous Lalacidae (otherwise indistinguishable from Cixiidae) and presumably in other extinct families.

First (earliest Cretaceous) Achilidae had a plectoderine-like venation. Achilids are common in some ambers, because their mycetophagous nymphs lived under the bark.

Late Cretaceous *Netutela* (related to extant *Protachilus*) is the earliest member of the (Dictyopharidae + Fulgoridae) lineage, the oldest of extant planthopper groups with long-legged, adult-like nymphs (the first such



nymphs are found in the Early Cretaceous). Most nymphs of pre-Cretaceous fulgoroids probably lived in soil or rotten wood.

Other extant planthopper families have at most a Cenozoic fossil record. No tettigometrid-like forms are known from the Mesozoic. The stem of the fulgoroid family tree consists of cixiid-like forms, and Delphacidae could be their direct descendants. Fossil fulgoroids seem to be more common in warmer palaeoenvironments and absent from some cooler faunas.

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## Evolutionary implications of insect radiations and extinctions in the Cretaceous

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The Cretaceous was a period of great significance in the evolution of terrestrial life, and we present abundant new fossil evidence and interpretations of this period regarding insects. The appearance of abundant amber in the Early Cretaceous provides a unique archive for extinct insect life 140-120 mya, as did the formation of major Plattenkalke deposits. Major groups that radiated during the Cretaceous were various Dictyoptera (especially mantises and termites), phytophagan beetles, aculeate Hymenoptera, cyclorrhaphan Diptera, and glossatan Lepidoptera. Several of these groups are the largest lineages of phytophagous and pollinating animals, radiations of which coincide with that of the angiosperms. An evolutionary mechanism as to how phytophagy and anthophily promotes insect diversification, however, remains obscure. The fragmentation of Gondwana created the vast rain forests of the Amazon and Congo River basins, and separated areas of temperate forest that were once contiguous in Antarctica, southern Africa, Chile, Australia, New Zealand, and surrounding islands (the Austral Region). Numerous living austral disjuncts suggest a pervasive effect of Gondwanan drift, but northern-hemisphere fossils of many presently austral groups indicate these were widespread in the Cretaceous and probably into the early Oligocene. Insects seem to have barely been affected at the family level by the K/T extinctions, but appear to have been profoundly affected by climatic change. The importance of phylogenetics in addressing evolutionary patterns like radiations and extinctions is stressed.

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## The palaeontological significance of insect trace fossils in palaeosols

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Insect trace fossils in palaeosols have been studied systematically since the eighties, contributing to different extents to geological, biological and palaeontological disciplines. In ichnology, new ethological categories, ichnofacies, and principles have been created to accommodate them. Stratigraphy and sedimentology have been benefited because of their importance in the recognition of palaeosols and for extracting palaeoenvironmental inferences. In contrast, the integration of this new information with palaeoentomology for reconstructing evolutionary histories of insects has still been scarce.

Insect ichnofossils are dominant in palaeosols from the Paleocene to the Recent. The key is that these structures, such as breeding and pupation chambers, are produced for larval development. In insect nests, larvae are confined to chambers that are provisioned with different kinds of organic matter. Chambers need to maintain very precise environmental conditions internal to avoid the destruction of provisions and larvae. These conditions are achieved by constructing walls, linings, and particular architectures, in order to isolate them from soil. These morphological devices increase the complexity of the structures. The incorporation of organic matter in the constructions is important for the formation of soils, but also because it increases the potential for preservation of these traces. Nests of bees, dung beetles and termites are the most common



ichnofossils in palaeosols because they are constructed or lined structures, not merely excavated ones. They are able to pass the taphonomic barrier. In turn, increasing complexity of the structure provides numerous diagnostic characters. In many cases these characters should be studied using 3D computer reconstructions, tomographic sections and micromorphological analysis, which can be used to identify and properly attribute trace fossils to insect taxa. In turn, these attributions provide the possibility to contribute to the knowledge of the evolutionary history of the producers. In Halictinae, the minimum ages of behavioral innovations, fossil evidence from the Cretaceous to the Middle Eocene, and from the Southern Hemisphere, came from the ichnofossil record.

Environmental conditions inside chambers are also achieved by their location in soils, which in turn can be analyzed on species and on individual scales. On species scale, the location of nests depends on the geographical distribution of producers, which depends on climate and vegetation. Fossil termite and ant nests have been used in comparison to the actual distribution of their supposed constructors to extract palaeoclimatic inferences. Most fossorial dung beetles and hymenopterans establish their nests in areas dominated by herbaceous plants. Recurrent associations of their trace fossils supported the creation of the archetypal *Coprinisphaera* ichnofacies, which is used as indicative of palaeoenvironments dominated by low vegetation. On an individual scale, females, after selecting a nesting site, locate chambers at a definite depth in the soil. Then, it is expected that the repetition of stratigraphic levels with the same nests in a succession will be indicative of stacked palaeosols.

In conclusion, insect ichnofossils in palaeosols, when studied with a specific methodology that enables a sound ichnotaxonomy, and reliable attributions to extant taxa controlled by the body-fossil record, are powerful tools for sedimentology, stratigraphy, palaeobiology, and for improving our knowledge of the evolutionary history of insects.

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### **Aptian (mid-Lower Cretaceous) weevils (Coleoptera: Curculionoidea) of Asia and Brazil: a comparison**

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The Early Cretaceous Curculionoidea are represented by all their extant families and one extinct one (Ulyanidae). The principal Lower Cretaceous curculionoid fossil sites include Santana in Araripe Basin (Ceara State, Brazil; Santana Fm., Crato Member, Aptian), Baissa in Transbaikalia (Vitim River; Zaza Fm., lower half of Neocomian), Bon Tsagan in Central Mongolia (Bon Tsagan Lake; Khurilt Rock Unit, Barremian or Aptian), and Khetana in Okhotsk Sea area (East Siberia; Emanra Fm., mid-Albian). The Brazilian fauna comprises only extant families of southern-hemisphere distribution (Rhinorhynchinae, Belidae, Eurhynchinae). In contrast, Asian fossil sites have yielded extant families now found either in both hemispheres (Nemonychidae, Anthribidae, Attelabidae, Brentidae, Curculionidae) or southern-hemisphere endemics (Belydae, Eccoptarthridae), and also the extinct family Ulyanidae, endemic to the Asian Lower Cretaceous sites.



## Chironomids in Dominican amber: a fossil tropical fauna

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Dominican amber originates from the Caribbean island of Hispaniola, in deposits dated 15-20 million years old. Although fossil chironomids in Dominican amber can be used to reconstruct the ancient environment, no studies have been undertaken until recently.

The fossil chironomids in Dominican amber are very similar to their recent relatives. An example for this striking similarity is a fossil specimen of the genus *Ablabesmyia*.

The percentage composition of chironomid subfamilies depends on habitat preferences and zoogeographical region. The patterns of subfamily composition in Dominican amber and today's neotropics will be compared.

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## Preservation of ichnofossils and body fossils in continental environments: understanding the depositional conditions, soil-forming processes and the taphonomic filter

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Debate has arisen recently concerning the use of ichnofossils and the degree to which they can be used to interpret the nature of the tracemakers as well as palaeoecologic, palaeohydrologic, and palaeoclimatic settings of continental deposits. For the most part, body fossils of all organisms are disproportionately under-represented due to taphonomic processes, given the enormous thickness of strata that recorded geologic time. Why is this so? The main reason is that the syn- and postdepositional processes in alluvial, palustrine, lacustrine, and eolian environments are highly variable through time and dominated by oxidizing conditions found typically above the water table. Palustrine and lacustrine environments are relatively shallow and mostly short-lived. Sedimentary deposits in many such settings record periaquatic conditions, indicating periods of submergence, emergence, desiccation, and soil development. As a result, organisms deposited in aquatic settings can be exposed subaerially later and destroyed due to an oxygenated soil atmosphere or groundwater.

The relationship between the burrowing behaviour of the terrestrial biota and the substrate environment should preserve a larger, disproportionate number of ichnofossils because they are impacted less taphonomically than body fossils. Ichnofossils are preserved abundantly in the geologic record because they were excavated or constructed in the shallow subsurface environment to various depths and reinforced by physical manipulation or bodily secretions. Ichnofossils were part of the pedogenic modification of continental deposits, and were preserved preferentially by soil chelates and microbial activity attracted to the organic material in the walls of burrows, nests, and roots.

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## Insect trace fossils – their use as proxies for biodiversity, and indicators of palaeoenvironment, palaeoecology, palaeohydrology and palaeoclimate

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Behaviour of organisms that is preserved in the geologic record occurs as ichnofossils (trace fossils). The recognition and interpretation of simple to complex ichnofossils as the product of the activities of insects and



other arthropods are major developments in the study of continental ichnology. The biota is related to the sediment through feeding, dwelling, locomotion, reproduction, and searching behavior evident as tracks, trails, burrows, nests of animals and roots of plants. Ichnofossils in continental deposits represent hidden biodiversity because the tracemakers are preserved only rarely as body fossils for that region or period of geologic time.

Ichnofossils indicate such climatic parameters as temperature, precipitation, evapotranspiration, and solar insolation because a well defined relationship exists between climate, hydrology, soil formation, and biodiversity. The lateral and vertical distribution of modern trace-making organisms within a sedimentary environment is controlled by ecological associations, sediment characteristics, soil moisture, and water-table levels. Similar factors impact soil formation, and include topography, parent material, biologic activity, and time. Continental ichnofossils also preserve major innovations in soil ecosystems that include food hoarding, adaptations to disturbance from flooding and precipitation, enduring unpredictable hypercapnic (rise in CO<sub>2</sub> levels) and hypoxic (fall in O<sub>2</sub> levels) conditions, and reproductive strategies that employ a subterranean, hemimetabolous or holometabolous life cycle.

Thus, ichnofossils in terrestrial and aquatic environments are ancient proxies for 1) hidden biodiversity not recorded by body fossils, 2) above- and below-ground ecological associations, 3) soil formation, 4) hydrology and groundwater profiles, and 5) seasonal and annual climate indicators and climate change.

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## The phasmid wing-recurrence debate: a palaeobiological perspective

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The recently proposed and controversial phasmid wing-recurrence hypothesis suggests that the ancestral phasmid was secondarily wingless and that wings then reappeared independently on at least four occasions in later lineages. The hypothesis is based on a molecular phylogeny of living stick and leaf insects and does not take into account morphological data or the phasmid fossil record. Well developed wings are present in all fossil stick insects, including *Susumanioidea Gorochov*, the likely sister-group of all living phasmids (Euphasmida = Phasmatoidea + Timematoidea). In contrast to fossil forms, the forewings of living phasmids are much reduced and thickened, suggesting that the ancestral euphasmid also had well-developed wings which subsequently underwent significant reduction prior to being lost in several lineages. This is the most parsimonious scenario in the light of fossil evidence and does not support the wing-recurrence hypothesis.

Evolutionary recurrence is a much-neglected phenomenon and, although largely rejected as an explanation for the distribution of winged vs. wingless character transformations in euphasmid phylogeny, deserves further investigation. The maintenance of developmental pathways over extended periods of time is well documented and the possibility of complex morphological features being switched on and off during evolution is of great interest to palaeobiologists and neontologists alike.

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## Insect/other-animal interactions in the Late Carboniferous

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The Coal forest is often perceived as primaevial and inhabited by a few creepy-crawlies (arthropods) of large size and/or unpleasant habits. Whilst not doubting the abundance of cockroaches (Blattaria) – the forest was a good larder – nor the likelihood of being eaten ('spiders' galore), there is evidence of more subtle interplay between animal species, including insects.



I shall demonstrate this with a selection of examples including evidence of cryptic and deimatic markings in insects and swallowing avoidance by horseshoe crabs. The mutual arms race sometimes led to gigantism but alleged mimicry is unlikely, although blood sucking remains an intriguing question.

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## Galls and mines on fossil leaves from the Late Cretaceous of southern Negev, Israel

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The recently described Late Cretaceous (Turonian) flora of Israel contains 46 species of angiosperms. The traces of galling and mining activity are exceptionally abundant and well preserved. In the collection of more than 1000 leaves of terrestrial and aquatic angiosperms, all the leaves are infected. The gall remains include acarocecidia of microscopic tarsonemid mites, as well as zooecidia, some of which show evidence of pupation in the gall, a supposedly advanced feature in the present-day gall midges, as is the detachment of the galls. The mines are linear and blotched, of several morphological types, showing various degrees of specialization in respect to the leaf histology. Unusual associations of galls and mines, with the miners probably acting as inquilines, suggest an elaborate cecidogenous system. These findings are evidence of an explosive evolution of mining and galling habits with the rise of early angiosperm-dominated communities. Some morphological innovations in angiosperms, such as marginal dentation, might have been stimulated by the gall production.

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## Pollen eaters and pollen morphology in Paleozoic and Mesozoic plants

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In each of the sequential periods of seed-plant evolution, there were pollen grains that can be called charismatic for they fascinated generations of palynologists. In the Permian, such peculiar pollen morphologies included the taeniate pollen (with the wall split into bands, or taeniae) of the *Protohaploxylinus* – *Lunatisporites* and *Vittatina* groups, as well as the discoid grains of the *Cordaitina* – *Cladaitina* group. Both types were found in the guts of hypoperlid, grylloblattid and psocid insects. The advent of the Mesozoic era was marked by a spread of smooth asaccate pollen of “*Ginkgocycadophytus*” type, virtually indistinguishable in the dominant orders of Mesozoic gymnosperms. Such pollen was never found in the guts. Charismatic through the Mesozoic was the rimulate pollen of *Classopollis* type. It was found as a monospecific load in the guts of large Jurassic katydids (*Aboilus*, Haglidae). The *Eucommiidites* group, related to gnetophytes, is peculiar in having additional apertures or leptomas parallel to the main sulcus. Recently this pollen type has been found in the guts of a xyelid genus, *Ceroxyela*. The reason why the Paleozoic and Mesozoic insects preferred just such pollen morphologies might have been that these were charismatic for them also: they recognized edible pollen grains by their surface features that evolved mainly for this purpose.



## Extinct Late Palaeozoic Arthropleurida and extant relatives (Diplopoda, Penicillata): relationship, functional morphology and ecological aspects

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Most probably the largest arthropods ever known, the arthropleurids with a total length of more than 2 m, have extant relatives in the tiny Pselaphognatha (Diplopoda), which scarcely exceed 3 mm. To ascertain this continuous existence of the clade, an analysis of the main characters is necessary, which we now interpret as apomorphies. The monophyly of the Penicillata (= Pselaphognatha + Arthropleurida) is based on the following synapomorphies: 1. “trilobitoid” dorsal plates composed of sytergites and lateral pleural folds; 2. a thin, relatively weak and unmineralized cuticula; 3. irregular diplopody; 4. presence of a “rosette plate” on the proteral side of the walking legs, in pselaphognaths represented by a “Y skeleton”; 5. special median sternites in combination with two additional lateral (B and K) plates.

Whereas *Eoarthropleura* is a somewhat inadequately known Arthropleurida, the Microdecemplicida are excluded. They form a separate group with the autapomorphies described by their original authors, which are not comparable to any other extant group of the diplopods: 1. head capsule; 2. constructional morphology of trunk diplosomites; 3. presence of terminal filaments. They may be related to the Chilognatha among diplopods. This proposal is based on: 1. Presence of a three-toothed clypeolabrum and 2. the presumed strict diplopody. They differ from the Penicillata by the absence of paraterga plus pleurites and the presence of only one ventral plate on both sides of the unpaired sternite.

The enormous size of the Arthropleurida is discussed in connection with a relatively weak exoskeleton. It may be that, like in caterpillars, the stabilization was achieved by means of musculature and antagonistic haemolymph hydraulics of the body cavity. This could have caused the functional exclusion of stigmata and tracheae and their replacement by K-plates. They obviously functioned as respiratory structures by plastron-breathing.

The largest known *Arthropleura* specimen shows paired paramedian holes close to the negatively preserved anterior end, not mentioned by previous authors. Similar (positive) structures, i.e. vulvae, are present in the extant Pselaphognatha (e.g., in *Polyxenus lagurus*) in an equivalent position. Hence, the paired holes in the fossil may be traces of corresponding structures.

A study of many remains of the arthropleurids shows that they are exuviae. Comparison with Recent exuviae from pselaphognaths leads to the conclusion that the plate previously interpreted as the head of arthropleurids is in fact the collum. The lack of any mouthparts of the arthropleurids in the fossil record indicates that they were comparatively weak as in Recent pselaphognaths. Therefore the presumed carnivory is denied and spores, including megaspores of associated plants which were produced in large masses during Carboniferous and Lower Permian times, are proposed as diet.

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## The early history of leaf mining on gymnospermous and angiospermous floras

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Leaf mining is a distinctive insect feeding strategy that has originated numerous times and features host-specific patterns of colonization on a wide range of modern land plants. Nevertheless, it is the only major insect functional feeding group whose earliest occurrence is documented in the Mesozoic rather than the Paleozoic.



Although leaf mining currently is overwhelmingly dominant on angiosperms, the earliest demonstrable fossil leaf mines are present on a variety of gymnospermous seed-plant clades. The most widely targeted clade is the ginkgooids, consisting of hosts from five major lineages, namely the shrubby to large woody trees *Dejersya* (Matatiellales), *Paraginkgo* (Ginkgoales), *Sphenobaiera* (Hamshawviales) and *Dicroidium* (Umkomasiales), and the herbaceous *Kannaskoppifolia* (Petriellales). In addition, the herbaceous and broad-leaved conifer *Heidiphyllum* (Voltziales), the cycad *Pseudoctenis* (Cycadales), and the fern *Cladophlebis* (Osmundales) also were colonized. These mines occur in the Late Triassic Molteno Formation in South Africa, placed in the Early Carnian at approximately 225 Ma, and precede the earliest angiosperms by at least 90 million years. From a current examination of approximately 47,500 leaves representing 29 localities, the most diverse leaf-mined clade are the ginkgooids, representing 5 of the 9 species; the greatest abundance is on *Heidiphyllum*, consisting of 119 of 137 total leaves. Four distinctive leaf-mining morphotypes are documented by patterns of mine shape and size, frass texture and trajectory, and other features; the culprits are probably coleopterans and also possibly lepidopterans.

With the exception of two other Gondwanan Triassic occurrences, a leaf-mining hiatus persists until the Jurassic-Cretaceous boundary, from which sinusoidal mines are found on another gymnospermous host, *Pachypteris*, from the Battle Camp Formation of northern Queensland, Australia. From three localities of the Dakota Formation from the United States, placed in the late Albian of the Early Cretaceous (about 104 Ma), 10 leaf-mine types have been found, representing the extant lepidopteran families Nepticulidae and Gracillariidae, and other unknown mining clades. These miners colonized basal dicotyledonous angiosperms, specifically the Platanaceae, Chloranthales, Laurales, Magnoliales, and a rosiid clade. Earlier Cretaceous leaf mines are not known for any angiosperm clade, although the slightly younger ginkgoalean *Pseudotorellia*, from the Cenomanian of Lebanon, is mined. These preliminary data indicate that leaf mining first originated in Gondwana, opportunistically invading several gymnosperms and a single fern clade, and later underwent a radiation on basal dicotyledonous angiosperms in Laurasia.

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## The Santana Formation palaeoentomofauna reviewed: Polyneoptera (Isoptera, Blattoptera, Dermaptera, Orthoptera) with description of six new species, one new genus and one new combination

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This contribution follows a wide review of the Santana Formation palaeoentomofauna. This part focuses on the Polyneoptera. The following new taxa are proposed: a species of *Lapsoderma* (Dermaptera, Labiidae?), one of *Araripetermes*, one of *Caatingatermes* (Isoptera, Hodotermitidae), two of *Cercopisblatta* (Blattoptera, Umenocoleidae? Cercopionidae?), and a new genus and species of Orthoptera, Ensifera.

*Cordulagomphus santanensis* Carle & Wighton, 1990, described as being a Gomphidae (Odonatoptera), was transferred to the Order Dermaptera by Bechly in 1998. A new genus, *Lapsoderma* Martins-Neto, 2001, was described for this species because it did not belong to any dermapteran genus then described from the Santana Formation. Here, another species attributable to the genus is proposed. *Cercopisblatta* shares characteristics with both *Cercopion* Hamilton (originally described as a hemipteran) and *Panopteryx* Vransky, a remarkable blattopteran with sclerotized and veined forewings. The ensiferan is large-sized, 40 mm in length or more, with the posterior femur short and robust, the posterior tibia shorter than the femur, and the posterior tarsi with four segments and pulvilli present on all of them. This new taxon is the biggest known Cretaceous ensiferan and shares no characteristics with the other 35 taxa described for the Santana Formation.

A checklist of all known Polyneoptera for the Santana Formation is also supplied.



## A review of South American Palaeozoic entomofauna with description of three new genera, two new species and four new combinations, from Bajo De Véliz locality (Upper Carboniferous, Argentina)

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A newly described insect *Taiophlebia niloriclasodae* Martins-Neto from the upper part of the Rio do Sul Formation at Taió municipality, Santa Catarina, Brazil (Upper Carboniferous, Paraná Basin) is a key taxon for the understanding of the Narkeminoidea-Cacurgidea complex in the South America Palaeozoic palaeoentomofauna. The venational traits such as ScP and RA distally fused, RP branched, originating about one fifth from the wing base, allow us to see a closest proximity with the Narkeminoidea representatives (*Grylloblattida sensu* Storozhenko), rather than Cacurgidea (“Paraplecoptera” *sensu lato* or Orthoptera). *Taiophlebiidae* Martins-Neto differs from *Narkeminidae* Pinto & Ornellas and its closest families by lacking the typical MP+CuA convergence, being the most basal group within the Cacurgoidea and Narkeminoidea complex. Another genus, *Cacurgulopsis* Pinto & Adami-Rodrigues, from Boituva, São Paulo (Paraná Basin, Upper Carboniferous) was also originally included in the family Cacurgidae. However, *Cacurgus* Handlirsch, the type genus of the family doesn’t exhibit ScP distally fused with RA, which is multibranched, and RP apparently not branched, whose origin is at about one third from the wing base. *Cacurgulopsis* and *Taiophlebia* are sister genera and included in the family *Taiophlebiidae*. *Archaeomegaptilus ferreirai* Pinto, from the Upper Carboniferous of Argentina, originally attributed to the palaeodictyopterans, clearly exhibits traits found in *Taiophlebia* Martins-Neto, so is removed to this genus. “*Paranarkemina*” *velizensis* Pinto & Ornellas, and “*Paranarkemina*” *kurtzi* Pinto & Ornellas, both which came from the Argentinean Carboniferous, share diagnostic traits with *Cacurgulopsis* Pinto & Adami-Rodrigues, so are removed to this genus, and a sister group of *Taiophlebia*, within *Taiophlebiidae*. *Rigattoptera ornellasae* Pinto, from the Upper Carboniferous of Argentina is also a sister group of *Taiophlebiidae*. *Narkemina rochacamposi* Pinto & Ornellas (Paraná Basin, Upper Carboniferous) is removed to the genus *Carpenteroptera* Pinto and *Proedischia mezzalirai* Pinto & Ornellas (Upper Carboniferous, Paraná Basin) is removed to the Narkeminoidea complex, being a sister genus of a new genus and species (Bajo de Véliz, Upper Carboniferous, Argentina), both sister groups of *Carpenteroptera*. For the Brazilian Carboniferous sediments, the species *Narkemina rohdendorfi* Pinto & Ornellas (apart from *Narkemina rochacamposi* Pinto & Ornellas, mentioned earlier) and *Paranarkemina martinsnetoi* Pinto are also known. For the Argentinean Carboniferous, apart from *Paranarkemina kurtzi* and *Paranarkemina velizensis* mentioned earlier, *Paranarkemina amosi* Pinto is known. *Narkemina rohdendorfi* is removed to a new genus and another new genus and species from Bajo de Véliz (Upper Carboniferous, Argentina) is proposed. A phylogenetic approach is also supplied.

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### The EDNA fossil-insect database – the first 20,000 species

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EDNA is a type-based database that at present covers about 3/4 of all fossil insect species. Accompanying systematic data includes family-group and ordinal information. Type localities are included and full references are given for each species. There is also lithostratigraphic and chronostratigraphic information for major divisions (bed/member/formation/group and stage/epoch/subperiod/period).



Using Microsoft Access, it is possible to sort and search each field and output any field combination. Thus synonyms can be extracted plus authors of taxonomic changes. Counts and graphs can also be generated.

A future challenge is extending the database to taxonomic ranges.

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## Completeness and bias versus adequacy of the spider fossil record

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The current state of knowledge of the spider fossil record is presented in the form of an evolutionary tree, by superimposing the accepted cladogram of spider phylogeny over geological time and calibrating it with fossil data. The importance of this technique is that it allows predictions to be made for taxa with an incomplete, or non-existent fossil record. It also graphically highlights biases associated with the spider fossil record in terms of rich and poor sources of fossil spiders and different modes of preservation. Combining neontological and palaeontological data in this manner provides an immense amount of information and thus the ability to investigate palaeobiological problems that could not be addressed adequately using solely palaeontological data. In this presentation recent and ongoing advances (since the previous amber congress) in fossil-spider taxonomy and palaeobiology are illustrated. The fossil record of spiders is very useful for addressing palaeobiological problems but it is still far from complete.

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## A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples

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A comprehensive comparison is provided for the first time for the arthropod composition in Rovno and Baltic ambers, based on representative samples from the Klesov and Dubrovitsy quarries (1246 fossils) and the Yantarnyi Quarry (700 fossils), respectively. The composition of arthropod fossils in different-sized fractions of Baltic amber is also compared for the first time. Results indicate the composition as different enough to consider the origin of Rovno and Baltic ambers as geographically different. The Rovno sample shows a distinctly lower share of Acari (16% vs. 24%), Homoptera (4.7% vs. 8.8%, due to the rarity of *Germaraphis* aphids and scale insects: 1.2% vs. 5.2%, and 0.7% vs. 1.3%, respectively), Chironomidae (22% vs. 40% of Diptera), Empididae (1.1% vs. 3.6% of Diptera), and a higher share of beetles (5.2% vs. 2%), Sciaridae (30% vs. 15% of Diptera) and Phoridae (2.9% vs. 0.9% of Diptera). For ants, Dolichoderinae are less abundant in the Rovno sample (43% vs. 64% of ants), with a particularly low share of *Ctenobethylus goepperti* (Mayr) (30% vs. 59%). The differences are most convincing in the species composition: 9 of 37 ant species found in Rovno amber are unknown in Baltic amber. The deficiency of aquatic and subaquatic arthropods and an excess of dwellers of the *Sciara* zone, indicate the partially ecological nature of the above differences.



## The underestimated importance of the Cretaceous amber of France

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Approximately 50 amber deposits of Cretaceous age were recorded for France at the beginning of the 20<sup>th</sup> century. However, only one analysis of the fossiliferous content was attempted towards the end of the 70's. Indeed, Schlüter recorded fewer than 100 fossil arthropods, mainly insects, from the Cenomanian amber of Durtal and Bezonnais (NW France). He described or figured 36 species in 11 insect families and 5 specimens of Arachnida. Schlüter also analysed some amber pieces from the Early Cenomanian deposits of Fouras and Aix Island in the Department of Charente-Maritime, but without any discovery of fossil inclusions.

New recent field investigations in the region of Charentes has led to the (re)discovery of six amber deposits of both Albian and Cenomanian age, including those of Fouras and Aix Island. Analyses have revealed biological inclusions in all these amber deposits, although only the locality of Archingeay is highly fossiliferous. The other deposits have provided fewer inclusions since they were either discovered more recently and need further analyses (localities of Cadeuil and Angoulême), or the outcrops are less accessible and thus provided a smaller amount of material (localities of Fouras, Aix Island and les Renardières).

More than 800 fossil inclusions have been recorded from the most fossiliferous amber of Archingeay so far. This fossil assemblage is mainly composed of insects but also provided other arthropods such as Arachnida, Crustacea or Myriapoda, vertebrate remains such as a reptile skin and some feathers of a putative dinosaur, and various micro-organisms (bacteria, fungi, algae, diatoms, dinoflagellates ...).

The records are the oldest known for numerous arthropod families or subfamilies: Orthoptera Gryllotalpidae, Heteroptera Gerridae, Coleoptera Rhipiphorinae, Hymenoptera Trigonalidae and Diapriidae (subfamilies Ambositrinae and Belytinae), and Araneae Zodariidae. The records of Formicidae are also the oldest for this family, together with those from the contemporaneous amber of Myanmar. Lastly, this amber deposit has provided representatives of some fossil families such as Palaeoescorpiidae and Lagonomegopidae for arachnids.

With a record of 22 arthropod orders and numerous other biological inclusions, the present analyses demonstrate the previously underestimated importance of the Cretaceous amber of France, which are, together with ambers from Lebanon, Spain, Myanmar, New Jersey, Canada and Siberia, amongst the seven major fossiliferous Cretaceous ambers.

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## Palaeobiology and taphonomy of amber and its inclusions: theoretical framework of their historical relationships

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Over the last few years several articles have been written about the palaeobiology and taphonomy of amber. A new approach to historical relationships between palaeobiological and taphonomical processes concerning amber and its inclusions is presented. Taphonomy is analysed following the methodology and concepts developed by Fernández-López in several publications. The main terms and concepts used in this work are defined as follows: production is the process from which taphonomic entities are originated from palaeobiological entities, this biogenic production implies the death of a palaeobiological entity and/or the realization of remains and/or traces by a palaeobiological entity; biostratinomy is a dispensable discipline of taphonomy that refers to modifications of taphonomic entities from production to burial.

Resin is a trace of biological activity and undergoes biostratinomic and/or fossildiagenetic modifications after its production by the plant. Production of fossils preserved in amber may occur immediately after or before their



inclusion in resin. Inclusion in resin represents a biostratinomic mechanism that allows the preservation in most cases of the three-dimensional shape and external morphology (with micrometrical detail and sometimes of internal soft tissues) by replication of the original remains. Fossildiagenesis of resin and its inclusions goes from burial in the lithosphere to the present day. Inclusion in resin prevents some mechanisms of taphonomic alteration like mineralisation and distortion by gravity, but not others like decay, dehydration, deformation, and thermal maturation.

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## Taphonomy of the Paris amber and its inclusions, early Eocene of France

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In 1996, the finding by the second author of a new Paris amber site enabled the prospecting and collection *in situ* (without biases) of a very rich and mainly unexplored amber layer. Amber comes from the locality of Le Quesnoy near Houdancourt. The age of this amber is considered to be Ypresian (early Eocene) in accordance with recent publications (co-authored by the third author). The aim of this work is to make a preliminary study of the functional taphonomy of Paris amber, to describe the material collected at Le Quesnoy, and to interpret the different taphonomical phases (biostratinomy and fossildiagenesis) involved in the formation of this amber and its inclusions. Fossil resin is preserved in spherical drops, stalactites, irregular pieces, and inside wood. This latter type of preservation allowed the determination (in a recent publication co-authored by the second author) of the producer tree as a member of the Caesalpiniaceae similar to the tribe Detarieae. Fossil inclusions are immersed (totally or partly) or imprinted in the surface. Traces include signals of movement, spider's webs and their prey. From 5127-recorded specimens, insects represent about the 89% of all fossil animals, along with myriapods, spiders, pseudoscorpions, mites, tardigrades, and vertebrates.

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## A new hangingfly (Insecta: Mecoptera: Bittacidae) from the Middle Jurassic of Inner Mongolia, China

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Bittacidae is a small family of insects, but a major family of mecopterans, with more than half of its genera known from the Mesozoic. Cenozoic records are scarce and in most cases are assigned to extant genera. Living bittacids are widespread in temperate and tropical climates. Hangingflies usually occur in mesic habitats, including stream margins, slowly flying short distances. Eggs are drought resistant and laid on the ground, where the larvae scavenge on dead insects. A new genus and species of Bittacidae is erected from the Middle Jurassic of Daohugou, Ningcheng County, Inner Mongolia, China. The new species is represented by a bi-dimensionally articulated specimen, without the head. The new genus appears to be related to the *Mesobittacus*-*Anabittacus* group because of the presence of three synapomorphies, i.e. MP4+CuA1+2 simple; *Kreuz der Bittaciden* not aligned; and crossvein c-sp absent. Its relationships and characteristics are explored.



## Ambush-predator guild of backswimmers in the Cretaceous of Argentina

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Notonectidae are rather frequent in the Cenozoic, but their Mesozoic record is much less complete, with several taxa of uncertain affinities. The present discovery of at least two species of Notonectidae belonging to the modern subfamilies Notonectinae and Anisopinae in the Aptian-earliest Albian of west-central Argentina is of great interest for the knowledge of this family. The specimens of Notonectinae belong to a new species of the recent genus *Notonecta*. The specimens of Anisopinae seem to belong to a new genus and species. Specimens are considered to be exuviae. Exuviae of both species are represented by different instars and preserved in the same strata. Bodies are exceptionally preserved, at least in the prospected position of the lake. Recent species of *Notonecta* may also live together with Anisopinae, exhibiting asymmetrical intraguild predation. They may live in the same space, in lentic - static water systems, but heterogeneity of environment can promote the coexistence of conflicting species. It is noteworthy that notonectids from La Cantera, 120 Ma, formed a guild homologous to the recent Notonectinae-Anisopinae ambush-predator guild in freshwater environments and it is likely this also presented IGP interaction.

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## Arthropod bioconstructions from the Miocene of Namibia and their palaeoclimatic implications

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Neogene deposits in Namibia contain abundant traces of arthropod activity, including bioconstructions. Many of the traces, such as burrows, are impossible to identify precisely, but three kinds of bioconstructions are sufficiently distinctive for their makers to be identified. These include fossil spider's webs attributed to *Seothyra*, termite hives considered to belong to *Hodotermes* and *Psammotermes* and honeycomb similar to extant examples made by *Apis*. These fossilised entomobioconstructions are similar to extant counterparts, meaning that they can be used to glean palaeoclimatic information about the deposits in which they occur. In addition to these readily identified bioconstructions, there are burrows which are less securely identified, but which were probably made by the arachnid *Leucorchestris*, and by coleopterans of various sorts.

On the basis of the identifiable bioconstructions such as the hives attributed to *Hodotermes*, it is considered that during the Early Miocene and at various times during the Pleistocene, the southern Namib Desert, which today experiences winter rainfall, used to experience summer rainfall of up to 750 mm per year. Today these areas receive less than 50 mm per year. The bioconstructions attributed to *Seothyra* and *Psammotermes* indicate that at other times during the Neogene the region was arid to hyper-arid, just as it is today. Hyper-aridity in the Namib commenced about 17-16 Ma.



## New data on *Pygocephalus* Huxley, 1857 and the correlate genera of the order Pygocephalomorpha

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Primitive mistakes about the characters of the genus *Pygocephalus* Huxley, 1857, such as those committed by H. Woodward (1907), H. K. Brooks (1962), F. Schramm (1947) and so on, induced the author to a basic revision of the general characters and taphonomic conditions of this Paleozoic crustacean genus, and correlate genera. For a better understanding they were compared with a similar living species of the genus *Aegla* Leach, 1820.

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## Insects about the Permian/Triassic boundary

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The longest sequences of insect assemblages across the Permian/Triassic boundary (PTB) (including unique faunas of intertrappean deposits and other boundary beds) are known in European Russia and Siberia. Permian zonal faunas diverged due to development of climatic zonality. In the Late Permian, thermophilic cockroaches and orthopterans still common at low palaeolatitudes (Europe) became absent from higher latitudes of both hemispheres. Considerable taxonomic turnover during the Permian was partly due to migrations. Successions of insect faunas in Angaria and Gondwana appear homotaxal.

Palaeodictyopteroids and other Carboniferous orders decreased sharply after the Early Kazanian, but persisted up to the PTB in refugia with favourable climates (mid-Kazanian faunal change seems to be overrated). In contrast to them, the groups of Permian origin (e.g. beetles, homopterans) increased and diversified. In some faunas near the biome boundaries, Paleozoic relicts coexisted with precursors of Mesozoic groups. Several taxa characteristic of the Triassic (Chaulioditidae, Titanoptera, etc.) are first recorded in the Tatarian of semiarid Subangaria.

Assemblages of boundary beds are dominated by groups rare in the Late Permian and contain few first occurrences of Mesozoic taxa. Disruption of climatic and biotic zonality about the PTB resulted in far-range polarward dispersal of some low-latitude taxa. Shortly after that the greatest extinction in non-marine biota took place, affecting small-sized forms connected with water and belonging to younger groups less.

Regeneration of biotic diversity started after the Early Triassic gap. Insects with aquatic immatures, rarely found in Paleozoic assemblages, increased and diversified in the Triassic. The origins of such major groups as Heteroptera, Coleoptera Adepaga and Polyphaga, and Diptera were possibly associated with fresh waters.

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## History of true bugs (Heteroptera)

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True bugs include over 40 000 recent species from nearly 80 families and ca 1 000 fossil (mostly Cenozoic) species from about 50 families, only a few of these families extinct (+). The earliest Heteroptera from the Middle and Late Triassic are shore or water bugs belonging to Nepomorpha: Ochteroidea (?), naucoroid



Triassicoridae†, Naucoridae, Belostomatidae and Notonectidae. The oldest terrestrial bugs are from the Latest Triassic (lygaeoid Pachymeridiidae†).

Heteroptera markedly diversified in the Early Jurassic, including the first recorded water-boatmen (Corixidae, Shurabellidae†), water-striders (Mesoveliidae?), littoral (Ochteridae, saldoid Archegocimicidae†) and terrestrial bugs (Velocipedidae, Pentatomoidea). In the Late Jurassic, more families enter the record: Nepidae (including the oldest extant hemipteran genus, *Laccotrephes*), pleoid Scaphocoridae†, Anthocoridae, Miridae, Coreidae, Alydidae, and pentatomoid Mesopentacoridae†. Jurassic assemblages are usually dominated by corixoids, archegocimicids and pachymeridiids. Shurabellids are very common in the Early–Middle Jurassic of Asia and virtually absent in the Late Jurassic.

The Early Cretaceous heteropteran fauna is similar to the Late Jurassic one, but contains further extant families: Saldidae (Enicocorinae†), Hydrometridae, Enicocephalidae (in Lebanese amber), Tingidae, Reduviidae, Aradidae (including the oldest extant genus of land bugs, *Aradus*), and Cydnidae. Early Cretaceous assemblages are often dominated by notonectids or naucorids, sometimes by corixids (Velocorixinae† or Diaprepocorinae) among water bugs, and cydnids or pachymeridiids among land bugs.

The Late Cretaceous heteropteran fauna, already more similar to the Cenozoic one, includes the first occurrences of Gerridae, Lygaeidae, Thaumastocoridae and Vianaididae (last two in New Jersey amber). All Mesozoic families went extinct, except for the pleoid Mesotrephidae† known from a single find.

During the Cenozoic, the number of living families and subfamilies representing nearly all groups further increased.

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### **Fossil resin with biological inclusions in early Paleogene deposits from the Bile Karpaty Mountains in eastern Moravia (Czech Republic)**

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The newly re-excavated locality of scarce amber resin at Studlov in eastern Moravia has been known for decades but biological inclusions have never been investigated. Stratigraphically, the site is attributed to pelagic marine sediments of the Belovez Formation (Paleocene to Middle Eocene) lying beneath the Zlin Formation (Middle to Upper Eocene). The amber resins were previously studied geochemically, which confirmed an affinity with the attached resinite coal and that the origin of the resin was angiosperm plants. The chemical and physical analyses proved that this amber does not contain “amber-acid” typical of the Baltic amber.

All arthropod inclusions are represented by only a few specimens (25) according to the sparse occurrence of resin at the quarry. In a preliminary study of the arthropod fauna, the following groups have been recognized: Arachnida, Acarina and Insecta represented by the orders “Orthoptera”, Psocoptera, Heteroptera, Coleoptera, Diptera and Hymenoptera. Representatives of Diptera are markedly the most abundant. The current research was focused on the taxonomy of new material of Diptera: Scatopsidae, Phoridae and Hymenoptera: Scelionidae which were systematically and palaeogeographically evaluated. The type material is housed at Charles University in Prague.



## History of the orders of winged insects

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The 125<sup>th</sup> anniversary of Andrey V. Martynov (1879-1938), the worldwide esteemed entomologist and the founder of the Russian palaeontological school, and the centenary of his successor Boris B. Rohdendorf (1904-1977), justifies this short review of some results produced recently by this school jointly with its associates.

A variety of approaches exists to reveal the history of a group of living beings through time, including the genealogical relationships of subtaxa, evolutionary scenarios dealing with the morphological, functional, ecological, and geographical changes of the subtaxa, as well as the timing of all these evolutionary events. All these approaches deserve attention and should be used whenever appropriate. However, the palaeontological data have special value, being unique in their ability both to date and sequence various evolutionary events and to display directly, even if incompletely, the past organic worlds in their diversity along with their interaction systems. Thus, the insect fossil record in its available detail, considered against the background of the entomological knowledge of its diversity and integrity, made it possible to reveal a different and rather unexpected picture of the history of the insects. The information available suggests the main distinction within the winged insects as opposing the former Polyneoptera (orthopteroid insects in the widest sense) to the rest of the Pterygota. Within the latter assemblage, the primary distinction appears to separate mayflies jointly with the dragonflies from the remaining orders, that is, from holometabolans, hemipteroids, palaeodictyopteroids, and a few minor extinct orders. The introduction of numerous other innovations of lesser generality was found necessary to balance the fossil record against other data concerning the extant and extinct winged insects.

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### Extending ancestry: two new hymenopteran fossils from the mid-Cretaceous of southern Africa (Hymenoptera: ?Jurapriidae, Evaniidae)

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The deposits at Orapa, Botswana, include several unique specimens of Hymenoptera which provide insights into relationships amongst various higher taxa, and into the probable characteristics of their ancestral forms. This paper describes two new monotypic genera and their type species. The first shows characteristics of Scelionidae (body and antennal form and some aspects of wing venation) and Chalcidoidea (form of pronotum, number of antennomeres and other aspects of wing venation), and may be a sister taxon to Chalcidoidea; it is provisionally placed in the family Jurapriidae. The second is clearly a member of Evaniidae, but shows a mixture of relatively plesiomorphic (intermediate number of antennomeres and form of mesosoma) and apomorphic (length of hind legs, wing venation and form of metasomal petiole) characters when compared with other species of the family; its placement at or near the base of Evaniidae is highly probable, but greater certainty requires additional specimens.



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## Palaeontology in South Africa

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Because of the unique antiquity of its geological record, with rocks dating back some 3600 million years, South Africa has a very long palaeontological record. For almost two centuries palaeontologists have collected and researched fossils from the rocks of South Africa, and these are curated at various centres in the country and in many countries of the world. These fossils include some of the oldest evidence of life on Earth, some of the oldest multi-cellular animals, an excellent record of the early history of dinosaurs, the most complete record of the more than 80-million-year ancestry of mammals, and a remarkable record of human origins and of human achievements through the last four million years. In particular, two areas of South African palaeontological endeavour which have gained international prominence are: the fossils from the Karoo rocks which record a largely uninterrupted terrestrial rock record covering the Carboniferous, Permian, Triassic and Jurassic periods, documenting a climatic shift from glacial polar conditions to subtropical desert; and the much younger, but nevertheless extended, history of human ancestry. Research in these fields by South African scientists, often in collaboration with people from the rest of the world, has a rich tradition and continues to maintain international prominence.

In relation to the fossil wealth of this country, South Africa suffers from a paucity of palaeontologists, in particular in the fields of invertebrates and palaeobotany. Earlier palaeontological research undertaken in this country has been related to the taxonomy and description of fossils, but now that much of the basic description has been done for many of the vertebrate groups, the emphasis has shifted to the application of fossils in biodiversity, taphonomic, palaeoclimatic, palaeoenvironmental and basin-development interpretation. In the rocks of the Karoo in particular, these studies have been of great assistance in interpreting the geological development of Gondwana.

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## Diversity changes in fossil insects from middle and northern Europe during the Paleogene

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The Paleogene of Middle and Northern Europe was characterised by a greenhouse climate during the Paleocene and Eocene with tropical to subtropical forests and species-rich insect faunas, which are well known from several fossil localities (e.g. Messel, Eckfeld, Mo-clay, Baltic amber). The global temperature drop at the end of the Eocene thermal maximum, lead to mixed subtropical/temperate, less diverse insect faunas in the Oligocene, which are documented in fossil localities like Enspel and Rott in Germany. It is still unresolved whether this climate transition was coupled with a major extinction event in insects, and even the reasons for the decrease of insect diversity (e.g. drop of temperature, change of food-web complexity, decrease of plant species) are still unknown. It is the aim of the presentation to discuss these points in the light of the record of fossil insects from several Middle and Northern European Paleogene localities and their taphonomic peculiarities.



## Fossils and phylogeny of spiders

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There has been considerable debate concerning the utility of fossils in reconstructing phylogeny. In this talk, some of the features and methods of interpretation of fossil spiders are described, and some problems and benefits of the use of fossils in phylogeny reconstruction are discussed. Recent case studies on the use of fossils in reconstructing the spider tree of life are presented.

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## Martynov and Handlirsch *versus* Rasnitsyn: are Palaeoptera primitive?

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Wings of Palaeoptera are derivable from a prototype represented by some Palaeodictyoptera: venation homonomous and regularly fluted in Sc–Cu interval (costal fan; simple convex ScA, RA, MA, and CuA alternating with branched concave ScP, RP, MP, CuP; anal fan); no basal braces and fusions; fore- and hindwings identical (including same fluting of Cu and A). Such wings are deformed automatically during the stroke and conform to the model with two spars (MA and CuA) diverging from the leading-edge spar (RA). Venal braces originate *de novo* in various Palaeodictyoptera and therefore are not homologous with MA or M5 in Neoptera.

Early Neoptera enhanced the cubital spar (basally independent from the radial one) to control wing folding in repose and deformation in flight, and lost the medial spar (restored in some advanced forms). Their 1A was singled out as Pcu, and the venation and fluting became different in the fore- and hindwings. Some neopterans possess a triple Cu with two concave branches of CuP-origin. Neopteran venation is heteronomous and incongruent with fluting.

Handlirsch considered Palaeodictyoptera ancestral to the remaining pterygotes, Crampton – only to the Neoptera. Martynov suggested that Palaeoptera and Neoptera diverged early in pterygote history. Rasnitsyn assumed instead that polyneopterans diverged first, and that palaeodictyopteroids and ephemeropteroids originated from different wing-folding ancestors. Characters used to support the latter hypothesis are weak (e.g. the position of 2A relative to the hindwing anal fold in some Blattodea and Plecoptera is the same as in Homoptera).

The ultraprimitive structure of mayfly nymphs and palaeopterous wings implies that Neoptera originated from mayfly-like ancestors via not-yet-sucking palaeodictyopteroids. The abdominal gills of primitive mayfly nymphs bear a quasi-neopterous tracheal pattern, later imported to the wings in Neoptera.

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## Arthropods in Mexican amber

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Mexican amber inclusions were systematically evaluated first in the 1960's. Since then research has focused on Baltic and Dominican amber. An analysis of the diversity of Mexican amber is presented here, which includes investigations of the climate and vegetation during the formation of the amber, as well as a comparison of the



inclusions found in Dominican and Mexican amber; because the proto-Antilles lay close to Central America during the Paleocene, similarities between the fauna from both amber deposits are to be expected.

What is the relationship between the species from the Mexican amber, extant species, and species found in Dominican amber? How stable has the ecosystem been since the formation of the amber, and what has happened to the fauna of the Mexican amber? These questions have been insufficiently investigated in the past. *Polyderis* (Erwin, 1971), *Procolobostema* (Amorim, 1998), *Trigona* and *Proplebeia* (Grimaldi, 2000), *Cephalotes* (Andrade & Urbani 1999), *Aphaenogaster* (Andrade 1995) and the plant of the fossil resin, *Hymenaea*, together with other new information, suggest a close relationship between Dominican and Mexican amber.

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## Palaeontomological associations in Lower Cretaceous lacustrine deposits from Spain: Las Hoyas and El Montsec fossil sites

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Las Hoyas and El Montsec are composed of lithographic limestones, formed by lacustrine deposits from the Barremian. In both sites fossil remains are very abundant, especially insects (more than 30% of total fossil specimens).

From El Montsec, 900 insect specimens belonging to 13 orders, 35 families, 68 genera and approximately 79 species, have been recorded. From Las Hoyas, 1000 insect specimens from 14 orders, 35 families, 51 genera and at least 53 species, have been sampled.

Despite some similarities between the insect composition of these two fossil sites (high diversity, majority of aquatic forms, some species in common), there are remarkable differences, mostly concerning diversity and abundance of taxa, and proportions of different ecological behaviours.

The El Montsec insect association is characterized by high diversity of hymenopterans, blattids and terrestrial coleopterans, while Las Hoyas is characterized by high diversity of neuropterans, odonatans and aquatic coleopterans.

In terms of abundance, El Montsec's most represented groups are ephemeropterans and odonatans (mostly larval remains), while in Las Hoyas the majority of insect remains belong to adults of aquatic heteropterans and coleopterans. These differences yield a contrast between the most represented breathing mechanisms among the insects of these two sites: at El Montsec more than 80% are aquatic-breathing insects, while at Las Hoyas more than 90% are air-breathing.

Even if some of these differences may be caused by interferences in sample method, they have to be related also to differences in the original characteristics of both palaeolakes (geographical or environmental) and to distinct taphonomical processes.

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## Fossil Achilidae and their significance for the phylogeny and classification of the group (Hemiptera: Fulgoromorpha)

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The earliest Achilidae are known from the Lower Cretaceous (Aptian). Representatives of the family were found in Santana Formation deposits, Burmese amber and Lebanese amber. Few specimens are recorded from Palaeocene deposits of Europe. The richest record of the family is to be found in Eocene Baltic amber, and the Oligocene record is scarce.



Lower Cretaceous representatives are quite distinct from later and extant forms, and none of them can be placed in recently recognized tribes. The most important differences are in venational pattern, but also in other morphological characters. In Palaeocene deposits, Achilidae are reported as abundant, but without formal descriptions or more detailed data available. The richest record of this group is in Eocene Baltic amber. Representatives of some extant tribes have been identified, as well as forms with particular characters, representing separate units. The most numerous are taxa to be placed in Achilini, but with sets of characters calling for further study. It is interesting that extant Achilini are not highly diversified in numbers of taxa, so the fossils seem to be more diversified. The placement of highly derivative Ptychoptilini is still controversial and not resolved. The most numerous tribe in the recent fauna, Plectoderini, is seldom found in Eocene but more commonly in Oligocene/Miocene Dominican amber.

The Achilidae is a group of Fulgoroidea placed close to the basal stock of the superfamily. The most recently proposed scheme of relationships is based on the extant fauna only. Fossils have characters different from extant forms, and could strongly influence the proposed evolutionary scenario of the Achilidae.

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### **Lower Cretaceous Fulgoromorpha (Hemiptera): their diversity and disparity**

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The order Hemiptera Linnaeus, 1758, is divided into 6 suborders: Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorrhyncha, Heteroptera and Palaeorrhyncha. Fulgoromorpha comprises one of the most ancient lineages of the Hemiptera, with a fossil record extending from the Lower Permian. The earliest Fulgoromorpha were represented by Permian Coleoscytoidea and Permian-Triassic Surijokocixioidea; the Fulgoroidea are known since the Jurassic.

Lower Cretaceous Fulgoroidea are represented by Achilidae, Cixiidae and Lalacidae. Achilidae are not numerous, but differ from extant taxa in some morphological characters. This is true for fossils from the Santana Formation as well as for taxa found in Burmese amber. Cixiidae are also not common, but very similar in general characters to extant forms. Lalacidae is an extinct family, characteristically of quite distinct disparity (morphological diversity). Some new fossils of this group were recently found. The present state of knowledge suggests that this family was highly differentiated in the Lower Cretaceous.

Recently, new data about representatives of Fulgoromorpha from the Lower Cretaceous have become available. A planthopper with a very particular set of characters was found in Jordanian amber. It seems that this fossil represents a new family of Fulgoroidea. Other planthoppers were found among inclusions in Lebanese amber. These insects are characterised by nymphal characters retained in the adults, particularly venation, hind-leg chaetotaxy pattern, and structure of female external genitalia. These fossils, highly derivative, without doubt represent another extinct family of Fulgoroidea. Representatives of other families, previously not recorded were also identified among Lower Cretaceous fossils.

It seems that the Lower Cretaceous was an age of Fulgoroidea differentiation.

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### **Rooting the insect phylogenetic tree: independent adaptations to terrestrial life**

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Ideas about the origin and evolution of insects can be traced back to Aristotle. One of the greatest controversies in entomology concerns the root of the phylogenetic tree for winged insects. Most hypotheses concerning the origin of insects can be accommodated in one of two models, an aquatic model or a terrestrial model. Although the terrestrial model received most support in the last century, recent evidence strongly supports an



aquatic origin and we may now be moving towards a point where the phylogenetic tree for all insects can be firmly rooted. Fossil and other evidence is discussed with a view to identifying crucial tests which could potentially resolve the controversy.

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## New chironomid flies from the Early Cretaceous Lebanese amber (Diptera: Chironomidae)

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Chironomid flies are frequent in the Jurassic and Early Cretaceous aquatic insect assemblages, even if the systematic positions of some of the described taxa remain debatable.

Some Late Jurassic or Cretaceous Chironomidae are attributed to Recent subfamilies, like Podonominae Thienemann and Edwards, 1937, Aphroteniinae Brundin, 1966, Diamesinae Edwards, 1929, Orthoclaadiinae Edwards, 1929, and Tanypodinae Thienemann and Zavřel, 1916. The Mesozoic fossil taxa currently attributed to this last subfamily are all either larvae or poorly preserved adults, consequently their attribution to Tanypodinae is uncertain.

Although the Chironomidae are the most abundant group of inclusions in the Lebanese amber, only one genus and species are so far described. We describe the first definitive fossil representatives of the Tanypodinae: Pentaneurini Fittkau, 1962, the oldest representatives of the Orthoclaadiinae and Prodiamesinae, and the male of the podonomine genus *Libanochlites*, previously only known from a female specimen.

The discovery and the study of chironomid flies in the Lebanese amber allow the understanding the historical biodiversity of this particular group and strongly increase our knowledge of them in the Early Cretaceous, a very crucial period for the diversification of the Recent entomofauna and development of the modern biotas.

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## The old wasp and the tree: estimating the age and size of the common ancestor of the Orussidae (Hymenoptera)

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The small parasitic wasp family Orussidae comprises 75 extant species distributed worldwide. Two amber fossils from the lower Upper Cretaceous, *Mesorussus taimyrensis* and *Minyorus luzzi*, have been assigned to the family. When analysed together with the extant species, the fossil taxa come out in an unresolved trichotomy with the rest of the Orussidae. This suggests a minimum age of the common ancestor of at least 95 Myr. Biogeographical patterns indicate that the earliest splitting events in the Orussidae are correlated with the initial breakup events in Pangea, approximately 160 Mya. The earliest representatives of the sistergroup to the Orussidae, the Apocrita, have a comparable age. Given the depauperate fossil record of the family, the biogeographical evidence is considered to provide the superior estimate for the age of the Orussidae. The anatomy of the Orussidae displays some reductional features (e.g., wing venation). It has been suggested that they underwent considerable body size reduction early in their evolutionary history. The small size of the fossil taxa (body length about 2 mm) seems to corroborate this. However, when tested more rigorously against the phylogeny, the size reduction hypothesis is not unequivocally supported. Refutation or acceptance of the hypothesis awaits the discovery of additional basal taxa within the Orussidae.



## Outstanding fossil insects from the Middle Eocene Eckfeld maar

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The rich insect taphocoenosis from the Middle Eocene lacustrine deposits of the Eckfeld maar is comprehensively presented for the first time, and permits detailed insights into Middle Eocene palaeoecosystems, the last epoch with a worldwide greenhouse climate. Furthermore, this study allows for an extensive reconstruction of this now-extinct ecosystem. The results are in congruence with other data; for example, from sedimentological and palaeobotanical research.

In total, the Eckfeld maar insect taphocoenosis contains 4617 fossil specimens. The fossil record documents a highly diverse terrestrial fauna and flora, while aquatic life is rather poor in species. The insect taphocoenosis is predominantly composed of Coleoptera (84%). The beetles represented consist of 21 families, among which the Curculionoidea (Curculionidae and Brentidae) is the dominant group, comprising 40% of all specimens. In second place are Chrysomelidae, which are quite common. Elateridae, Scarabaeidae, Buprestidae, and Tenebrionidae are also frequently found. Odonata are extremely rare, only represented by isolated wings but in one instance preserved with the original wing pattern. Dermaptera, Blattaria, Isoptera, Diptera, Plecoptera, and Phthiraptera are represented by only a few fossils. Much more common are Auchenorrhyncha and Heteroptera. Trichoptera are recorded from the Eckfeld maar in the absence of any body fossil on the basis of four different kinds of portable tube-cases.

Analysis of the giant ants from the extinct subfamily Formiciinae, known only from Eckfeld and Messel as complete specimens, shows that the intraspecific variability over the Geiseltalian time period (4-5 Ma) is negligible. Specimens from both localities are probably conspecific. Similar results could be proposed for representatives of Elateridae, Buprestidae, and Chrysomelidae. In these groups, as well as some others, the original structural colouring is preserved, comparable with taxa from Messel and Geiseltal.

Altogether there are numerous xylophagous and parasitic insect taxa present. They indicate densely wooded surroundings, with a highly complex palaeoecosystem. The disposal of heteropteran taxa over the digging profile clearly shows that some kind of temporary xerothermic habitats (e.g., small, temporary areas restricted and free of vegetation) were present, with surrounding areas of sea.

The systematic revision of the Eckfelder taphocoenosis reveals that most of the taxa are generally allied with lineages that now inhabit tropical or subtropical climates. Taxa with a Palearctic or Holarctic distribution are less common. The main palaeobiogeographic pattern shows a strong relationship to faunas from South America and SE-Asia, continents formally allied to Gondwanaland. The composition of the Apinae shows a strong alliance with groups currently known from the roughly contemporaneous and geographically close Baltic amber. This also applies to some other insect taxa (e.g., Carabidae: Paussinae, and Gerromorpha).

The Eckfeld maar insect taphocoenosis shows no striking evidence for a cooling at the end of the Middle Eocene. By contrast, the fossils represent a paratropical rainforest community, similar to those now found in SE-Asia, and supposed for the generally warm climate conditions prevailing in central Europe for the early Paleogene (PETM = Paleocene-Eocene Thermal Maximum).

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### Antiquity of lice

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A 44 million-year-old fossilized louse was discovered with the remains of feathers in its gut, suggesting that even ancestral birds were plagued by ectoparasites. This is the first example of a bird-lice fossil. The finding also suggests that early feathered dinosaurs may have suffered the same itchy symptoms.



The 44 million-year-old specimen, collected from the Eckfeld maar, is exceptionally well preserved. The evolutionary relationship of this louse to other parasitic lice suggests that the co-evolutionary history between parasites and birds spans more than 120 million years. This raises the possibility that the ancestral host for parasitic lice was not a modern bird or mammal as is generally accepted, but an early feathered dinosaur. Since vertebrates fossilize well, much is known of their evolutionary history.

In contrast, our understanding of the invertebrate fauna is scant, since there are very few fossilized remains of the parasites that might have plagued ancestral vertebrates.

This parasite specimen is extraordinary because of its incredible preservation and its last feathery meal is still evident in its foregut. We compared this fossil with extant species of louse. It closely resembles modern menoponids, species restricted to seabirds, shorebirds and ducks.

The Eocene Eckfeld maar is situated 100-150 km from the sea, ruling out seabirds as likely hosts. However, fossilized ancestors of both shorebirds and ducks are present at Messel. So it is very likely that they were also present in Eckfeld.

Tracing the louse phylogenetic tree back to its roots, the co-evolutionary history between parasites and birds spans more than 120 million years. Since the first feathered dinosaur is estimated to be 147 million years old, it is not unlikely that dinosaurs also had such parasites.

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## Aquatic life in a Tertiary lake ecosystem

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The sediments of fossil lakes often yield numerous invertebrate fossils. These finds are usually dominated by terrestrial-living taxa while autochthonous, water-living forms are only rarely found. This is the case for the Eocene maar lake of Messel (Germany). Thus, analysis of the fossils may give interesting clues to the terrestrial environment of the former lake but is often not able to yield information on the ecosystem of the lake itself.

Our examination of fossil faeces from planctivorous fish of the fossil site Messel, has for the first time revealed that larvae of phantom midges (Diptera, Chaoboridae) and biting midges (Diptera, Culicidae) existed in the former lake. The identification of the larval midges was possible on the basis of isolated mouthparts, i.e. mandibles and filter tufts. Due to the quantity of these remains in the coprolites it can be concluded that the aquatic midges formed large populations in the former lake. Therefore, the larvae, and to a lesser degree also the pupae, of these midges were very important factors of the food web and are crucial elements for the understanding of the former lake ecosystem.

Another important taxon of the food web in the former Messel lake are water fleas (Crustacea, Cladocera). They are documented by their ephippia found in great numbers in certain sediment layers and by parts of their bodies found in some fish coprolites.

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## Remarkable steps of the origin of Odonata

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The oldest dragonflies we know are three species from the uppermost Namurian B of the brickyard quarry of the German carboniferous locality at Hagen-Vorhalle, which are rather completely preserved, showing many details of wings, body, head and legs. This are *Namurotypus sippeli* Brauckmann & Zessin, 1989; length of



wings ca. 150 mm, *Erasipteroides valentini* (Brauckmann, 1985), wing length 80 mm and *Zessinella siope* Brauckmann, 1988, wing length 40 mm. The largest, *Namurotypus*, with two pairs of wings, a lot of cells and a characteristic venation, pleating, and a complex tergal, alar and pleural wing articulation, as well as spines along the costal margin and on the main longitudinal veins. *Erasipteroides* Brauckmann & Zessin, 1989 and *Zessinella* are smaller and have fewer large wing cells like *Namurotypus*. The species with the highest number of cells is *Stephanotypus schneideri* Zessin, 1983 from the Stephanian of Ploetz, near Halle in Germany. Some of the old fossil dragonflies show small prothoracic winglets. These prothoracic protowings, never adapted to powered flapping flight, bore a complete set of branched veinal sectors, similar to that of Palaeodictyoptera (after Kukalova-Peck) like *Stenodictya lobata* (Brongniart, 1885).

Similar, but with a different wing size, is *Carpertertypus* Zessin, 1983 from the Carboniferous of North America.

The Mesozoic was the great time of the Anisozygoptera and Protomyrmeleontidae (*Protomyrmeleon* Geinitz, 1887, *Obotritagrion* Zessin, 1991 and *Zirzipanagrion* Zessin, 1991) with a specialised wing venation, never found after the Cretaceous. Recently, two great groups of Dragonflies (and Damselflies) dominate the fauna. Only one genus of the Anisozygoptera, *Epiophlebia* Asahina, 1954 with specialised wing venation, is found in the recent fauna of Japan and the Himalaya region.

Recently, the Anisoptera and Zygoptera are dominant. The wing venation of some Gomphidae (*Microgomphus* Selys, 1857, *Macrogomphus* Selys, 1857, *Lamelligomphus* Fraser, 1922, *Sieboldius* Selys, 1854) especially shows that animals with small differences in venation may possess large differences in body size of larval and imaginal development, with great ecological differences. This, and knowledge of the variability of the wing venation, can be important for estimates of the fossil record of Odonata.



## ABSTRACTS OF POSTERS

(\* = in attendance)

### Permian plant-insect interactions in a Gondwana flora of southern Brazil

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Leaf compressions and impressions from Gondwanan floras of Permian age in the state of Rio Grande do Sul, Brazil, provide evidence for several types of external interactions by insects. The material analyzed originates from the Rio Bonito (Artinskian to Kungurian) and Irati/Serra Alta (Kungurian-early Kazanian) Formations and was collected from horizons interpreted as representing wet palaeoenvironments: marginal accumulations of ancient peat or deposits that formed close to the shoreline. The principal groups of phytophagous insects inferred as the herbivore culprits are orthopteran-like, homopterous Hemiptera and holometabolous Coleoptera. A qualitative analysis of plant-insect interactions from these deposits indicates eleven categories of damage inflicted on the vascular plants: continuous and discontinuous external foliage feeding activity of the foliar edge and apex, removal of the foliar lamina, mining, skeletonization, small incisions related to piercing and sucking, oviposition scars, and galling. Among the damages related to herbivory, the first five types mentioned above were detected in 8,24% of the specimens (total = 352). A quantitative analysis allowed us to determine the proportion of herbivorized area removed (0.47% ) and the herbivory index (0.48%) which, in spite of its low value, give us a relative idea, per taxon, of the incidence of herbivorization of the floral assemblages studied. The present study concludes that possibly these phytophagous insects had a preference for *Glossopteris* and less of a specific preference for *Cordaites* and *Gangamopteris* foliage.

### Preliminary notes on the record of Protanisoptera (Insecta: Odonoptera) in Itu varvite, Itararé Subgroup (Permo-Carboniferous), Paraná Basin, Brazil

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Protanisoptera is a group of Odonoptera that apparently flourished all over the world during the Permian (recorded from Russia, USA, Australia and Brazil) and became extinct before or at the end of this period. A single Paleozoic record of Odonoptera (Permaeschnidae, Protanisoptera) so far, for Brazil, is *Condvanoptilon brasiliense* Rösler, Rohn & Albamonte, 1981, from a gray limestone of Permian age (Passa Dois Group, Irati Formation). In the present work, samples from Itararé Subgroup (Permo-Carboniferous) were opened and 3 insect wings were found, preserved as impressions, apparently from the same stratigraphic level. The Itararé Subgroup in the vicinity of Itu municipality, is located in the central-eastern region of São Paulo State, Brazil and is known as Itu varvite. It is made up of rhythmites and consists of a lower, coarser, light-colored bed/lamina of fine sandstone/siltstone overlain by a thin, dark lamina of siltstone/argillite. The wings are preserved as impressions on the sandstone level. The wingspan is about 6.5 cm; the wing venation (C(+), R+M, RP3/4, CuA) and possibly the arculus could be observed under a stereomicroscope. Besides the incomplete preservation of the wing venation, we concluded that these structures correspond to fore- and hindwings of Protanisoptera, which provides the oldest record of specimens of that suborder for Brazil.



## Lebanese amber: “an exceptional trip into the past”

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Lebanese amber is well known to be the oldest with intensive biological inclusions. Its age ranges from the terminal Jurassic to the Cretaceous period. Most of the outcrops belong to the Lower Cretaceous, which is a crucial period in the coevolution between insects and flowering plants.

Amber is found in different localities in Lebanon from north to south, and more than 200 outcrops have been discovered, which cover about 10% of Lebanese land.

The mythical foundation of the city of Tyre is related to amber. According to some authors the presence of amber in Lebanon was known for a long time; amber was collected and marketed by the Phoenicians until the Baltic amber, which is of better commercial quality, became available. The earliest “modern” report of Lebanese amber goes back to 1843.

Lebanese amber contains a lot of extinct families 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 old fauna and the modern one, and improve our knowledge of the Past.

Study of the different inclusions in Lebanese amber has allowed the reconstruction of palaeoenvironment, palaeoclimate and palaeogeography.

The Lebanese amber is very important, and efforts are being made to classify this natural treasure on the list of the Heritage of Humanity. The different Lebanese outcrops are not yet officially protected against vandalism. Their destruction or pillaging would be a great loss to the human heritage, and to scientific knowledge.

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## A palaeoenvironmental and palaeoecological reconstruction of the Upper Permian insect beds at Belmont, New South Wales, Australia

Robert G. Beattie\*

see under PAPERS

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## The aquatic Lower Cretaceous ecosystem of Las Hoyas (Spain): ecological interactions

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The aquatic ecosystem of Las Hoyas (Lower Cretaceous, Barremian) is characterised by highly diverse benthos and nekton, but poorly diverse plankton and pleuston. The benthonic community was mainly formed by several species of charophytes (which indicates a low trophism for the lacustrine system), early aquatic angiosperms, aquatic insects, crayfishes and molluscs, whilst the nekton was mainly composed of small adult fishes and freshwater shrimps. The normal status of the aquatic system was oligotrophy, but punctual eutrophication events have been recorded, which may produce the destruction of the charophyte and plant cover and the subsequent mass mortality of benthic animals.

Aquatic arthropods are represented by ostracods, pericarids (isopods and speleogriphaceans), decapods, and insects (ephemeropterans, odonatans, heteropterans, phasmatodeans, dipterans and coleopterans). The studies on arthropod and plant communities of the Las Hoyas palaeolake suggest the presence of several relationships



between arthropods and the palaeoenvironment and between the other organisms that live in the aquatic ecosystem that suggest not only a complex trophic chain in the ecosystem, but also plant-insect, plant-crustacean, and fish-insect interactions.

The charophyte *Clavatoraxis robustus* bore a heavy coat of spine cell-rosettes suggesting an adaptation against herbivory, most probably by coleopterans.

Planktonic inhabitants (Chaoboridae-like pupae) are supposed to be the usual food for other insects and fishes, like *Gordichthys*, a teleostean fish that had a body remarkably similar to recent *Gambusia*. *Chresmoda* was a pleustonic representative; its long and serrate female ovopositor suggests endophytic oviposition. Epipleustonic beetles are represented by coptoclavids; these beetles would feed on insects on the water surface, or diving into the water.

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### Spanish Mesozoic amber localities

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The most ancient mention of the existence of amber in Spain was published by Gaspar-Casal in 1762. During the XIX<sup>th</sup> century and at the beginning of the XX<sup>th</sup>, quite a lot of general publications about Spanish coals and minerals included new references about the occurrence of amber in different localities and mines. Nevertheless, until 1996 no palaeobiological inclusions in these ambers were recorded. This amber (for the first time including palaeobiological specimens) was found in Peñacerrada and Moraza, in Álava and Burgos Provinces respectively, and until today it has yielded about 1500 specimens of insects and other arthropods, mainly arachnids and hexapods.

The scientific research carried out during the last five years in Spain have shown the existence of more than 110 fossil sites with amber, mainly located in the northern and eastern regions. This area corresponds to a Lower Cretaceous palaeogeographic limit of the Iberian Plate, and the majority of amber deposits are associated with deltaic coal-rich palaeoenvironments.

Although the majority of these amber fossil sites are Aptian - Albian in age, several Triassic, Upper Cretaceous and Tertiary amber-bearing deposits are also documented. Nevertheless, only in 7 amber localities from the Lower Cretaceous have recognizable insect inclusions been found. These are: Moraza (Burgos Province), Peñacerrada (Álava Province), El Caleyú and Pola de Siero (both in the Asturias Principate), Rubielos de Mora and San Just (both in the Teruel Province), and La-Hoya (Castellón Province). In these localities 21 orders of arthropods (17 of insects) are known.

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### A diverse insect fauna from the Late Triassic of Virginia, USA: summary and new findings

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A deposit of the lacustrine Cow Branch Formation (Carnian- to Norian-aged), from the town of Cascade in southernmost Virginia, yields the only significant assemblage of Triassic insects in North America, and is also the



most significant such deposit in the Western Hemisphere. The deposit lies in the Danville Basin, which is part of a series of Triassic and Jurassic rift-basin lake sediments along the eastern coast of North America. The insects are found in a thin layer of fine-grained, black shale along with diverse plants (*Pagiophyllum*, *Brachyphyllum*, *Compsostrobus* conifers; bennettitaleans; pteridophytes; ginkgos), various fish, and the small aquatic reptile *Tanytrachelos*. All of the fossils are preserved as silvery films, composed of alumina silicates. The insects are commonly fully articulated, which is unique among the world's Triassic insect deposits and greatly improves phylogenetic interpretation.

Thus far 10 orders and an estimated 40 species of terrestrial arthropods have been excavated and are the following: ARACHNIDA: Araneae; INSECTA: Blattodea, Odonatoidea (family indet.), Orthoptera (Elcanidae [3 species], Locustopseidae [1 sp.]), Plecoptera (family indet.), Thysanoptera (*Triassothrips virginicus* Grimaldi and Fraser, 2004), Hemiptera: Sternorrhyncha (Archescytinidae: 3 spp.), Hemiptera (Auchenorrhyncha: 2 spp.), Hemiptera: Heteroptera (Dipsocoromorpha, Belostomatidae, Naucoridae), Coleoptera (Caraboidea [1 sp.], Cupedoidea [1 sp.], Holcoptera/Dytiscidae [1 sp.], Staphylinoidea [1 sp.], assorted families indet. [10 spp.]), Mecoptera (Pseudopolycentropodidae n.gen., n.sp.), and diverse Diptera. There are 15 species and 8 families of Diptera from the Cow Branch Formation, making this the most diverse dipteran fauna from the Triassic. Diptera include families Limoniidae (n.gen., 2 spp.), a new family in the Psychodoidea (n.gen., n.sp.), Procrampptomysiidae (*Yala*, *Alinka*), Protorhyphidae (n.gen., n.sp.), Crosaphididae (1 n.sp.), Paraxymyiidae (*Veriplecia*, 1 n.gen., 2 n.spp.), a family in the Culicomorpha (2 spp., one of which has a long proboscis and may have been a blood feeder), and 2 species (n.gen.) representing a new family that is a possible stem group to the Brachycera (but which has moniliform antennae). The Diptera come from a time during the initial radiation of the order into infraorders. The thrips are among the oldest and most primitive for Thysanoptera. Belostomatidae and Naucoridae indicate an autochthonous lacustrine fauna and one of the earliest faunas of freshwater aquatic insects. The Staphylinoidea is the oldest and only known Triassic species of this group, and the earliest definitive polyphagan beetle; the Cow Branch Formation is also one of the most diverse assemblages of early Coleoptera. Significant absences are Ephemeroptera, Titanoptera, Neuropterida, and early Hymenoptera (i.e., Xyelidae).

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### 300-million-year trace-fossil record of terrestrial and freshwater burrowing crayfish from North America

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Our understanding of the fossil record and evolutionary history of crayfish (Decapoda: Astacoidea) has changed dramatically in the last decade through studies that integrate continental ichnology, palaeontology, sedimentology, and palaeopedology. The fossil record of crayfish was considered no older than 135 to 140 million years (Early Cretaceous) in Europe based on body fossils found there and in Asia, and no older than 55 million years (early Eocene) in North America based on body fossils from Wyoming. The recent discovery of trace and body fossils in the southwestern United States in 220-million-year-old continental deposits demonstrates that crayfish lived in freshwater and terrestrial environments by the Late Triassic. Moreover, the distribution of extant crayfish in North America, Europe, Asia, South America, and Australia indicate a wide distribution prior to Pangea's initial breakup in the Late Triassic. Additional evidence from Pennsylvanian-Permian rocks in New Mexico suggests that crayfish evolved 300 million years ago.

Recently discovered trace and body fossils come from the Upper Triassic Chinle Formation in southeastern Utah. Trace fossils in Triassic rocks interpreted as crayfish burrows occur also in Arizona, Colorado, New Mexico, and Wyoming. Crayfish body fossils occur also in Arizona's Petrified Forest National Park. Comparisons of the Triassic burrows and body fossils with extant crayfish anatomy and burrow morphology demonstrate that their behaviour, anatomy, and environmental distribution have changed little in the past 220 million years. For example, the depth and architecture of crayfish burrows are related to the depth and fluctuation of the water table since at least the Triassic.



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## Fossil Therevidae (Diptera, Asiloidea) - How the past can change our view of the present

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Several species of fossil "Therevidae" had to be placed outside the family Therevidae, some even outside the order Diptera. The remaining fossil Therevidae from the Florissant shale and the Mexican and Baltic amber belong to the subfamilies Phycinae and Xestomyzinae. The oldest "higher" Therevidae fossil is *Ambradolon grimaldii* Metz & Irwin, 2000 from Dominican amber, which is about 18 Mya old. The oldest Phycinae and Xestomyzinae are from the Baltic amber (40 Mya). The supposedly oldest therevoid fossil, *Rhagiophryne bianalis* probably belongs to the Rhagionidae *sensu lato*. The family Apsilocephalidae, which is closely related to the Therevidae, is known from several Cretaceous deposits up to 100 Ma old. But because of the rarity of fossil Therevidae, the lack of older fossils does not necessarily conclude that Therevidae are younger than the Upper Cretaceous.

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## Frequency of inclusions in Baltic and Bitterfeld amber from unselected material, with special reference to the order Diptera

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A first report on the frequency of arthropod inclusions in Baltic amber was published by Prof. Richard Klebs of Königsberg (Kaliningrad) in 1910.

The basis for this current assessment of the frequency of inclusions is unselected material from different localities with Baltic amber deposits and from the Bitterfeld mine, collected by the authors between 1987 and 2001. For this purpose, arthropod inclusions are determined to the level of order, and dipteran inclusions to the level of family.

The results are presented in 5 tables and 2 diagrams.

Both amber sources have an identical ranking of: the six main orders within the Insecta (1. Diptera, 2. Collembola, 3. Hymenoptera, 4. Coleoptera, 5. Hemiptera, 6. Trichoptera); the six most frequent families within the order Diptera (1. Chironomidae, 2. Sciaridae, 3. Dolichopodidae, 4. Mycetophilidae, 5. Ceratopogonidae, 6. Phoridae); male and female individuals within four dipteran families (1. female Chironomidae, 2. male Sciaridae, 3. male Chironomidae, 4. female Dolichopodidae, 5. female Sciaridae, 6. female Ceratopogonidae, 7. male Dolichopodidae, 8. male Ceratopogonidae).

Klebs' statistics for Baltic-amber arthropods, which have been followed since 1910, are now confirmed and actualized through this research.

Commercial exploitation of the Bitterfeld amber was stopped for ecological/political reasons, and the remaining resources were "guaranteed" by illegal private collectors until flotation of the mine in 1999. During this period, the hypothesis of an autochthonous Bitterfeld amber and its arthropod fauna was the subject of a lively controversy. This hypothesis has not been confirmed by the present authors' results.



## Revision of proctotrupid parasitic wasps (Hymenoptera: Proctotrupidae) described by Ch.T. Brues from the Baltic amber

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Types of six proctotrupid species (Hymenoptera: Proctotrupeoidea) described by Charles T. Brues from the Baltic amber and stored in the Museum of Comparative Zoology, Harvard University, Cambridge, USA, are carefully re-examined. It has been demonstrated that none of six species described in the recent genus *Cryptoserphus* actually belongs to it, but each represents a separate new genus. Thus, six new genera of proctotrupid parasitic wasps have been added to the fauna of the Baltic amber.

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## Bittacidae (Mecoptera) from the Baltic amber revised (Upper Eocene)

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Snake-flies (Mecoptera) are represented in the Baltic amber by eight species of three families: Panorpidae (2 spp.), Ponoropodidae (2 spp.) and Bittacidae (4 spp.), the latter being most numerous in collections. A revision of Bittacidae from Baltic amber revealed one new species, and the fact that all these specimens had only one pterostigmal cross-vein. This allowed the transfer of all these species from the genus *Bittacus* to *Hylobittacus*.

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## The oldest Diptera and their importance to the phylogeny of the order

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The oldest known Diptera come from the famous collection of L. Grauvogel & J.-P. Gall and are aged at Lower/Middle Triassic (240 Ma; Voltzia-Buntsandstein of Alsace, France). Five new species of this collection are presented: one each in Grauvogeliidae (1), Nadipteridae (2), Archilimoniidae (3), Protorhyphidae (4) and Rhagionidae (5). *Grauvogelia arzwilleriana* (Grauvogeliidae) (6) was previously described by us. These species are shown on the background of a phylogenetic tree of the Diptera based on wing venation of fossil and Recent species. They are distributed between four of the five main suborders: Diarchineura (1, 2, 6), Polyneura (3), Anisoneura (4) and Brachycera (5), and demonstrate radiation into these lineages before the Lower Triassic. Only *Neoneura* are not known before the Upper Triassic (*Rhaetania diana*). The tree is illustrated by 43 wings (mostly fossil species).

Homology between the wing veins of Mecoptera and Diptera is presented.



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## Cladocerans (Branchiopoda: Anomopoda) from the Miocene Barstow Formation: Mojave Desert, California

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This is the first report of three-dimensional cladoceran fossils from the Miocene Barstow Formation. Exceptional SEM images of silica-preserved soft-tissue structure allows study of these fossils as if they were modern organisms (sub-micron detail). Both body fossils and ephippia occur in early diagenetic carbonate nodules associated with lacustrine sediments of the Middle Member of the Barstow Formation. The new fossils are found adjacent to the type section of the Barstow Formation, and are confidently correlated with known biostratigraphic and chronostratigraphic markers.

The cladocerans are 0.7 mm to 1.0 mm in length. The carapace covers the thorax, abdomen and thoracic legs. The carapace margin is curved ventrally. The carapace surface exhibits a fine reticulate pattern. The first antennae are five times longer than they are wide and are attached to the head away from the carapace margin. The second antennae are biramous. The dorsal branch contains four segments and four swimming setae. The ventral branch contains three segments and five swimming setae. There is a row of feathered lateral setae on the post-abdomen and a distal bident tooth near the base of the post-abdominal claw. The ephippia are 0.5 mm in length. Two embryos are evident. These characteristics are consistent with placement of this cladoceran in the family Moinidae.

The occurrence of cladoceran “resting eggs” may indicate changing palaeoenvironmental conditions such as temperature, pH, or even periodic lake desiccation. All specimens observed are fully articulated implying high sedimentation and/or high mineralization rates.

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## New data on Fulgoromorpha (Hemiptera) from Lower Cretaceous Santana Formation, Brazil

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Fulgoromorpha (Hemiptera) recorded from the Lower Cretaceous, Upper Aptian, Santana Formation comprise representatives of Achilidae, Cixiidae and Lalacidae. There are some other families listed (Delphacidae, Ricaniidae and Flatidae) but no formal or closer description of representatives of these taxa is available. Lalacidae is represented by a number of highly differentiated taxa, but Achilidae and Cixiidae are scarce. In the newly collected material, representatives of Lalacidae also constitute the commonest group. Only a few of them are to be ascribed to previously known taxa. The others represent new genera and species. Among the specimens recorded, a representative of Fulgoridae was found, the oldest record of the family. This fossil bears some particular characters and needs further examination. Some other specimens are of particular interest – one of them could represent the oldest Derbidae, but with open clavus, which is regarded as an “achilid-like” feature (symplesiomorphy of these sister-groups?). Placement of the next specimen is still not clear; it also could be related to the earliest Derbidae. The position of another specimen remains unresolved; it bears some common characters with Lalacidae, but differs in venational details and head-capsule structures.

It seems that Fulgoromorpha from the Upper Aptian Santana Formation are highly diversified. Comparing them with other fossils of similar age, high specificity (e.g. number of highly diversified Lalacidae, presence of only a few other groups) is evident. It is clear that this locality presents data from the period of formation of more recent Fulgoromorpha faunas. The taxonomic diversity and morphological disparity of Fulgoromorpha from Santana call for further research.



## A scolopendromorph centipede from the Cretaceous Crato Formation of Brazil

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Preliminary morphological interpretation of a new, exceptionally preserved Mesozoic fossil scolopendromorph chilopod from the Crato Formation of the Araripe Basin, N. E Brazil, is presented. The centipede is preserved in right lateral view and shows features, including a tracheal spiracle, not seen in previously described fossil scolopendromorphs from this locality. All four known fossil centipedes from this Formation are morphologically indistinguishable from modern forms, while extant genera from other terrestrial invertebrate orders are known from Cretaceous fossils. Therefore, the new specimen cannot be placed in a fossil taxon on the basis of age alone. Rigorous morphological comparison with extant specimens is required before the correct taxonomic status of the specimen can be determined.

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## *Chresmoda*, an enigmatic Mesozoic insect that is finally placed

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The genus *Chresmoda* (= *Pygolampis*) was named in 1839 by E.F. Germar for an insect found in the Upper Jurassic lithographic limestones of Solnhofen, in Germany. Handlirsch in 1906-08 erected for the species *Chresmoda obscura* the family Chresmodidae. Today the genus is also known and reported from China, Spain, Mongolia, Lebanon and Brazil, and ranges from the Upper Jurassic to the Upper Cretaceous. The genus is not infrequent and diverse semaphoronts, larvae, females and usually males, are found. Larvae and males are apterous, whereas females are winged; unfortunately the wing characters are not well known because wings usually rest folded above the abdomen. The lack of information has prevented any positive placement among several insect groups. The general habitus is similar to that of recent water striders, in relation with a similar life habit, but with mandibles instead of a sucking mouth. The recent discovery of a specimen with fore- and hindwings not folded, in the Lower Cretaceous of El Montsec (Spain), and several specimens with well preserved ultra-articulated tarsi (> 40) in the Upper Cretaceous of Namoura (Lebanon), Solnhofen (Germany) and Las Hoyas (Spain), suggest that *Chresmoda* was a member of Phasmatodea (but not related to the Recent order Phasmida), possibly with carnivorous/insectivorous alimentary habits, and with very specialized leg structures indicating a water-surface skating locomotion mode.



## An exceptional biocenosis in Miocene Dominican amber (Diptera: Phlebotominae; Vertebrata: Mammalia)

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Evidence of fossilized blood-feeding insects associated with mammal hosts include a *Pulex* flea and an argasid (“soft”) tick, each preserved with strands of very rare mammal hair in Miocene amber from the Dominican Republic. Here we report another very rare instance of a fossilized blood-feeding association. From among more than 100,000 pieces of Dominican amber we have found three pieces that contain small swarms of the phlebotomine genus *Lutzomyia* (family Psychodidae) with strands of mammal hair, along with debris presumably from a nest. Given the rarity of mammalian hair in Dominican amber, the probability of finding hair along with *Lutzomyia* based on chance alone is extremely remote. Thus, these blood-feeding midges were probably feeding on the mammal that shed the hairs, and some of the female midges are even bloated, presumably with a blood meal. Detailed maps of the pieces are presented, which aid the taphonomic interpretation of the assemblage. Pending the possible identification of the hair based on fine structure, we hypothesize that the phlebotomines were swarming and feeding around the arboreal nest of the mammal host. New World phlebotomines today harbour various pathogenic microbes, including *Leshmania*, *Bartonella*, and various trypanosomes, and given the remarkable cellular preservation in amber it should be possible to determine if these fossil *Lutzomyia* also harbored microbes that were pathogenic to mammals.

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## Hispaniolan spiders: extant and extinct compared

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Extant and extinct (in Miocene Dominican Republic amber) Hispaniolan spiders are compared graphically at family level using the evolutionary tree of Araneae. Overall, the two faunas are similar but some distinct differences are apparent. The families Cyrtoucheniidae, Microstigmatidae, Ochyroceratidae, Palpimanidae, Tetrablemmidae, Hersiliidae, Agelenidae, Anapidae and Mysmenidae are known only from amber, whereas Drymusidae, Deinopidae, Desidae, Amaurobiidae, Prodidomidae and Zoridae are known only from the extant fauna. Hispaniola is unique in that more spider families are recorded from fossil species than are recorded from extant species. Many spider families are known as fossils only from Dominican amber. Detailed comparisons of these faunas with other Neotropical faunas should allow us to elucidate the origins and palaeobiogeography of the Greater Antillean faunas, and also help us determine taxonomic biases associated with amber preservation.

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## Hymenopteran inclusions from the Cretaceous amber of France

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Since 1999, the Early Cretaceous (Albian) amber of Charente-Maritime (France) has contributed about 1000 fossil arthropods, mainly insects. Hymenoptera is the second-largest group, after Diptera, in terms of the number of specimens (14%) but the largest in terms of diversity, with more than 14 families recognized (26%).



This hymenopteran fossil assemblage found in the French amber is somewhat distinct both in present groupings and relative abundance, compared to the rest of the fossiliferous Cretaceous ambers.

Only Apocritans have been discovered in the French amber, and Parasitica make up 85% of the total hymenopteran specimens belonging to 11 families: Trigonalidae, Megalyridae, Scelionidae, Diapriidae, Ibalidae, Braconidae, Ichneumonidae and undetermined families of the Ceraphronoidea, Proctotrupoidea, Chalcidoidea and Cynipoidea. Aculeata belong to the three families Scolebythidae, Sphecidae and Formicidae. Scelionidae dominate this assemblage with 16% of specimens collected in four distinct species, and Formicidae is the next largest family with 12%, although Chalcidoidea and Proctotrupoidea are still not studied at the family level but seem to be well diversified.

The Trigonalidae is the first and oldest accurate fossil representative of this family. The records of Belytinae and Ambositrinae are the oldest for these diapriid subfamilies, which were not previously known before the Eocene. The Protorhyssalinae is the second and the oldest known representative of this extinct braconid subfamily which was only previously known from the Turonian New Jersey amber. Lastly, the formicid specimens also are the oldest known records for ants, together with those from the contemporaneous amber of Myanmar.

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### Centenary of Boris B. Rohdendorf and 125<sup>th</sup> birthday of Andrey V. Martynov

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In 2004 we celebrated two dates especially remarkable for Russian and world palaeoentomology. It was a centenary year for Boris B. Rohdendorf and the 125<sup>th</sup> birthday of Andrey V. Martynov. The origin and development of palaeoentomological studies in Russia is closely linked to these two names. A. Martynov started to collect fossil insects in various parts of the Soviet Union from the mid-1920s, working for the zoological and geological museums in Leningrad (currently St. Petersburg). He realised deeply that the only successful way for palaeoentomology is in effective specialisation within a group of palaeoentomologists, and undertook efforts to organise such a group. In January 1936, the Arthropoda Laboratory was established in the Palaeozoological (currently Palaeontological) Institute of the USSR Academy of Sciences (currently Russian Academy of Sciences), and A. Martynov became its first head. Sadly, he was happy to lead the laboratory for only 14 months before his death, and B. Rohdendorf, who joined the laboratory in 1936, became the second head of the laboratory for some 40 long years. Under his supervision, the team began growing, and eventually reached 12 specialists during the mid-60s of the last century, becoming and remaining the world's leading research unit in palaeoentomology.

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### New ommatids from the Late Jurassic of western Liaoning, China (Coleoptera: Archostemata)

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Although the family Cupedidae was described in the 1900s, its phylogenetic position was poorly understood until the early part of the 20<sup>th</sup> century. In Lacordaire's major work, *Omma* (*Omma* Newman, 1839) was tentatively placed at the end of the Cucujides, while the family Cupesides (*Cupes* Fabricius, 1801) was placed between the Lymexyloides and Ptiniores (Lawrence, 1999). On the basis of hind-wing venation, Ganglbauer placed the cupedids in the suborder Adephaga, believing them to be a modified family of that group (Atkins, 1963). However, Klobe in a later work considered the group to be a subdivision (Archostemata) of the suborder Symphiogastra (Lawrence, 1999). It was Forbes (1926) and Böving and Craighead (1931) who recognized the



Archostemata as a suborder equivalent to Adephaga and Polyphaga, based on wing venation and larvae respectively, and considered that this suborder included Cupedidae and Micromalthidae.

The family Cupedidae includes some of the earliest known fossil beetles and some of the most primitive living beetles (Lawrence, 1999). This group is small, including only 25 extant species and 9 extant genera (Neboiss, 1984), but it was quite diverse in the Permian and the Mesozoic (Lubkin, 2003). Consequently, the study of Mesozoic cupedid fossils has been important in understanding their relationships.

Although scattered fossil beetles were described before the middle of the 20<sup>th</sup> century, the most abundant and complete specimens of Archostemata were not described until the publication of Ponomarenko's major work. Ponomarenko (1969) defined Archostemata in a very broad sense to encompass the modern archostematan genera and all fossil taxa. He placed all of the typical cupedid-like species from the Triassic to the Recent in the family Cupedidae, which was subdivided into three subfamilies: Triadocupedinae, Cupedinae and Ommatinae.

The phylogenetic position of the subfamily Ommatinae has been the subject of much controversy. Based on the aedeagal difference between *Omma stanleyi* Newman and *Tenomerga mucida* (Chevrolat) (as *Cupes clathratus* Solsky), Sharp and Muir (1912) first proposed Ommatidae. However, most subsequent workers continued to include *Omma* in the family Cupedidae. Lawrence (1999) found there was a deep sensorial cavity on the apical palpomere uniting *Omma* and *Tetraphalerus*; this cavity is absent in Cupedidae. And he discussed the relationships of Ommatidae and Cupedidae and ticked off the differences between them. At last, Lawrence thought that it would be preferable to elevate Ommatinae to Ommatidae and described the features of this family.

A large fossil archostematan assemblage has been found in the Mesozoic non-marine sedimentary strata from northern China and 16 extinct genera and 22 extinct species of Cupedidae have been erected. Recently many well preserved fossil cupedids were recovered from the Yixian Formation in Chaomidian village, Beipiao city, Liaoning Province, by us. A late Jurassic age is indicated by the evidence of abundant fossil insect remains. The discovery of these fossils is very significant because most other Mesozoic cupedids in China are not complete, which made studies on them confined solely to isolated elytra. So the complete preservation enables us to determine accurately the body characteristics of the primitive cupedids and to document a more definite concept of the affinities of these species with existing and extinct groups.

One new genus and four new species of Archostemata from Yixian Formation is erected and can be assigned to the family Ommatidae because its two procoxal cavities are contiguous and the articulations of the abdominal ventrites are abutting. The new genus is similar to *Notocupes* Ponomarenko, 1964, *Tetraphalerus* Waterhouse, 1901, *Rhobdocupes* Ponomarenko, 1966 and *Sinocupes* Lin, 1976, but can be distinguished from other genera according to the following characters: the second joint of the antennae is shorter than the third; the basal joint of the posterior tarsi is obviously shorter than the three following taken together; the antennae reach the posterior ridge of the prothorax in length, and the sides of prothorax have a serrulate margin. Four new species of the new genus are described and figured. A key to species within this new genus is provided. All the specimens are collected from the Late Jurassic Yixian Formation of western Liaoning and are now housed in the College of Life Science, Capital Normal University in Beijing, China.

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## The true identity of the supposed giant fossil spider *Megarachne*

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*Megarachne servinei* Hünicken, 1980, from the Permo-Carboniferous Bajo de Véliz Formation of San Luis Province, Argentina, was described as a giant mygalomorph spider ('tarantula') and, with its body length of 339 mm, the largest spider ever to have lived on Earth. The interpretation was based on: the carapace shape, position of the eye tubercle, interpretation of the carapace anterior protrusion with median ridge as a pair of chelicerae, and a posterior, circular structure as the abdomen. Morphology hidden in the matrix was suggested



by x-radiography: cheliceral fangs, sternum, labium and coxae; and so a reconstruction of *Megarachne* as a giant spider was presented. Difficulties with the interpretation (unusual cuticular ornament, suture dividing the carapace, and spade-like anterior border of the chelicera), together with nonpreservation of synapomorphies of Araneae, provoked debate about its interpretation as a spider. Now, the holotype and a new specimen have become available for study. *Megarachne* is not a giant fossil spider; its true identity will be revealed!

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## New cupedids (Coleoptera: Cupedidae) from the Lower Cretaceous of Spain

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The fossil sites of Las Hoyas and El Montsec are formed by lithographic limestones, the result of sedimentation in shallow lakes during the Lower Cretaceous (Late Barremian). The entomofauna registered in these sites includes 15 orders of insects. The coleopterans are composed of families belonging to three suborders: Archostemata (Cupedidae), Adephaga (Coptoclavidae, ?Trachipachidae, Dytiscidae, and ?Gyrinidae) and Polyphaga (Buprestidae, Elateridae, Peltidae, Parandrexidae, Ptilodactylidae, ?Hydrophyllidae, Scarabaeidae, Staphylinidae, Mordellidae, Nemochnidae, Eccoptarthridae, Belidae, and Anthribidae).

The record of the family Cupedidae is mainly Mesozoic, with about 35 recent species and more than 500 fossil species. At the moment the only species of this group recognized in the Lower Cretaceous of Spain was *Tetraphalerus brevicapitis* Ponomarenko & Martínez-Delclòs, 2000. Recent studies have yielded the presence in Las Hoyas and El Montsec of at least 14 species of the family Cupedidae, belonging to 6 genera and 2 subfamilies.

The diversity of this family in the Spanish fossil sites is comparatively higher than in other European Mesozoic sites, such as Sohlhofen (Germany) or the English Weald. Moreover, the exceptional degree of preservation in most of the Spanish material allows us to study not only the external features in detail, but even to study some internal structures.

The best-recorded subfamily is Ommatinae, represented by the genera *Notocupes* (6 new species), followed by *Tetraphalerus* (2 new species), *Cionocoleus* (2 new species) and *Brochocoleus* (1 new species). The subfamily Cupedinae is recorded by the presence of the genera *Anaglyphites* (2 new species) and *Priacma* (1 new species).

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## Lower Toarcian (Lower Jurassic) cockroaches (Insecta: Blattodea) of Germany and England

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Cockroaches are rather rare insects in the Lower Toarcian marine insect taphocoenoses of Germany (Dobbertin 4.3%, Grimmen 2.0%, Lower Saxony 0.4%). After restudy of the Lower Jurassic types of cockroaches described by Geinitz, Scudder, Handlirsch and Bode, and study of new material from the Lower Toarcian of Germany and England, 45 previously described species are synonymized into only six species. The most common is *Blattula langfeldti* (Geinitz, 1880) (Blattulidae) known from dozens of isolated fore- and hindwings and a few complete specimens with associated fore- and hindwings. The second, however, extremely rare blattulid *Blattula dubia* (Handlirsch, 1939) is considerably smaller.



*Mesoblattina protypa* Geinitz, 1880 with sclerotized forewings is the only Lower Toarcian species of the subfamily Mesoblattininae (Blattidae) which comprises the genera *Mesoblattina* Geinitz, 1880, *Hispanoblattina* Martínez-Delclós, 1993, *Archimesoblatta* Vršanský, 2003, *Praeblattella* Vršanský, 2003, *Breviblattina* Vršanský, 2004 and a new genus represented by "*Artitocoblatta*" *colominasi* Meunier, 1914.

The large *Caloblattina mathildae* (Geinitz, 1883) (Caloblattinidae) and *Liadoblattina blakei* (Scudder, 1886) are rare species, as well as *Eublattula crassivena* Handlirsch, 1939 which is known only from the holotype. *Liadoblattina* Handlirsch, 1906 and *Eublattula* Handlirsch, 1939 are representatives of new families (in preparation). The absence of *Caloblattina* and *Liadoblattina* from Grimmen might indicate that these larger roaches did not live in the source area of this site, presumably offshore islands.

In comparison with Upper Jurassic and Lower Cretaceous sites worldwide, the diversity of Lower Jurassic cockroaches is remarkably low. On the other hand the variability of fore- and hindwings of the dominant Lower Toarcian roach *Blattula langfeldti* (Geinitz, 1880) is much higher compared with the Lower Cretaceous Blattulidae of the same size.

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### The age of Baltic amber: could Eckfeld resolve this problem?

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Pieces of Baltic amber can be easily identified by a number of diagnostic features. The chemical composition of Baltic amber, however, is relatively uniform and diagnostic by comparison with all other amber deposits. Additionally, Baltic amber frequently includes numerous stellate trichomes (hairs of plants). At the moment it is still not possible to date individual amber specimens directly. Nevertheless, the age of Baltic amber was controversially discussed during the last decades. Caution should be used when interpreting older publications, whereas an Oligocene age is proposed for Baltic amber (e.g. Carpenter's Treatise).

The amber predominantly occurs in the "*blaue Erde*" (blue earth), which is spread over northern Europe. New, absolute dating analyses of glauconites show that the Formation *Blue Earth* is allocated to the Middle Eocene (Lutetian:  $44.1 \pm 1.1$  Ma) and is thus significantly older than previously assumed.

Mounting evidence for a possible Middle Eocene origin of Baltic amber now comes from limnic sediments within the Eckfeld maar, which correlate perfectly in age with the K-Ar radiometric data from the Kaliningrad district, the main deposit of Baltic amber. Biostratigraphically, Eckfeld corresponds to the Middle Eocene mammal reference level MP 13 of the ELMA. In the maar crater, basalt fragments could be recovered by drilling. The  $^{40}\text{Ar}/^{39}\text{Ar}$  dating of the basalt presents for the first time a direct numerical calibration mark for an Eocene European mammal locality. The Eckfeld basal isochron has an age of  $44.3 \pm 0.4$  Ma. There is now little doubt about the Middle Eocene age of Baltic amber. This is partly revealed by insect groups, in particular by genera of the Coleoptera, Hymenoptera, and Hemiptera. Comparing taxa exclusively from the Eckfeld taphocoenosis with their occurrence in Baltic amber, the Eckfeld maar insects are found to contain an interesting mix of palaeofaunal elements that shows a strong alliance with groups currently known only from the roughly contemporaneous and geographically close Baltic amber. †*Balticarthropterus* (Coleoptera: Paussinae), †*Electrogerris* (Heteroptera: Gerromorpha), and the extinct hymenopteran genera †*Protobombus* and †*Electrapis* are taxa that have so far been found only in Baltic amber.

Based on the distributions of these index taxa, it is likely that the Baltic amber is Middle Eocene in age.



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## Pictures of the German Carboniferous localities Hagen-Vorhalle and Ploetz

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There are eight sequences of pictures of the German Carboniferous localities Hagen-Vorhalle and Ploetz with pictures and drawings of some fossil insects.

Sequence 1: a map of Northwest Germany with the Carboniferous locality Hagen-Vorhalle and some photographs of the uppermost Namurian B of the brickyard quarry of this famous German carboniferous locality made in the early 1980s by Wolfgang Sippel, Ennepetal and Wolfgang Zessin, Jasnitz;

Sequence 2: reconstructions of the Carboniferous life with dragonfly (painted by Wolfgang Sippel, Ennepetal);

Sequence 3: fossil Dragonflies: photographs and drawings (by Carsten Brauckmann, Elke Groening and W. Zessin of *Namurotypus sippeli* Brauckmann & Zessin, 1989; *Erasipteroides valentini* (Brauckmann, 1985); *Zessinella siope* Brauckmann, 1988);

Sequence 4: other fossils (insects, plants);

Sequence 5: a map of East Germany with the locality Ploetz near Halle and some photographs of the Stefanium C coal dump;

Sequence 6: photographs and a drawing of the forewing of the giant dragonfly *Stephanotypus schneideri* Zessin, 1983;

Sequence 7: other fossils (insects, spider, plants);

Sequence 8: the coal dump Ploetz in art: a patchwork of Christa Gabriel, Halle and an oil painting by Lothar Gruenewald (1935-2001, Halle).



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