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COMMENTARY

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Alexandr Pavlovich Rasnitsyn, (palaeo)entomologist extraordinaire – a personal appreciation

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This note is not meant to be an exhaustive account of the many achievements of Alex Rasnitsyn over the 75 years of his life thus far. Apart from anything else, I have little knowledge of his activities outside of my professional interactions with him. Also, there will undoubtedly be several other biographical essays this year to celebrate his accomplishments in many fields. So, my intention, after providing the essential details to place him in context, mainly derived from his personal page on the Paleontological Institute's website (Rasnitsyn 2011) and a note in the Paleontological Journal (Laboratory of Arthropods, in press), is to give my personal impressions of our interactions, his influence on my own life and work, and on hymenopterology in general.

Alexandr Pavlovich Rasnitsyn was born in Moscow, Russia, on 24 September, 1936, and has lived there since. His interest in insects and general natural history soon became apparent, and he joined the Club of Young Biologists at the Moscow Zoo. In 1955 he enrolled at the Moscow State University, and in 1960 graduated with honours and a masters degree in entomology, his thesis being on "Hibernation in the ichneumon flies subfamily Ichneumoninae", showing that his passion for Hymenoptera was developed right from the start. That same year he joined the Arthropoda Laboratory, headed by Professor Boris Rohdendorf, in the Paleontological Institute of the USSR (now Russian) Academy of Sciences, Moscow. From this start as a young man (Figure 1), he worked his way up sequentially from positions as Technician, Junior and Senior Research Worker, to becoming the Head of the Laboratory (1979–1996), Principal Research Worker (since 1996) and then again Head of the Laboratory (from 2002 after

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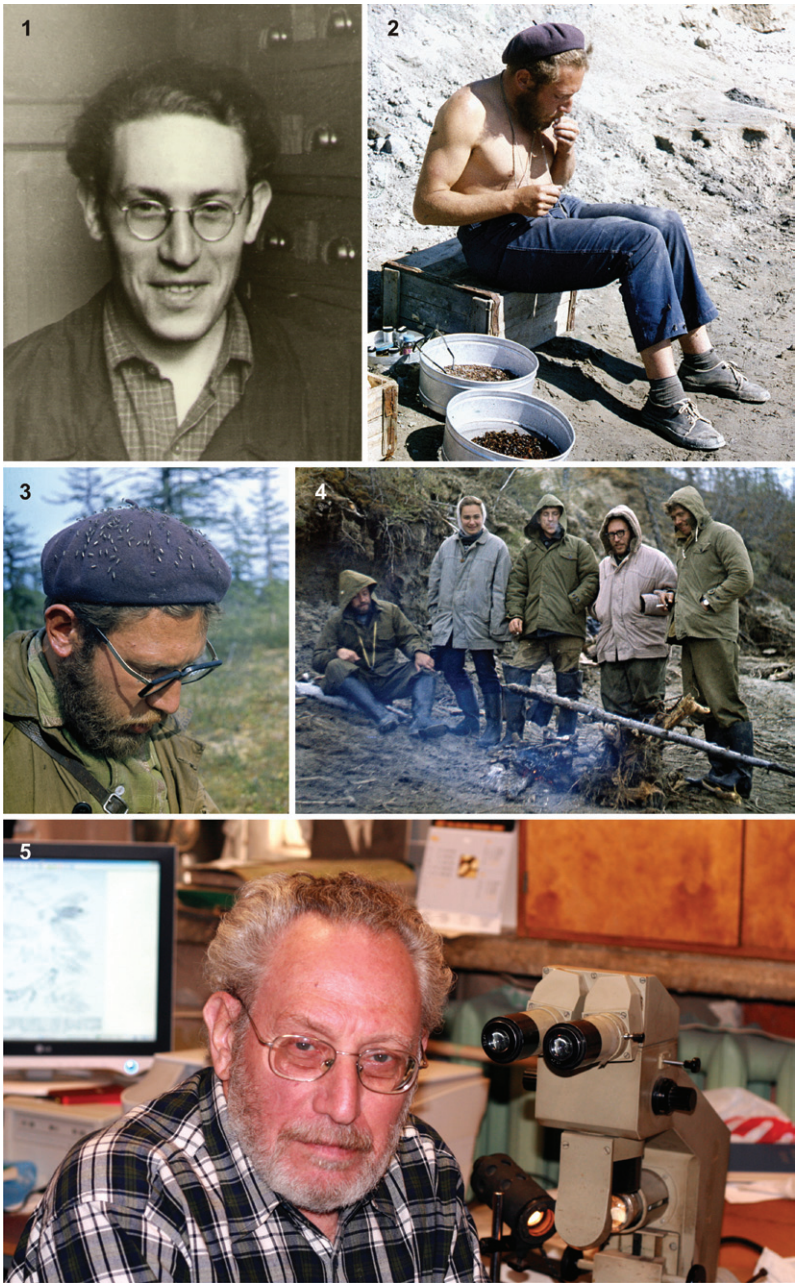
the sudden death of his successor, Vladimir Zherikhin, to the present, Figure 5). He has thus headed the most productive and influential group of palaeoentomologists in the world for 28 years. During his employment he also earned two doctorates from the Paleontological Institute, a PhD in 1967 on "Mesozoic Hymenoptera Symphyta and early evolution of Xyelidae", and a DSc in 1978 on "Origin and evolution of Hymenoptera". In 1991 he was awarded the title of Professor, and in 2001 he was given the award of "Honoured Scientist" by the Russian Federation. He served as the first President of the International Palaeoentomological Society (2001–2005), and was given Honorary Membership of the Russian Entomological Society (2004) and has been a member of their Council since 2007. He has long held an honorary appointment at the Natural History Museum, London, England.

By his own account, Alex's interests encompass not only the palaeontology, phylogeny and taxonomy of Hymenoptera and of insects in general, but also broader biological problems, including evolutionary theory, dynamics of taxonomic diversity, and methodology of phylogenetics, taxonomy, and nomenclature. His fascination with the natural world is unquenchable, as shown by his participation in or leading collecting expeditions over 22 field seasons (starting in 1956) to many famous fossil-insect localities in Central Asia, North Caucasus, Siberia (Figures 2–4), Transbaikalia, Mongolia, England, Germany, USA and Israel. He has also visited collections to study specimens, both fossil and modern, in many countries: Canada, China, Denmark, England, France, Germany, Poland, South Africa, Spain and USA. He has participated in many conferences around the world and in several international research collaborations.

Alex's incredible productivity and breadth of interests are graphically shown by his publications. The most complete list available to me, a late precursor to Engel and Shcherbakov (2011), includes 366 items produced from 1959 onwards. This output is both prodigious and diverse. I broke the items down into ten broad categories and discovered the following, arranged in descending order of items per category (Table 1):

Table 1. Items authored or co-authored by Alex Rasnitsyn, including abstracts.

Field of contribution	Year of first item	Year of latest item	Number of items	Items per year	Median year	Modal year
Palaeontology of Hymenoptera	1963	2011	117	2.39	2000	2000
Palaeontology of other insects	1974	2011	111	2.92	2002	2002
Theory of systematics	1966	2010	36	0.80	1992	1991
Theory of evolution	1965	2005	20	0.49	1974	1971
Modern Hymenoptera	1959	2010	17	0.33	1986	1981
Evolution of Hymenoptera	1965	2006	15	0.36	1980	1971
Ecology, biodiversity, etc.	1963	1995	15	0.45	1989	1989
Miscellaneous topics	1977	2008	13	0.41	2003	2004
Evolution of insects	1976	2003	11	0.39	1996	1976
Editorial work (books)	1980	2008	11	0.38	1988	1985
Total	1959	2011	366	6.91	1997	2002



Figures 1–5. Alex Rasnitsyn in Russia, in the laboratories of the Paleontological Institute, Moscow, and in the field. **1** In 1961 (photo by Oleg Amitrov). **2** In 1971, sorting amber at Yantardakh, Maimecha River, Taymyr Peninsula, northern Siberia (71°18'30"N 99°34'12"E) (photo by Alexandr Ponomarenko). **3** In 1971, with mosquitoes near Yantardakh (photo by Alexandr Ponomarenko). **4** In 1971, at Gubina Gora near Khatanga, Taymyr Peninsula (71°59'54"N 102°34'22"E); left to right: Alexandr Ponomarenko, Irina Sukacheva, Pol' Perov, Alex Rasnitsyn, Vladimir Zherikhin (photo probably by Anatoly Mikheev). **5** In 2008 (photo by Roman Rakitov).

Obviously, some items would span more than one category, but I have merely assigned each to what I judged to be the single most relevant category. Of the 366, 189 have Alex as sole author, 105 have two authors, 43 have three, 14 have four, 12 have five to nine, and 3 (tributes or obituaries) have more than twenty authors; the average number is 2.1. The frequency of co-authorships has increased over the years, from an average of 1.3 over the first 20 years to 2.6 for the last 20, indicating increasing requests for collaboration from colleagues. The above items include co-authorship with 187 different colleagues, a remarkable spread.

It is no surprise that most of Alex's contributions have been on Hymenoptera, specially their palaeontology, but also on modern groups and, probably of most general influence, the evolution of the order, the relatively few items in that category building on the others and comprising large and major contributions (specially Rasnitsyn 1969, 1980, 1988). He has produced 149 items on Hymenoptera, at a rate of 2.81 per year since 1959, the median and modal years being 1999 and 2000 respectively. Not only his sheer productivity, but even more his encyclopaedic coverage and integration of his ideas into pioneering systems outlining the evolution of the members of the order, mean that he is unquestionably the greatest current authority on the Hymenoptera as a whole. His analyses, relying extensively on fossils, often produced results somewhat different from those obtained by cladistic methods using the morphology of modern representatives, including some of my own (e.g. Brothers 1999); even cladistic re-analyses using his own characters produced less conclusive results (Ronquist et al. 1999), reflecting the difficulty of integrating information about incomplete fossils and modern forms in a single analysis. Nevertheless, many of his proposed groupings are corroborated in some of the latest analyses incorporating both morphological and molecular information from representatives across the order (e.g. Sharkey et al. 2011), illustrating his remarkable insights and unique encyclopaedic knowledge of the order as a whole. Alex's unparalleled breadth and integration of research on the Hymenoptera was formally recognised in 2008 by the award of the Distinguished Research Medal of the International Society of Hymenopterists, only the fourth such award, following similar recognition of the legendary Charles Michener, Zdeněk Bouček and Richard Bohart.

I was surprised, however, to discover that Alex's contributions to the palaeontology of other insect groups, although starting about 15 years after his first contribution on Hymenoptera, have been almost as numerous as those on hymenopteran palaeontology, with the same average number of co-authors (one), and at a higher annual rate over the period of their production. The groups covered range across the entire spectrum of insect orders, including several enigmatic ones whose relationships remain obscure. In all of the other categories his output has been much less and generally earlier in his career, although he has continued to make contributions in all (except for more ecological areas) until recently. Although the bulk of his editorial work was done before about 1991, it included two very significant and influential compilations on insect palaeontology and evolution (Rohdendorf and Rasnitsyn 1980, and Rasnitsyn and Quicke 2002), the latter being the first large-scale work of its sort in English. He

has developed and propounded a mode of systematic analysis to estimate the pathways of evolution and phylogenies which is considered idiosyncratic by many, but which is firmly grounded in his extensive knowledge of fossil insects, and which certainly provides an important alternative way of looking at such issues, a recent paper (Rasnitsyn 2010) providing comparisons between various methods. The accompanying list of Alex's publications (Engel and Shcherbakov 2011) must be consulted for a proper appreciation of the volume and variety of his contributions.

It is obvious from the above that Alex has a fearsome intellect and exhibits boundless dedication and hard work in pursuit of his passion. He is much sought as a collaborator, and he is certainly not slowing down – he produced 19 items in 2010 alone. One might consider that such a person must be self-centred, forceful and entirely focused on his work, but this is not true of Alex. He is a real gentleman, very thoughtful of the needs of others, humble, and ready to participate in non-work-related activities which might expand his appreciation and understanding of the natural world. These are qualities which I have experienced in my many interactions with him.

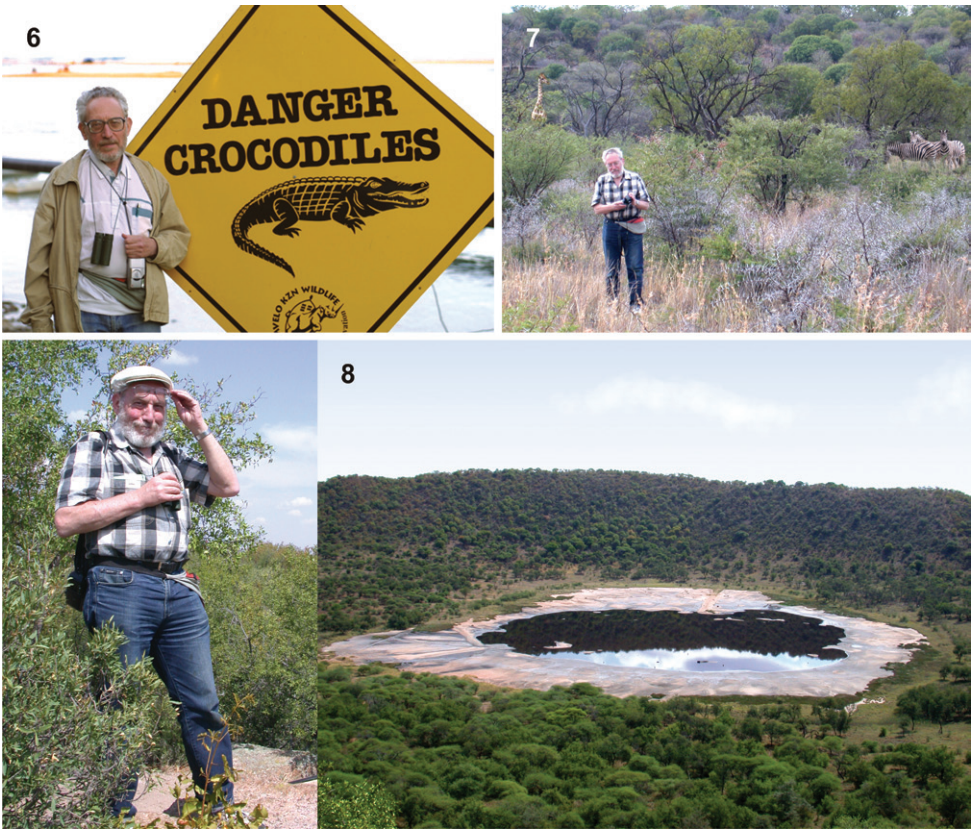
I first met Alex in 1988 at the XVIII International Congress of Entomology and meeting of the International Society of Hymenopterists, in Vancouver, Canada. We both enjoyed the exchanges with colleagues and chatted about our mutual interests in hymenopteran phylogeny (mine restricted to Aculeata) but prospects for closer collaboration seemed poor, given the political systems in place at the time. At that stage I had no idea that I might become involved in hymenopteran palaeontology myself. The turning point for me came in early 1991 when I was made aware of an extensive collection of Cretaceous insect fossils from the Orapa diamond mine in Botswana, which were housed under the care of Dr Richard Rayner, a palaeobotanist, at the Bernard Price Institute of Palaeontology (BPI), University of the Witwatersrand, Johannesburg, South Africa. This piqued my curiosity, and I was able to look at several of the blocks containing the most spectacular of the insect fossils. I was immediately struck by a most beautifully preserved specimen of some sort of wasp, which I was able to photograph. On my return home, I fortuitously found the latest issue of the journal Psyche on my desk, and on looking through it discovered that the first paper dealt with Mesozoic Vespidae (Carpenter and Rasnitsyn 1990). I immediately compared my photographs with the figures in the paper, and became convinced that the Orapa specimen was a new species of *Curiosivespa*, a genus previously known only from north-eastern Asia. This was an exciting serendipitous discovery and led to my first palaeoentomological paper (Brothers 1992).

As a consequence, I had even more in common with Alex when we met again later in 1991 at the Second Quadrennial Meeting of the International Society of Hymenopterists in Sheffield, England. We were also both at the Third Quadrennial Meeting of the Society in Davis California, USA in 1995. Then, in 1998, we were both participants in an important symposium and workshop investigating the phylogeny of Hymenoptera, organised by Fredrik Ronquist in Uppsala, Sweden (see Ronquist 1999), part of it devoted to reanalysing Alex's ideas from a rigorous cladistic perspective, with somewhat different results from his original proposals (see Ronquist et al. 1999). A lesser person might have taken this personally, as some sort of repudiation of their

work, but Alex, as the true scientist that he is, considered it to provide new perspectives which warranted further exploration, and, perhaps in response, soon produced a paper analysing ways to test cladograms using fossils (Rasnitsyn 2000). Also in 1998 the First Palaeoentomological Conference was held, in Moscow at the home of the world's greatest concentration of palaeoentomologists. It was an eye-opener for someone like me who had entered the field late and almost accidentally, not least because of Alex's evident mastery of the entire field and his varied contributions. A lasting memory of that visit is Alex's and his wife, Irina Goncharova's, hospitality. I had stayed on for a few days after the conference and was invited, together with Conrad Labandeira, to share a Sunday with them. This involved a walk from their apartment across the multi-lane road encircling the city, past several rather run-down farmhouses and into the forest, Alex carrying a heavy load of equipment and food items. After walking for a considerable distance, collecting wild mushrooms and investigating unfamiliar biological phenomena along the way, we reached a small clearing where Alex collected firewood and made a fire for our lunch. We enjoyed a marvellous relaxing time, eating and drinking the excellent provisions and chatting about many topics, before we had to make our way back. We then spent more time in their apartment, being provided with further refreshments. Thanks again, Alex and Irina, for that wonderful afternoon.

In 1999 I was sent an Eocene fossil wasp wing from Canada for my opinion on its placement, and I immediately referred it to Alex, who identified it as a new genus of primitive sphecid and suggested that it be included in a paper he was currently involved with; Pulawski et al. (2000) was the result. At about the same time Alex told me about a couple of specimens from New Jersey Cretaceous amber which he thought were Plumariidae (putatively the first fossils for that family) and arranged for them to be sent to me. I initially agreed with this placement, but after various analyses became convinced that they should probably rather be placed in a separate closely related family, described in an accompanying paper as Plumalexiidae (Brothers 2011).

After 1992 I was unable to do any further work on the Orapa material (it being housed 500 km from my home in Pietermaritzburg) for a long time. But I remained painfully aware that there was a treasure trove of Cretaceous material awaiting study in Johannesburg, and could think of no-one better to evaluate its significance than Alex. So I managed to secure funding in 2001 to invite him as a plenary speaker to an entomological conference in Pietermaritzburg and then to spend about three weeks examining the fossils in Johannesburg. During that period I scanned about 2000 rock pieces (containing about 5000 insect fossils) for Hymenoptera and Alex examined the 68 blocks on which I had found at least one hymenopteron, identifying and listing all the fossils and making drawings of the 108 hymenopterons found. I also managed to photograph them. Alex's experience, persistence and encyclopaedic knowledge permitted us to make an estimate of the insect diversity in the collection (Brothers and Rasnitsyn 2003), and laid the basis for our further collaborative work on the Orapa fossil Hymenoptera (Dlussky, Brothers and Rasnitsyn 2004; Rasnitsyn and Brothers 2007; Brothers and Rasnitsyn 2008; Rasnitsyn and Brothers 2009; Kopylov, Brothers and Rasnitsyn 2010), work as yet far from completion.



Figures 6–8. Alex Rasnitsyn in South Africa. **6** At the Lake St Lucia estuary mouth, northern KwaZulu-Natal (28°22'58"S 32°25'12"E), July 2001 (photo by Justin Waldman). **7** At Buffelsdrift residential nature reserve, north of Pretoria, Gauteng Province (25°33'41"S 28°20'48"E), February 2005 (onlookers added although also photographed there). **8** Surveying the Tswaing meteorite crater (right), north of Pretoria, Gauteng Province (25°24'38"S 28°05'14"E), February 2005.

The year 2001 saw further contact, since we both attended the Second International Congress on Palaeoentomology in Krakow, Poland, where Alex was elected the first President of the International Palaeoentomological Society to much acclaim at its founding meeting, and where it was decided that the next such congress would be held in South Africa. This provided another opportunity for him to visit me, and in 2005 he spent some time in Pietermaritzburg, courtesy of funding from the South African government in support of Russian academics visiting our country, before Fossils X 3: 3rd International Congress of Palaeoentomology with 2nd International Meeting on Palaeoarthropodology and 2nd World Congress on Amber and its Inclusions, held in Pretoria. He was also able to do further work on the Molteno Formation (Triassic) fossils amassed by John Anderson at the South African National Botanical Research Institute in Pretoria (a collection now also housed at BPI, Johannesburg). Then Alex came to South Africa again in 2006 for the Sixth International Conference of Hymenopterists, held at Sun City.

I have thus been extremely fortunate to benefit from extensive interactions with Alex, to have him sharing his vast knowledge of Hymenoptera diversity, and patiently explaining palaeontological conventions and practices to someone without any training in palaeontology or even geology. I have always been amazed at his readiness to spend time addressing my concerns and yet obviously being able to spend even more time simultaneously on all his other projects. Nothing has been too much trouble for him. I can only assume that the level of interaction I have had has extended to all of his other collaborators, a very wide diversity of people from all over the world. Obviously, colleagues in all areas of palaeoentomology turn to his advice and participation when faced with interesting problems. To my mind, he embodies the ideal scientist, someone filled with an inexhaustible curiosity about the natural world and its history, able to focus intently on the task at hand and yet able to interrupt that task when necessary and return to it as if the interruption never happened (a skill needed by any manager), and also to enjoy doing something completely different when the opportunity arises. I remember his delight when we travelled from Pietermaritzburg to Johannesburg in 2001 and were able to visit places such as St Lucia (Figure 6) and the Hluhluwe-Mfolozi game reserve where we stayed overnight. He was thrilled by the diversity of game animals and birds, from rhinoceros, elephant and buffalo to oxpeckers and weavers. When we had to leave the reserve he leaned back and said he had been "Alex in Wonderland". The same enjoyment was in evidence in 2005 when we stayed for a few nights at an eco-estate north of Pretoria (Figure 7) and also when we visited the impact crater about 1 km in diameter and 100 m deep at Tswaing (Figure 8), also north of Pretoria.

The celebration of Alex's 75th birthday is a wonderful opportunity to look back at his many accomplishments, let him know how much we all appreciate them, and admire his continuing energy and drive in pursuit of his passion. Long may it continue. Happy birthday, Alex, and we certainly wish you many more to come.

Acknowledgments

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Scientific contributions of Alexandr P. Rasnitsyn, 1959 to present

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Introduction and format

The following list provides citations for 363 scientific contributions, including 13 edited volumes and books, produced by Alexandr P. Rasnitsyn. Naturally, the list presented here is a static representation of Alex's contributions and we look forward to years of his forthcoming publications to our shared science. Thus, this list only encompasses those papers published as of 1 August 2011. We have published it here so as to bring to the attention of colleagues Alex's numerous and multifaceted accomplishments, and why he so richly deserves our admiration. In addition, we believe the following list is the most thorough and accurate accounting of his published scientific activities. Given that many of his works are in his native Russian, we believe this list will serve as a tool for directing interested individuals to English translations, where available.

In elaborating this list we have taken a detailed approach to cataloguing Alex's numerous publications, adopting the philosophy that bibliography is a science of its own and provides an accurate description of a work or contribution to a work (e.g., Gaskell 1972). It is with this philosophy in mind that the list was constructed and how to determine what should, or should not, constitute an individual citation, the appropriate form of citation, etc.

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To the best of our ability we have checked article and serial titles, as well as dates of publication and complete citations against original sources, either from the original series or official reprints. In addition, some serials and edited volumes have been checked against library copies at the University of Kansas (Lawrence) or the Library of Congress (Washington DC). Several of Alex's contributions appear in special edited issues of otherwise serial publications. These are cited as they appear in the journal series, with the editors and titles of the special issues following in parentheticals.

Serial titles

Understandably many of the serials in which Alex has published have titles in Cyrillic. The transliterated versions of these are used throughout the bibliography and we have provided here a summary of those titles and their English equivalents.

Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, Otdel Biologicheskiy [Bulletin of the Moscow Society of Naturalists, Series Biology]

Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, Otdel Geologicheskiy [Bulletin of the Moscow Society of Naturalists, Series Geology]

Doklady Akademii Nauk SSSR (since 1992, *Doklady Akademii Nauk*) [Transactions of the Academy of Sciences, USSR (since 1992, of the Russian Academy of Sciences), or sometimes appearing simply as "Doklady" followed by the English name of the particular section, e.g., "Doklady. Biological Sciences Section"]

Doklady Moskovskogo Obshchestva Ispytatelei Prirody, Zoologia i Botanika [Reports of the Moscow Society of Naturalists, Zoology and Botany]

Entomologicheskoe Obozrenie [Entomological Review]

Izvestiya Akademii Nauk, Seriya Biologicheskaya [Bulletin of the Academy of Sciences, Biology Series]

Paleontologicheskiy Zhurnal [Paleontological Journal]

Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR (since 1992, …*Rossiyskoy Akademii Nauk*) [Transactions of the Paleontological Institute, Academy of Sciences, USSR (since 1992, Russian Academy of Sciences)]

Trudy Russkogo Entomologicheskogo Obshchestva [Proceedings of the Russian Entomological Society]

Trudy Sovmestnoy Sovetsko-Mongol'skoy Paleontologicheskoy Ekspeditsii [Transactions of the Joint Soviet-Mongolian Paleontological Expedition]

Uspekhi Sovremennoy Biologii [Achievements in Modern Biology]

Vestnik Permskogo Universiteta, Geologiya [Bulletin of Perm' University, Geology]

Vestnik Zoologii [Zoological Herald]

Zhurnal Obshchey Biologii [Journal of General Biology]

Zoologicheskiy Zhurnal [Zoological Journal]

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New Middle Permian palaeopteran insects from Lodève Basin in southern France (Ephemeroptera, Diaphanopterodea, Megasecoptera)

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Abstract

Three new palaeopteran insects are described from the Middle Permian (Guadalupian) of Salagou Formation in the Lodève Basin (South of France), viz. the diaphanopterodean Alexrasnitsyniidae **fam. n.**, based on *Alexrasnitsynia permiana* **gen. et sp. n.**, the Parelmoidae *Permelmoa magnifica* **gen. et sp. n.**, and *Lodevohymen lapeyriei* **gen. et sp. n.** (in Megasecoptera or Diaphanopterodea, family undetermined). In addition the first record of mayflies attributed to family Syntonopteridae (Ephemeroptera) is reported. These new fossils clearly demonstrate that the present knowledge of the Permian insects remains very incomplete. They also confirm that the Lodève entomofauna was highly diverse providing links to other Permian localities and also rather unique, with several families still not recorded in other contemporaneous outcrops.

Keywords

Insecta, Palaeoptera, Syntonopteridae, Alexrasnitsyniidae fam. n., Parelmoidae, gen. n., sp. n., Middle Permian, palaeodiversity.

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Introduction

Before the tremendous effort of collect of Dr Jean Lapeyrie who brought together a large collection of thousands of fossils, the 'red' Middle Permian Salagou Formation (Lodève Basin) was considered devoid of fossils. Palaeoenvironment of Lodève Basin could be characterized as climate controlled playa with ephemeral pools colonized by aquatic clam shrimps (Conchostraca) and tadpole shrimps (Notostraca) together with insects (Lopez et al. 2008). This palaeoenvironment was rich of insects those preservation exhibit considerable high diversity. Representatives of the orders Palaeodictyoptera, Diaphanopterodea, Odonatoptera, Orthoptera, Caloneurodea, Grylloblattodea, Hemiptera, and Glosselytrodea have already been described (see the state of the art in Béthoux 2008; plus Nel pers. comm.).

We describe herein four new fossil insects from the Salagou Formation those correspond to important new taxa. Unfortunately the great majority of this entomofauna is represented by isolated wings. The insect bodies have been destroyed by the abundant necrophagous animals (mainly *Triops* Schrank, 1803) and the decay due to taphonomic process (Gand et al. 1997). This limitation renders difficult the attribution of some fossils, as can be seen below.

Material and methods

The material described in the present paper comes from the Middle Permian deposits of Salagou Formation found in several localities in the Lodève Basin, Hérault, France (Garric 2000; Béthoux et al. 2002; Nel et al. 2009). Insects are preserved as compressed fossils and deposited in a playa palaeoenvironment. All specimens come from the Lapeyrie collection, currently housed at the Musée of Lodève, France.

The material was observed under stereomicroscope Olympus SZX-9 and venation pattern drawings were drawn directly through stereomicroscope by camera lucida. Photographs were made using digital camera Nikon D80 with macro lens Nikon AF-S VR Micro-Nikkor 105 mm by single sided cross-light exposure.

We follow the wing venation nomenclature of Kukalová-Peck (1991). Abbreviations of wing veins: C costa, ScP subcosta posterior, RA radius anterior, RP radius posterior, MA media anterior, MP media posterior, CuA cubitus anterior, CuP cubitus posterior, AA anal anterior, AP anal posterior.

Systematic part

Order Ephemeroptera Hyatt & Arms, 1890
Family Syntonopteridae Handlirsch, 1911

Genus indet.
Figs 1A–B

Material. Specimen Ld LAP 483 (Lapeyrie collection, imprint of proximal part of forewing), stored at the Musée of Lodève, France.

Age and locality. Middle Permian, Guadalupian, Lodève Basin, Salagou Formation, Lodève, Hérault, France (Garric 2000; Béthoux et al. 2002).

Description. Counter-imprint of a fore wing without trace of preserved coloration, strongly developed corrugation of longitudinal veins; basal part of fore wing 22.7 mm long and 11.6 mm wide, estimated total length about 45 mm; area between ScP and C rather broad with numerous simple cross-veins; concave ScP straight and basally running close to radial and medial veins; RA nearly straight; RA and RP extremely approximate between wing base and a point situated 17.5 mm distally at which RP strongly diverges from RA; convex MA diverging from MP nearly at right angle and directed towards radial veins, 11.3 mm from wing base; MA distally closely parallel to RA and RP for 5.4 mm, then nearly touching RP at one point; RP emerging 6.4 mm distal of base of MA; concave MP nearly straight; convex CuA diverging from CuP close to wing base and running parallel to medial veins, CuA with two visible terminal branches; simple CuP strongly concave and only weakly curved; anal area partly preserved, first anal vein of neutral polarity ending with two main branches, second anal vein convex and distally pectinate with several branches connected by rather dense network of cells; along posterior wing margin a broad area between CuP and first anal vein; a small pentagonal elongate cell below second anal vein, near wing base.

Discussion. This fossil bears a combination of the main characters of ephemeropterid family Syntonopteridae, i.e., a strong corrugation of the main longitudinal veins connected by mainly simple transverse crossveins also present in Odonatoptera and some Palaeodictyopterida (e.g., Breyeriidae), MA with a strong anterior curve at its base, shortly connected with RP distally; CuA with a short terminal twigging and anal area with well-defined cell(s). We can argue that this fossil is a forewing fragment for the absence of a characteristic constriction of concave vein IN- between AA1+2 and AA3+4 (Prokop et al. 2010). The specimen can be possibly attributed to a new genus and species for the long part of MA closely parallel to extremely approximate bases of RA and RP; a broad area between CuP and first anal vein near posterior wing margin, and CuP simple (differences with all other genera *Lithoneura* Carpenter, 1938, *Syntonoptera* Handlirsch, 1911, *Anglolithoneura* Prokop & al., 2010, except maybe *Gallolithoneura* Garrouste et al., 2009 based on a rather incomplete wing) (Garrouste et al. 2009). However, we prefer to maintain this specimen as Syntonopteridae gen. et sp. indet. for its incompleteness. Nevertheless this fossil represents the first undisputed record of mayflies from Salagou Formation in the Lodève Basin.

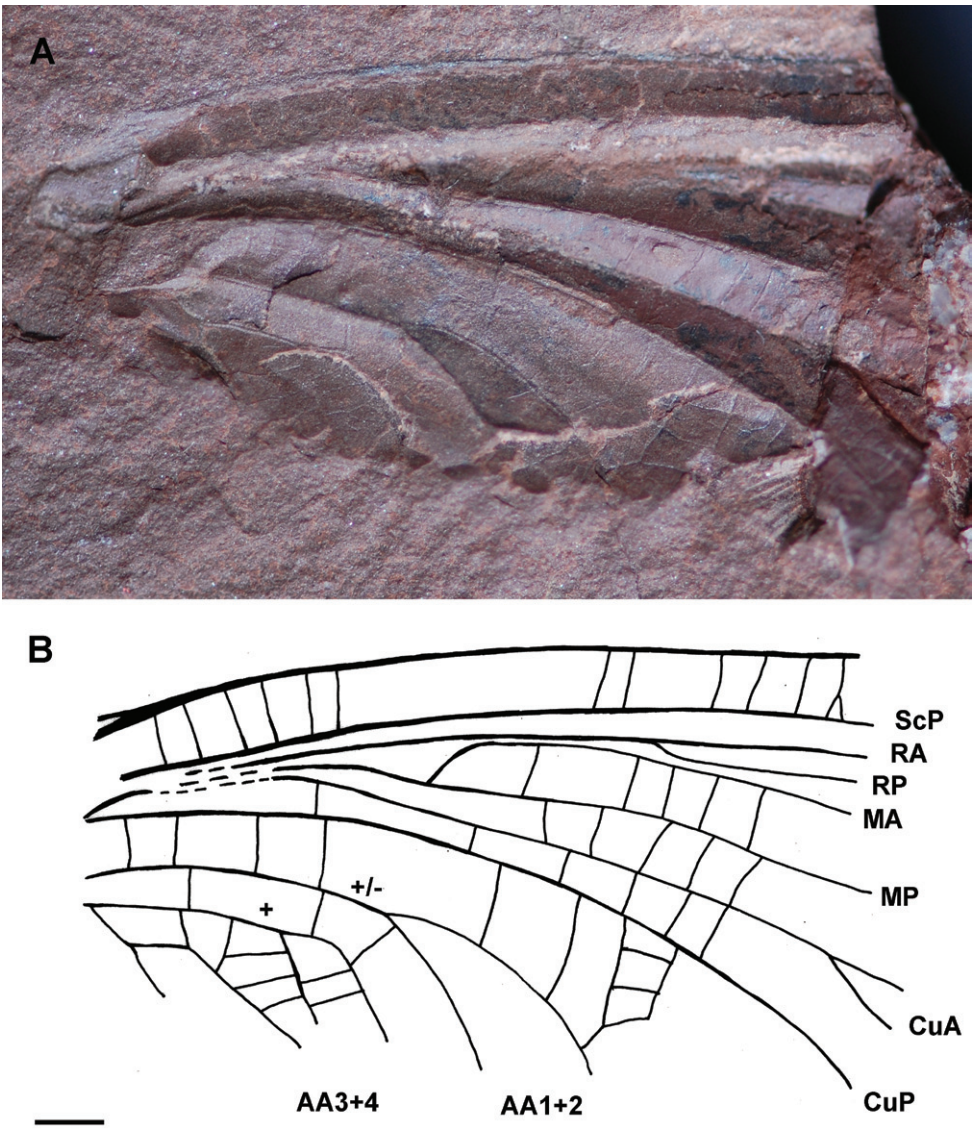

Figure 1. Genus and species indet. (Ephemeroptera: Syntonopteridae), specimen Ld LAP 483: **A** photograph of forewing **B** drawing of forewing (Scale bar represents 2 mm).

Order Diaphanopterodea Handlirsch, 1919

Family Alexrasnitsyniidae fam. n.

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http://species-id.net/wiki/Alexrasnitsyniidae

Type genus and species. *Alexrasnitsynia permiana* gen. et sp. n.

Diagnosis. Wing venation only. ScP ending on anterior wing margin near mid part of wing; stems of CuA, M and R very close; CuA, MP and MA diverging at the same point; MA and radial stem very closely parallel; MA distally fused for a short distance with RP; a very broad area between RA and anterior wing margin with several long simple oblique crossveins; a very broad area between CuA and CuP; CuA with weak secondary posterior branches.

Genus *Alexrasnitsynia* gen. n.

urn:lsid:zoobank.org:act:

Type species. *Alexrasnitsynia permiana* sp. n. by monotypy.

Etymology. Named after Prof. Alexandr Rasnitsyn.

Diagnosis. That of the family.

Alexrasnitsynia permiana sp. n.

urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Alexrasnitsynia_permiana
Figs 2A–B

Material. Holotype LdLAP 318A (Lapeyrie collection, prints of two identical wings), stored at the Musée of Lodève, France.

Type strata and locality. Middle Permian, Guadalupian, Mérifons Member, Salagou Formation, Lodève, Languedoc, France (Garric 2000; Béthoux et al. 2002).

Diagnosis. That of the family.

Description. Wing 11.8 mm long, 3.9 mm wide; ScP simple, ending in costal margin near mid part of wing, a narrow area between it and C without visible crossveins; area between C and RA relatively broad, 0.6 mm wide, with a row of simple oblique crossveins; RA simple ending on anterior wing margin 0.4 mm from wing apex; RP separating from RA 2.6 mm from wing base; RP with six-seven branches and covering a broad area with series of crossveins; CuA, MP, and MA diverging at the same point, 1.3 mm from wing base; MA very closely parallel to radial stem and reaching RP, fused with it for 0.6 mm, and separating again distally, MA simple, slightly curved; MP simple; CuA with three short distal branches; a series of crossveins

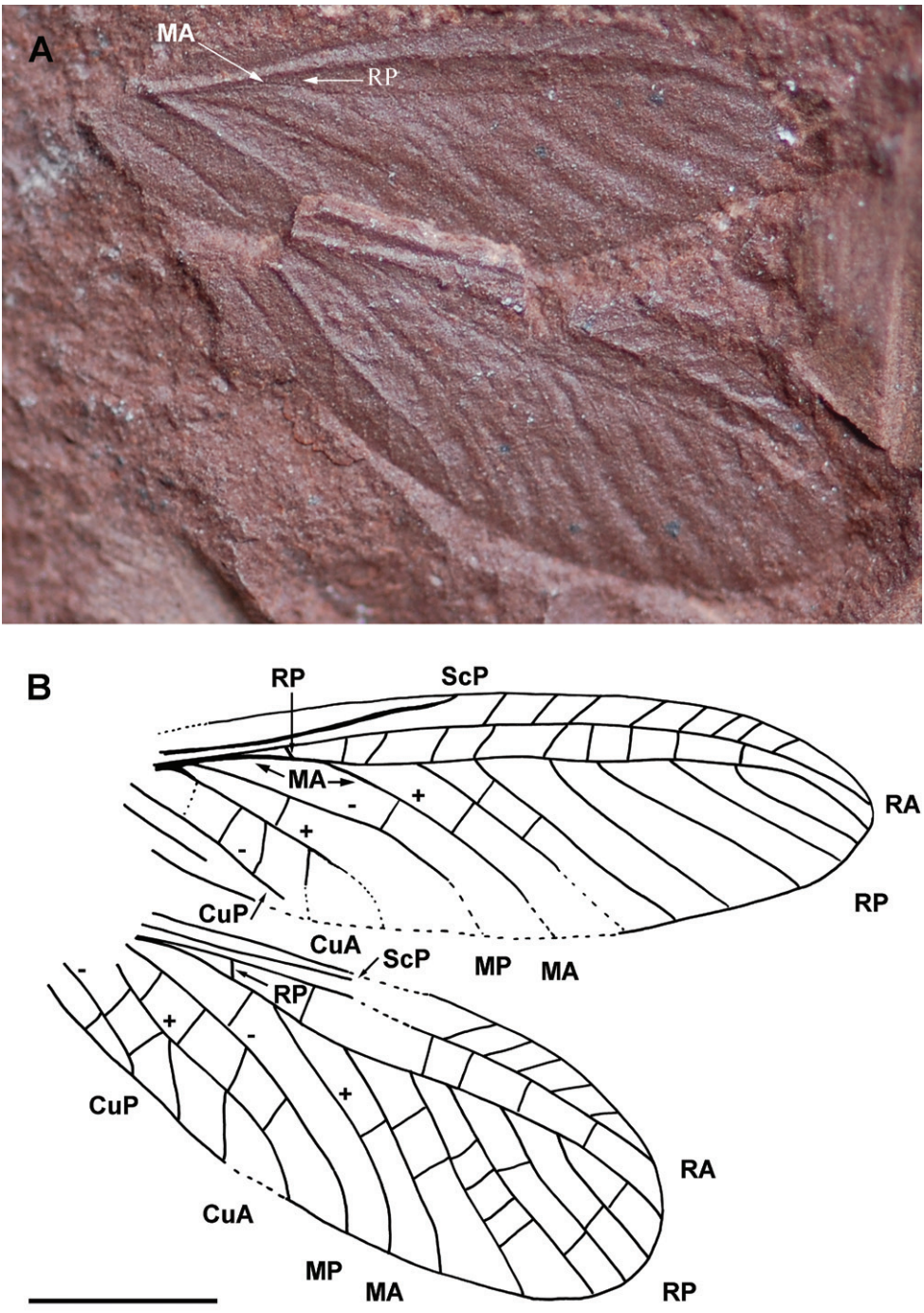

Figure 2. *Alexrasnitsynia permiana* gen. et sp. n. (Diaphanopterodea: Alexrasnitsyniidae fam. n.), holotype LdLAP 318A: A photograph of wings, B drawing of wings (Scale bar represents 3 mm).

between MP and CuA; a broad area between CuA and CuP with crossveins; one anal vein preserved at least.

Discussion. As the two wings show the same convexity of the veins and are very close, they are likely to be a fore- and a hindwing of the same specimen, but it is impossible to determine which one is the forewing. *Alexrasnitsynia* has a pattern of wing venation characteristic of many Diaphanopterodea (Martynoviidae, Biarmohymenidae, Asthenohymenidae, Rhaphidiopsidae, etc.), i.e. crossveins distinct, archedictyon absent, stems of M and R very close; CuA, MP and MA diverging at the same point; MA very closely parallel with radial stem and distally fused for a short distance with RP. *Alexrasnitsynia* differs from all the known representatives of this order, except *Parelmoa* Carpenter, 1947 and *Permuralia* Sinichenkova & Kukalová-Peck, 1997 in the very broad area between RA and anterior wing margin with several long simple oblique crossveins. It differs from these two last genera in vein MA strongly approximating radial stem, a very broad area between CuA and CuP, and CuA with weak secondary posterior branches (Carpenter 1947, 1992; Kukalová-Peck and Sinichenkova 1992; Sinichenkova and Kukalová-Peck 1997).

Note that the Upper Carboniferous monotypic family Velisopteridae Pinto & Adami-Rodrigues, 1997 is based on a fossil that seems to have none of the diaphanopterid characters listed above (Pinto and Adami-Rodrigues 1997). Its attribution to this order should be verified. The Permian genus and species *Walasua maculata* Tan, 1980 is based on a very fragmentary wing. It has some similarities with *Alexrasnitsynia* in the posterior branches of RP regularly organised, partial fusion of MA with RP, MA closely parallel to R, but structures like area between RA and costal margin, CuA, or CuP are not preserved in *Walasua*, rendering difficult the comparison with *Alexrasnitsynia* (Tan 1980). Nevertheless, the area between RA and RP is broad and with numerous crossveins in *Alexrasnitsynia*, unlike the situation in *Walasua*.

Alexrasnitsynia bears similar pattern of wing venation to monotypic *Sypharoptera* Handlirsch, 1911, based on *S. pneuma* known from the Upper Carboniferous of Mazon Creek (USA). Handlirsch (1911) established a separate order Sypharopteroidea for it, which he thought represented an offshoot of Palaeodictyoptera, with possible relationship to Megasecoptera. Martynov (1938) considered this group an offshoot from Spilapteridae (Palaeodictyoptera) or their ancestors, but did not include it in the latter order. Further placement was done by Rohdendorf (1962) who assigned *Sypharoptera* to Diaphanopterodea on the basis of position of wings. Carpenter first provided revision considering position of *Sypharoptera* in Neoptera contra all previous authors, but resulting with placement to Insecta incertae sedis and later reconsidered as Palaeoptera incertae sedis (Carpenter 1967, 1992). Finally Rasnitsyn (2002: 80) considered *Sypharoptera* to be possibly related to neopterous group Caloneurida on the basis of roof-like wing position, elongate wings with narrow costal space and simple and straight CuA and CuP. However, the holotype of *Sypharoptera* is not in a position that allows determining with accuracy that the wings were in a roof-like position in the living animal (Fig. 3), while the narrow costal space and simple, straight CuA and CuP can be found in many Diaphanopterodea and are not sufficient for an attribution to another clade.

Figure 3. *Sypharoptera pneuma* Handlirsch, 1911 (?Diaphanopterodea: Sypharopteridae), holotype YPM No. 0064 (Upper Carboniferous,Carbondale Formation, Mazon Creek (Illinois, USA): photograph (Scale bar represents 5 mm).

Sypharoptera shares with *Alexrasnitsynia* rather short ScP, RA and RP widely separated and connected by a series of transversal crossveins, but the organisation of RP, MA, MP, and CuA at their bases is unknown in the former. So we cannot be sure of its possible affinities with our fossil. In particular, it is not possible to determine on the photograph of the holotype of *Sypharoptera* if it has a MA very closely parallel to radial stem and reaching the short oblique basal part of RP, fused with it for short distance, and separating again distally, as in *Alexrasnitsynia*.

The other structures of wing venation are similar in *Sypharoptera* and *Alexrasnitsynia*, with the main difference in the greater number of branches of RP in the latter (6–7 branches) than in the former (3–4 branches). One might be tempted to consider that *Alexrasnitsynia* and *Sypharoptera* belong to the same family of Diaphanopterodea. Nevertheless several important structures diagnostic to the family to which *Alexrasnitsynia* belongs are unknown in *Sypharoptera,* so we prefer to consider *Alexrasnitsynia* in a separate new family.

Family Parelmoidae Rohdendorf, 1962

Type genus. *Parelmoa* Carpenter, 1947.

Other genera. *Pseudelmoa* Carpenter, 1947, *Permuralia* Sinichenkova & Kukalová-Peck, 1997, *Permelmoa* gen. n.

Genus *Permelmoa* gen. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Permelmoa

Type species. *Permelmoa magnifica* sp. n.

Etymology. Named after the Permian and the genus *Elmoa* Tillyard, 1937.

Diagnosis. Wing venation only. ScP long, terminating to C close to wing apex; absence of 'trifurcation between R, M, and CuA near wing base; CuA never touching M; MA and RP never touching.

***Permelmoa magnifica* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Permelmoa_magnifica
Figs 4A–B

Material. Holotype Ld LAP 365ab (Lapeyrie collection, imprint and counterimprint of a complete wing), stored at the Musée of Lodève, France.

Type strata and locality. Middle Permian, Lodève Basin, Salagou Formation, Les Vignasses, Lodève, Hérault, France (Garric 2000; Béthoux et al. 2002).

Description. Complete wing without trace of coloration; wing 11.7 mm long and 3.3 mm wide; ScP simple and parallel to RA ending on costal margin close to wing apex (about 0.5 mm); stems R+M basally distinctly curved, with R and M separating about 1.8 mm from wing base; convex simple RA nearly straight, and ending in wing apex; RP separating from RA about 1/3 of wing length, RP with three long branches ending on posterior wing margin; simple convex MA shortly connected to RP by a crossvein; concave MP deeply forked 0.9 mm from division R and M; anterior branch of MP secondary bifurcated, posterior branch simple; simple convex CuA, basally close to R+M; no apparent 'trichotomy' R/M/CuA; simple concave CuP; anal area with three or four veins.

Discussion. *Permelmoa* is clearly attributable to the Parelmoidae because of combination of the following characters: ScP terminating on C; RP ending with three long branches; MA not coalescent with RP, but shortly connected by crossvein; MP deeply forked. *Permelmoa* differs from *Parelmoa* and *Pseudelmoa* in the absence of trifurcation between R, M, and CuA near wing base, and in the presence of a longer ScP terminat-

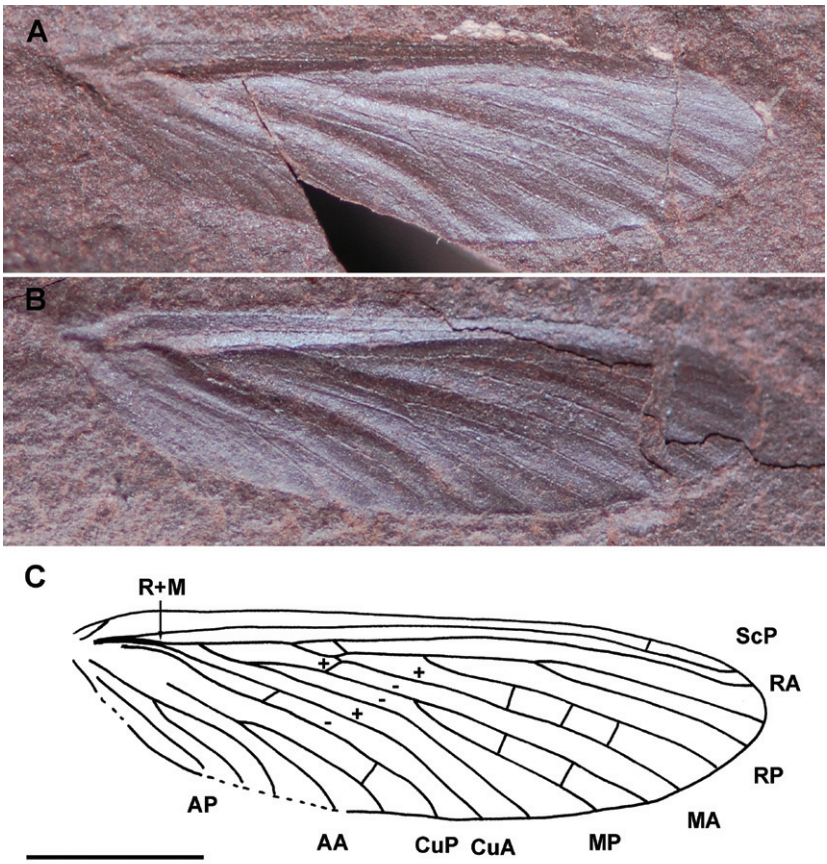

Figure 4. *Permelmoa magnifica* gen. et sp. n. (Diaphanopterodea: Parelmoidae), holotype Ld LAP 365ab: A photograph of wing imprint, B photograph of wing counter-imprint, C drawing of wing (scale bar represents 3 mm).

ing to C close to wing apex. In *Permuralia*, ScP is rather short and terminating on RA, CuA is touching M, and MA and RP are fused for a short distance, unlike in *Permelmoa*.

Family undetermined

Genus *Lodevohymen* gen. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lodevohymen

Type species. *Lodevohymen lapeyriei* sp. n.

Etymology. Named after Lodève town and Hymen.

Diagnosis. Wing characters only. Presence of basal fusion of M with CuA; broad areas between C and ScP and between ScP and RA without apical 'pterostigma'-like

structure, RP with five posterior parallel branches; strong convexity of basally connected veins R, M, and CuA, forming a curve.

***Lodevohymen lapeyriei* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lodevohymen_lapeyriei
Figs 5A–B

Material. Holotype LdLAP 556 (imprint of nearly complete wing, basal part not well preserved, Lapeyrie collection), stored at the Musée of Lodève, France.

Type strata and locality. Middle Permian, Lodève Basin, Salagou Formation, Les Canals, Lodève Basin, Hérault, France (Garric 2000; Béthoux et al. 2002).

Description. Wing elongated and basally narrow with no trace of coloration preserved, wing fragment about 16.5 mm long, estimated length about 19.5 mm width 4.2 mm in widest part; anterior margin nearly straight, ScP straight ending to C close to wing apex; areas between costal margin and ScP and ScP and RA rather broad; stem of R basally connected to M diverging 1/3 of wing length; division of RA and RP about 8.5 mm from the wing base, RA simple and straight ending in wing apex; RP pectinate with five branches ending on posterior wing margin, crossveins organized in rows between branches of RP; simple MA strongly diverges from MP 1.2 mm from division of stems R and M, and well connected with RP for distance; MP, CuA separates from CuP near wing base, CuA and M basally fused and closely parallel to R, separating 3.0 mm from base of CuA; CuA and CuP simple and straight with a few crossveins between them; anal area reduced , one anal vein present close the wing base.

Discussion. *Lodevohymen* shares with the diaphanopterodean taxa *Asthenohymen* Tillyard, 1924 (including *Karoohymen* Riek, 1976) (Asthenohymenidae Tillyard, 1924) and *Biarmohymen* Zallesky, 1937 (Biarmohymenidae Zallesky, 1937), but also with the megasecopteran taxa *Permohymen* Tillyard, 1924, *Ivahymen* Martynov, 1932, *Protohymen* Tillyard, 1924 (Protohymenidae Tillyard, 1924), *Scytohymen* Martynov, 1937, *Oceanoptera* Shcherbakov, 2009 (in Shcherbakov et al. 2009), and *Tshekardohymen* Rohdendorf, 1940 (Scytohymenidae Martynov, 1937), the presence of basal fusion of M with CuA (Carpenter 1992; Riek, 1976; Shcherbakov et al. 2009). This important character together with a very similar pattern of venation present in all these taxa would suggest that their attribution to different orders is weakly supported.

Nevertheless *Lodevohymen* strongly differs from all these taxa in the broad areas between C and ScP and between ScP and RA without apical 'pterostigma'-like structure. Other Diaphanopterodea and Megasecoptera have not a long fusion CuA-M in basal part of wing (Carpenter 1992).

The genus *Sunohymen* Hong, 1985, currently included into the Protohymenidae, shares with *Lodevohymen* the rather broad areas between C and ScP and RA, but they differ in RP with only two branches in the former. Also all its structures of basal half of

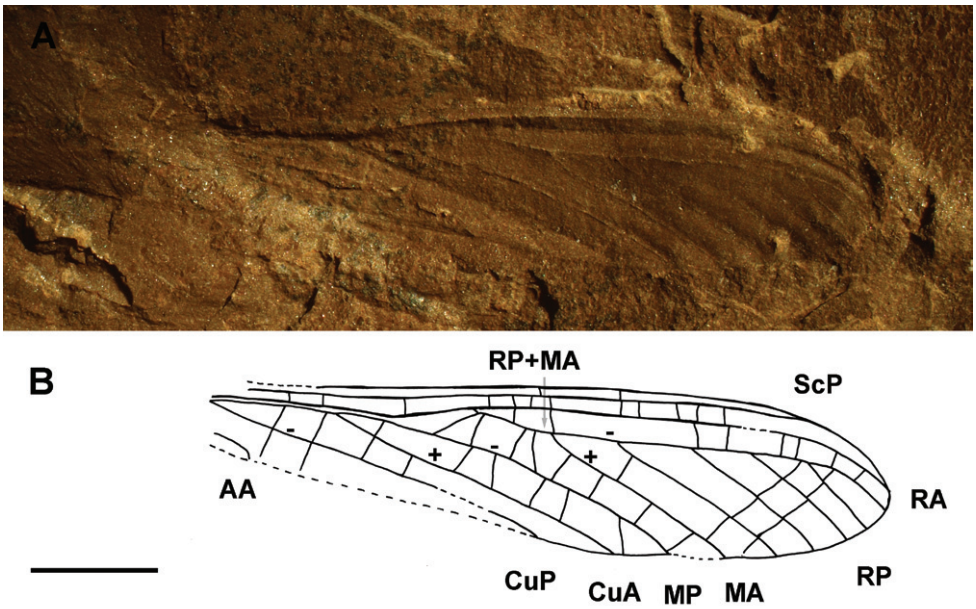

Figure 5. *Lodevohymen lapeyriei* gen. et sp. n. (?Diaphanopterodea), holotype LdLAP 556: A photograph of wing, B drawing of wing (Scale bar represents 3 mm).

wing are unknown, so that its attribution to the Protohymenidae, family in which M is basally fused to CuA, remains undemonstrated (Hong 1985).

Lodevohymen is obviously strongly different from all other Diaphanopterodea and Megasecoptera.

Lodevohymen could be better attributed to the Diaphanopterodea rather than to the Megasecoptera for the strong convexity of the basally connected veins R, M, and CuA, forming a curve. Nevertheless, as already noted by Carpenter (1992), it is very difficult to attribute isolated wings of this kind to one of these two orders. It is better to avoid creating a new family as the phylogeny of these two orders is still to be done and the limits of the described families not clearly defined.

Conclusion

We described in the present study two new representatives of Diaphanopterodea, including a new family, plus one enigmatic taxon that could be either related to this order or to the Megasecoptera, and the first representative of the order Ephemeroptera in the Salagou Formation. These new fossils confirm that this fauna is very rich, diverse and rather unique. It also confirms the general impression that the current knowledge on the Permian insects remains very incomplete. Interestingly, the Coleoptera and other holometabolous orders remain nearly unrecorded in the Lodève basin while these insects are already present in the Lower Permian and dominate all the fossil entomo-

faunas after the Triassic of Vosges (Papier et al. 2005). This confirms the hypothesis of Nel et al. (2007) about the delayed diversification of the Holometabola after the Permian-Triassic crisis. The Middle Permian appears as a period of renewal of the 'ancient', Carboniferous, groups of insects, especially in the palaeopteran clades, before the great extinctions that took place during the period between the Upper Permian and Lower Triassic.

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RESEARCH ARTICLE

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Rasnitsynala sigambrorum gen. et sp. n., a small odonatopterid ("Eomeganisoptera", "Erasipteridae") from the early Late Carboniferous of Hagen-Vorhalle (Germany)

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Abstract

Besides *Erasipteroides valentini* (Brauckmann in Brauckmann, Koch & Kemper, 1985), *Zessinella siope* Brauckmann, 1988, and *Namurotypus sippeli* Brauckmann & Zessin, 1989, *Rasnitsynala sigambrorum* **gen. et sp. n.** is the fourth species of the Odonatoptera from the early Late Carboniferous (Early Pennsylvanian: Namurian B, Marsdenian) deposits of the important Hagen-Vorhalle Konservat-Lagerstätte in Germany. With its wing-span of about 55 mm it is unusually small even for the "Eomeganisoptera". Its venation resembles other small "Eomeganisoptera", in particular *Z. siope*. This is why it is here assigned to the probably paraphyletic "Erasipteridae" Carpenter, 1939.

Keywords

Odonatoptera, "Eomeganisoptera", "Erasipteridae", gen. et sp. n., early Late Carboniferous, Namurian B, Marsdenian, Hagen-Vorhalle, Germany

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Introduction

Up to now three species of Odonatoptera: Neodonatoptera have been described from early Late Carboniferous (Early Pennsylvanian: Namurian B, Marsdenian) deposits of the important Konservat-Lagerstätte of Hagen-Vorhalle in Germany, i.e. *Erasipteroides valentini* (Brauckmann in Brauckmann, Koch & Kemper, 1985), *Zessinella siope* Brauckmann, 1988 (both "Eomeganisoptera": "Erasipteridae") and *Namurotypus sippeli* Brauckmann & Zessin, 1989 (Euodonatoptera: Meganisoptera). Due to the nearly completely preserved specimens, in particular *E. valentini* and *N. sippeli* enlarged the knowledge of the morphology and presumed behaviour of Late Palaeozoic Odonatoptera essentially (Brauckmann and Zessin 1989, Bechly et al. 2001, Zessin 2008b). With a wing-span of about 17 cm and 32 cm, respectively, these two species are both large when compared with *Z. siope*, which only reaches a wing-span of about 8 cm. *Rasnitsynala sigambrorum* gen. et sp. n. is the fourth species of the Odonatoptera of this collecting site. With its wing-span of only 55 mm it is unusually small even for the "Eomeganisoptera".

The previously described species from Hagen-Vorhalle are among several findings of Odonatoptera from other Late Carboniferous (Pennsylvanian) collecting sites, in particular in Germany (Zessin 1983, Brauckmann 1983) and Argentina (Riek and Kukalová-Peck 1984) which were discovered in the years between 1980 and 1990. After a long period of stagnation of scientific investigations in Odonatoptera, these new materials gave rise to further interest in this group. Subsequently several contributions have been published, in particular during the last decade, including descriptions of newly discovered materials of already described taxa (Beckemeyer 2000, 2006, Beckemeyer and Hall 2007) as well as of new species and genera (Zessin 2006, Zhang et al. 2006, Ren et al. 2008, Nel et al. 2008, Prokop and Nel 2008, Zessin and Brauckmann 2010), detailed morphological interpretations (Kukalová-Peck 2009), phylogenetic studies (Bechly et al. 2001, Jarzembowski and Nel 2002, Kukalová-Peck 2009), revisions of larger parts and compilations (Zessin 2008a, Nel et al. 2009), and even research concerning the presumed flight adaptations and behaviour (Wootton et al. 1998, Wootton and Kukalová-Peck 2000, Bechly et al. 2001, Zessin 2008b).

Material, methods and terminology

The nomenclature of the wing venation follows Redtenbacher (1886), Riek and Kukalová-Peck (1984), and Bechly (1996). Abbreviations used in this contribution are: PC, Precosta; CA+ = Costa anterior; CP– = Costa posterior; ScA+ = Subcosta anterior; ScP– = Subcosta posterior; R = Radius; RA+ = Radius anterior; RP– = Radius posterior; M = Media; MA+ Media anterior; MP– = Media posterior; Cu = Cubitus; CuA+ = Cubitus anterior; CuP– = Cubitus posterior; A = Analis; AA+ = Analis anterior; AP– = Analis posterior; JuA+ = Jugalis anterior. Attached + and – indicate the corrugation of

the wing. The corrugation is not distinctly preserved in *Rasnitsynala sigambrorum* gen. et sp. n. The nomenclature of the areas between the main veins follows Zessin (1987).

The photograph and drawing of the holotype was prepared by digital camera Nikon D3 and Corel Draw 12.

Systematic palaeontology

Remarks. The systematics of early Odonatoptera as used in the present article follows Bechly (1996), Bechly et al. (2001) and Zessin (2008a). Rohdendorf and Rasnitsyn (1980) as well as Rasnitsyn and Pritykina (2002) introduced a different nomenclature based upon the name of a type genus of each group, a nomenclatural method that has long been used in botany. Since these two points of view use different ranks they cannot easily be compared at each level, at least in early Odonatoptera.

Odonatoptera Martynov, 1932 = Libellulidea sensu Rasnitsyn and Pritykina, 2002
Neodonatoptera Bechly, 1996
"Eomeganisoptera" Rohdendorf, 1962
"Erasipteridae" Carpenter, 1939

Remarks. As shown by Brauckmann and Zessin (1989) and Bechly et al. (2001), both the "Eomeganisoptera" and "Erasipteridae" are most probably paraphyletic.

***Rasnitsynala* gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Rasnitsynala

Type (and only known) species. *Rasnitsynala sigambrorum* gen. et sp. n.

Diagnosis. As for the type species (due to the temporarily monospecific status). Thus far the physically smallest genus of the "Erasipteridae" with typical morphology of distal venation: kink between CuA+ and CuP– very short, ICu area forming a high triangle, and angle between AA1+ and CuA+ nearly 45°.

Discussion. In its general characters (small size, venation, and cell configuration) *Rasnitsynala* gen. n. closely resembles the previously described genera of the "Erasipteridae" as defined by Brauckmann and Zessin (1989), in particular *Zessinella* Brauckmann, 1988, and is therefore placed in this family. It differs from all other "Erasipteridae" in the basal course of CuA+ and CuP– with very short kink. In the mesothoracic wing, AA1+ runs steeply towards the posterior margin, only similar to *Aulertupus tembrocki* Zessin & Brauckmann, 2010 (Fig. 1). The basal intercubital area (ICu area) resembles a relatively high triangle with its point downwards. In *Erasipteron* Pruvost, 1933, *Erasipteroides* Brauckmann and Zessin, 1989, *Erasipterella* Brauckmann, 1983 and *Zessinella* this area is more a parallelogram with relatively

Figure 1. *Aulertupus tembrocki* Zessin & Brauckmann 2010, holotype, left mesothoracic wing, preserved length 63 mm; Late Carboniferous (Pennsylvanian): Westphalian C/D; Morris, Mazon Creek, Illinois, USA, nomenclature of wing venation. From Zessin and Brauckmann (2010).

short branch-lines. *Whalleyala* Brauckmann and Zessin, 1989 is much larger, and AA1+ is subparallel to the distal Cu; in contrast AA1+ forms an angle of about 45° with the distal Cu, in particular CuA+, in *Rasnitsynala* gen. n. Additionally *Campyloptera* Brongniart, 1893 again differs distinctly in this distal part of the venation as well as in its larger size.

Etymology. In honour of Professor Dr Alexandr P. Rasnitsyn (Moscow).

***Rasnitsynala sigambrorum* gen. et sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Rasnitsynala_sigambrorum
Figs 2–3

v 2008a Kleine, neue unbeschriebene Art von Vorhalle (= small, yet undescribed new species from Vorhalle). Zessin: 5.

Holotype. Former Sippel collection no. 182 A and B, now collection of the LWL-Museum für Naturkunde, Westfälisches Landesmuseum mit Planetarium in Münster (Germany), positive imprint: no. WMf.N P27781, negative imprint: no. WMf.N N3182B.

Type locality. Abandoned brickyard quarry in Hagen-Vorhalle, North Rhine-Westphalia, Germany (topographic map 1 : 25,000 sheet no. 4610 Hagen/Westfalen; 51°22.88'N; 007°26.77'E, ~115 m a.s.l.).

Stratum typicum. Early Late Carboniferous (Early Pennsylvanian: late Namurian B, late Marsdenian), Ziegelschiefer Formation.

Diagnosis. Thus far the smallest species of the „Erasipteridae" with the following main characters: Mesothoracic wing: (i) Length: 27 mm; (ii) anterior margin very slightly convex; (iii) ScP– very long, nearly reaching apex; (iv) subcostal area (Sc area) distally very narrow between ScP– and "PC/CA+/CP–/ScA+"; (v) AA1+ short, forming an angle of about 45° with Cu and CuA+; (vi) basal parts of CuA+ and CuP– rather long; (vii) basal intercubital area (ICu area) a relatively high triangle with its point downwards; (viii) kink between CuA+ and CuP– very short. Metathoracic wing: (i) Length: 22 mm; (ii) anterior margin very slightly convex. Body: (i) Preserved length (without head and posterior 3 abdominal segments): 24.5 mm, estimated total length: 32 mm; (ii) abdominal segments narrow and long.

Preservation. The rather well preserved fossil lies in dorsal view. The head with antennae, legs, the posterior three abdominal segments and the left wings are lacking as well as the posterior regions of the right wings. Nevertheless, the preserved parts of the right wings clearly exhibit the main diagnostic features. The original corrugation is nearly completely flattened by tectonic processes but can be reconstructed by comparison with the characters of the ground plan (Kukalová-Peck 2009). The body is compressed, too, and a part of the thoracic segments seems to have been split off. Possibly the right mesothoracic wing was basally disconnected.

Measurements (in mm). (i) Length of mesothoracic wing, 27; (ii) length of metathoracic wing, 22; (iii) preserved length of body (without posterior three abdominal segments), 24.5, estimated total length, 32.

Description. Mesothoracic wing: Anterior margin very slightly convex; ScP– very long, nearly reaching apex; subcostal area (Sc area) distally very narrow between ScP– and complex PC/CA+/CP–/ScA+; AA1+ short, forming an angle of about 45° with Cu and CuA+; basal parts of CuA+ and CuP– rather long; basal intercubital area (ICu area) resembling a relatively high triangle with its point downwards; kink between CuA+ and CuP– very short. Metathoracic wing: Anterior margin very slightly convex, nearly straight. Body: Abdominal segments slender and long.

Etymology. After the Latin name of the Germanic tribe Sigambri (or Sugambri) who inhabited the type region of the species.

Discussion. With a wing-span of about 55mm, *Rasnitsynala sigambrorum* gen. et sp. n. represents the smallest species known to date of the presumably paraphyletic "Erasipteridae". It shows some characters already known from the very plesiomorphic Geroptera: Eugeropteridae (metathoracic wing of *Eugeropteron lunatum* Riek in Riek & Kukalová-Peck, 1984) or Meganisoptera: Aulertupidae (*Aulertupus tembrocki*), e.g. (i) the morphology of the intercubital area (ICu area) and (ii) the course of AA1+. The abdominal morphology is unknown in most Palaeozoic Odonatoptera and cannot be compered. In *R. sigambrorum* gen. et sp. n. it is extremely slender and longer than the

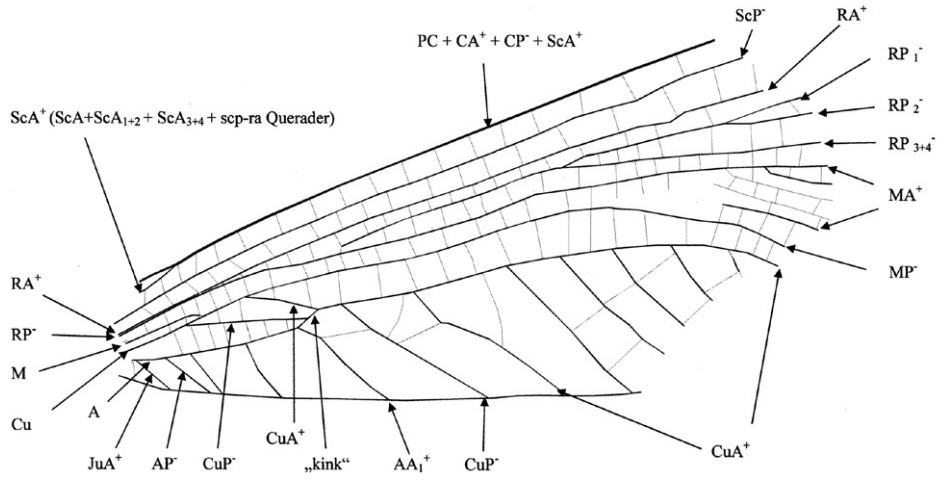

Figure 2. *Rasnitsynala sigambrorum* gen. et sp. n., holotype, former Sippel collection no. 182 A, now collection of the LWL-Museum für Naturkunde, Westfälisches Landesmuseum mit Planetarium in Münster (Germany), positive imprint WMf.N P27781, nearly complete specimen; Early Late Carboniferous (Early Pennsylvanian: Namurian B, Marsdenian); abandoned brickyard quarry, Hagen-Vorhalle (Germany). Preserved length (= without head and posterior three segments): 24,5 mm, length of mesothoracic wing: 27 mm. Photograph by LWL- Museum für Naturkunde, Berenika Oblonczyk.

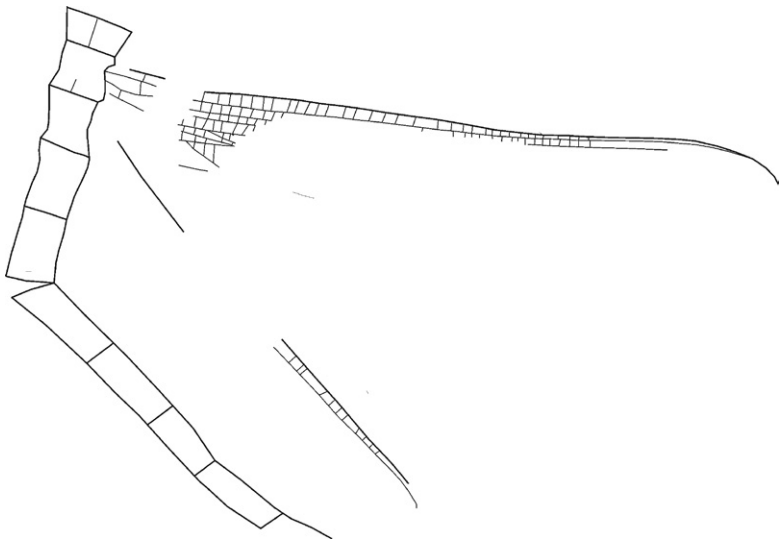

Figure 3. Drawing of *Rasnitsynala sigambrorum* gen. et sp. n., holotype, former Sippel collection no. 182 A, now collection of the LWL-Museum für Naturkunde, Westfälisches Landesmuseum mit Planetarium in Münster (Germany), positive imprint WMf.N P27781, nearly complete specimen; Early Late Carboniferous (Early Pennsylvanian: Namurian B, Marsdenian); abandoned brickyard quarry, Hagen-Vorhalle (Germany). Body structure schematized. Preserved length (= without head and posterior three segments): 24.5 mm, length of mesothoracic wing: 27 mm. Drawing by Wolfgang Zessin, Jasnitz (Germany).

wings. It is even relatively longer and narrower than in the contemporaneous *Namurotypus sippeli* and *Erasipteroides valentini* but seems to be similar in *Zessinella siope*, again of the same age and locality. This character is common in several Recent Zygoptera. It demonstrates that the basic ground plan of Odonatoptera was already established in the very early phase of their evolution, presumably long before the Namurian B (about 319 m.y. ago).

Conclusion

Though extremely rare, Late Palaeozoic Odonatoptera are famous for the giant size of some of their species with a wing-span of more than 70 cm. On the other hand, *Rasnitsynala sigambrorum* gen. et sp. n. shows once more that they include small relatives, too. Previous collections were largely accidental or concentrated on easily recognizable moderate to large insects. We expect that focussing further prospection onto small and tiny species will significantly broaden our knowledge of early Hexapoda. Another vivid example for this is most recently given by Ilger and Brauckmann (2011).

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RESEARCH ARTICLE

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The diversity of Odonata (Insecta) and their endophytic ovipositions from the Upper Oligocene Fossillagerstätte of Rott (Rhineland, Germany)

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Abstract

A commented list of fossil Odonata from the Oligocene outcrop of Rott is given, together with descriptions of new traces of oviposition in plant tissues, very similar to ichnotaxa already known from the early Eocene Laguna del Hunco floras of Patagonia. The joint presences of odonatan larvae and traces of oviposition demonstrate the autochthony of these insects in the palaeolake of Rott, confirming the existence of a diverse and abundant aquatic entomofauna, a situation strikingly different to that in the contemporaneous Oligocene palaeolake of Céreste (France).

Keywords

Insect reproduction, plant-insect interactions, Zygoptera, Odonata, palaeoecology, Oligocene, Rott

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Introduction

Since the first half of the 19th century the Oligocene lake deposits of Rott are well known for their high diversity of fossil insects. Until the middle of the 20th century about 630 species have been described (e.g., Lutz 1996). With almost 11.5 % of insect fossils, the odonates are quite common, mainly represented by their nymphs, but also by a variety of adult specimens with at least 11 species as well as by oviposition traces on fossil plant material. Females of most odonate species lay their eggs into plant substrata. Endophytic oviposition in these insects is performed by means of the ovipositor valves, which penetrate and cut substrate tissues inserting eggs in the prepared slits (e.g., Wesenberg-Lund 1943). Damselflies and dragonflies can use both live and rotten plants as oviposition substrates. The Cenozoic record of odonate endophytic oviposition is rather numerous and of modern aspect. Previous records have been recently summarized in Sarzetti et al. (2009). However, Hellmund and Hellmund (1991, 1996c, 2002a) were the first to described two scar patterns for the Rott fossil site. They recognized the most common "Coenagrionid Type", for which the arcuate and zigzag arrangements are the modal configurations, and the less common "Lestid Type", in which the files of paired egg scars follow the stronger veins. The arcuate/linear and zigzag arrangements of ovipositions could also be attributed to the damsel-dragonflies (represented in Recent by the relic family Epiophlebiidae), or to aeshnid dragonflies (for explanation see below). Furthermore, the locality is characterized to have a rather high diversity of body fossils of Odonata with at least 11 species based on adults and nymphs (*vide infra*).

The Rott fossil locality, lying between the town of Hennef and the Pleisbach River in the northern Siebengebirge close to the city of Bonn, is known for its abundance of exceptionally well-preserved fossil plants and animals (e.g., von Koenigswald 1996) as well as abundant insect damage on the bulk flora (Wappler 2010). Due to early mining activities, its stratigraphy is well-known (e.g., von Dechen 1884; Kaiser 1897; Laspeyres 1900; Wilkens 1927), and the fossiliferous layers were already discovered in several mines by the 19th century. 200 plant taxa and 35 vertebrate taxa, as well as over 600 insect taxa have already been described (numerous works of Statz in the years 1930–1952), although most of these descriptions are in need of revision, being nearly 150 to 70 years old (Lutz 1996; Fikáček et al. 2010). No new finds from Rott are expected, since only overgrown and weathered small dumps of rocks remain there.

The earliest notes on plant remains from Rott can be found in Weber (1852). Leaves that could be morphologically classified and identified were especially featured in this comprehensive study, as was the fashion at the time. In the following years, he collaborated with Philipp Wessel (1855) and they expanded the faunal inventory. Between 1937 and 1948, the leaf flora was updated, especially by Herrmann Weyland – this involved not only the original studies by Weber and Wessel, but also new material, particularly from the so called Statz collection.

Over 120 studies about the fossil insects from Rott have been published, making it as relevant as other famous Cenozoic localities, like Enspel and Céreste, but no

taphonomic study of the Rott insects has been done yet. Besides small correspondences about specific taxa (e.g., Statz 1931, 1936, 1940), the extensive revisions of single dipteran groups (e.g., Statz 1943, 1944a,b,c) stimulated further research on the insect fauna of Rott (see Fikáček et al. 2010). The dominance of different *Plecia* species (Diptera: Bibionidae) and the large diversity of isopterans is indicative for a warm, paratropical climate (Collomb et al. 2008); this is also supported by the palaeobotanical finds.

According to Lutz (1996), the Rott insect taxa are percentually distributed as follows: Diptera (26%), Coleoptera (24%), Hymenoptera (19%), and Orthoptera (18%). In contrast to similar localities (e.g., Enspel, Messel, Eckfeld, Céreste or Aix-en-Provence), aquatic insect larvae are quite common; sometimes they have been even found en masse (Statz 1938, 1950). Besides heteropterans and odonates, aquatic Coleoptera represent around 25% of the finds.

Nevertheless, additional screening of private and historical collections reveals new and undescribed plant material. Based on distinctive morphologies and damage patterns of elongate, ovoid, lens-, or teardrop-shaped scars in the leaves, we could assign these insect damages to the ichnogenus *Paleoovoidus*, consisting of the ichnospecies, *P. rectus*, *P. arcuatus* and *P. bifurcatus* (Table 1, Figs 11–23). The data support recent palaeobiological studies of insect damage on fossil plants and thus can provide valuable information about insect diversity, ecological interactions, and evolutionary adaptation (e.g., Labandeira 2002: Fig. 2).

Material and methods

Material

The fossils examined in the present work are from a number of collections. Fossil leaves and insects from the Upper Oligocene of Rott are housed in the Steinmann Institute, University of Bonn (represented by the Statz Collection, Kastenholz Collection, the Geological–Palaeontological–Institute Collection [GPIBo] at Bonn); in the Collection of Heinz Winterscheid, Cologne (HW-Ro); the Staatliches Museum für Naturkunde (SMNS), Stuttgart, all in Germany; plus a great part of original collection of Statz with many types stored at the Natural History Museum of Los Angeles County (Sphon 1973).By far the most important collection of fossils from Rott was accumulated between 1930–1940 by private collectors, in particular Georg Statz and Anton Kastenholz. Heinz Winterscheid and Meinolf Hellmund also collected valuable material over the last 30 years. Fossils were examined in dry conditions using a binocular microscope, and photographed using a Nikon Coolpix 4500 digital camera, free or attached to the ocular piece of the microscope. The nomenclature of the dragonfly wing venation is based on the interpretations of Riek and Kukalová-Peck (1984), amended by Nel et al.(1993) and Bechly (1996).

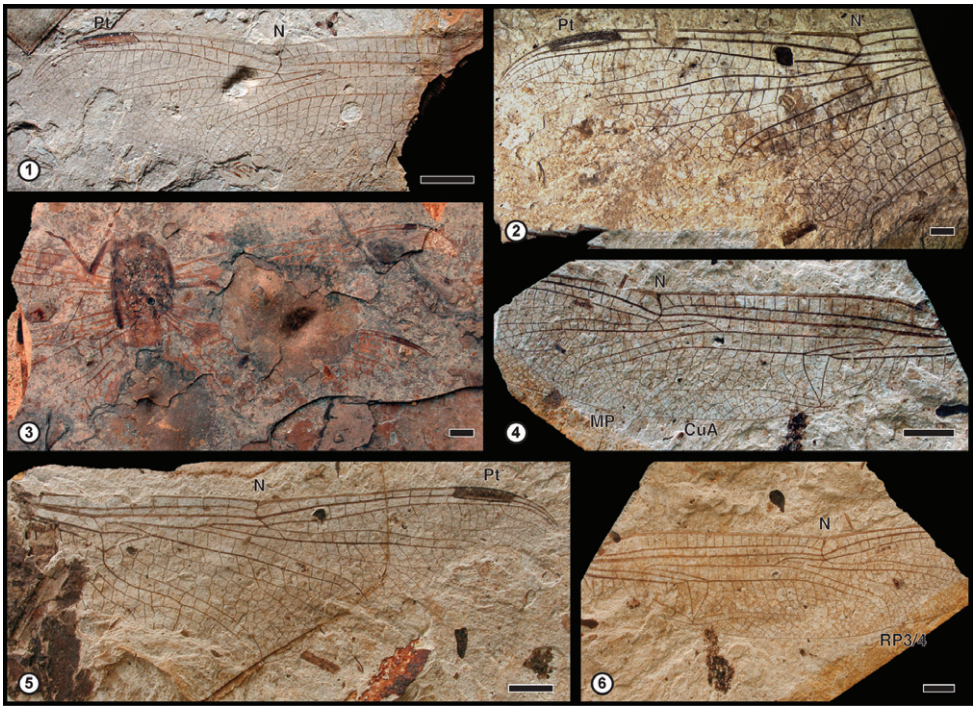
Geological Setting

Locality and stratigraphy

The fossiliferous sediments, also known as the "Sapropelite- and Diatomite-Layers", consist of alternating sapropelites, diatomites, radiolarites, bituminous clays and lignite layers reaching a height of 3–5 m. They partly rest on the weathered tuffs (e.g., Mörs 1995). Absolute dates are only available from volcanic rocks from the Siebengebirge (Todt and Lippolt 1980; Vieten et al. 1988; Wijbrans et al. 1995); in the central Siebengebirge, they have been dated to 26.4–23.0 Ma (Upper Oligocene, Chattian sensu Gradstein and Ogg 2004). Chronostratigraphically, the sediments belong to the uppermost Upper Oligocene, biostratigraphically (according to the mammal fossils) to Zone MP 30 (Mörs 1995); MP 30 ranges from Subchron C7An to the top of Subchron C6Cn.2r (see Agusti et al. 2001). Therefore, the absolute age of the Rott locality is 24–23 Ma (e.g., Kempf et al. 1997; Böhme 2003). The estimated mean annual temperature (MAT) in this area at the accumulation time of lake sediments was 17.5±1.2°C, based on leaf margin analysis (Winterscheid 2006a, b).

Diversity of body fossils of Odonata

The site of Rott is characterized to have a nice diversity of body fossils of Odonata with at least 11 species based on adults and nymphs. The Libellulidae are the most frequently encountered both nymphs and adults. This group has four species, the Libellulidae: Trameinii *Paleotramea cellulosa* (Hagen, 1863) (Nel and Paicheler 1993b), represented by adults (see Figs 1–6), and other three indeterminate species. Hagen (1863) attributed several nymphs to the genus *Libellula* under the names *Libellula ceres* Hagen, 1863 and *Libellula cassandra* Hagen, 1863, but this generic determination is uncertain, and they have to be considered as Libelluloidea *incertae sedis*. A new libellulid species A is described herein by an adult specimen (Fig. 7). *Aeshna dido* Hagen, 1963, based on a nymph, can be considered as an Aeshnidae *incertae sedis*. Other undeterminate Anisoptera (Nel and Paicheler 1994b) complete the odonatan diversity: *Ictinogomphus* (*Ictinus*) *fur* Fraser, 1957, based on an adult specimen, and five 'species' of damselflies. These are: one Lestidae, *Lestes statzi* Schmidt, 1958 (Nel and Paicheler 1994b) represented by adults; an adult of Coenagrionidae *incertae sedis* described herein (Figs 8–10); and several nymphs, viz. *Agrion icarus* Hagen, 1863 (Coenagrionoidea *incertae sedis*, after Nel and Paicheler 1993a), and *Coenagrion* (*Agrion*) *thais* Hagen, 1863 and *C.* (*A.*) *mysis* (both in Zygoptera incertae sedis, after Nel and Paicheler 1993a). In Rott there is also present the basal epiproctophoran family Sieblosiidae, with one described species, *Oligolestes grandis* (Statz, 1936) (Statz 1936; Schmidt 1958; Nel and Paicheler 1994a).

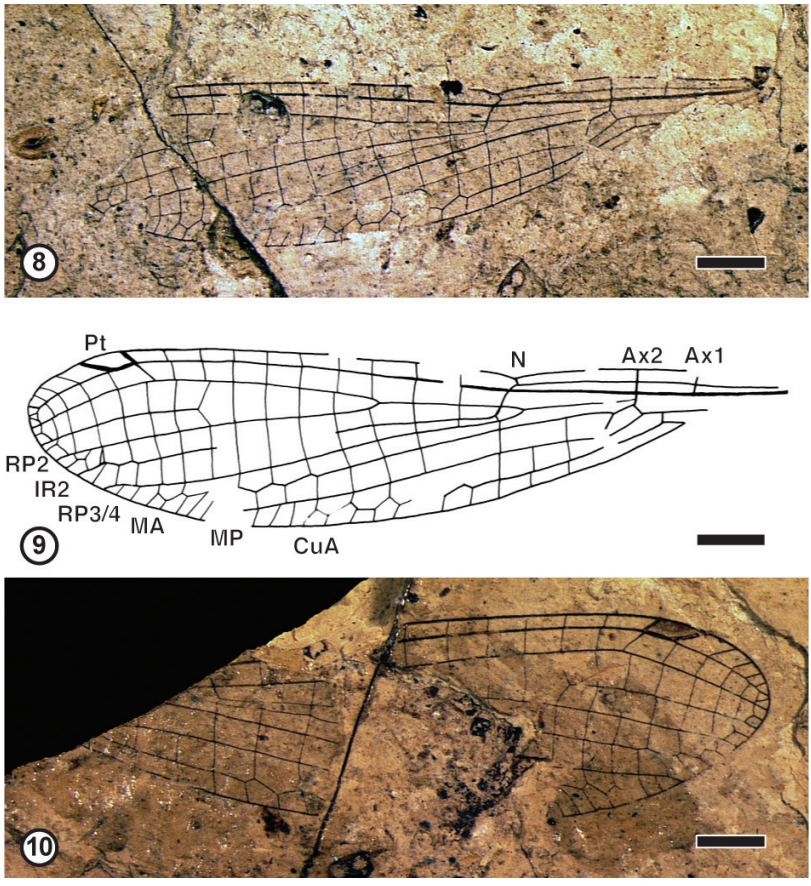


Figures 1–6. *Paleotramea cellulosa* (Hagen, 1863) from the Upper Oligocene Sapropelite- and Diatomite-Layers of Rott **1** Photograph of GPIBo A-626 **2** Photograph of GPIBo A-637a **3** Photograph of GPIBo A-624 **4** Photograph of GPIBo A-636b **5** Photograph of GPIBo Ro-2032 **6** Photograph of GPIBo A-636 a. Abbreviations: **N** – nodus; **Pt** – pterostigma; **RP3/4** – posterior radius; **MP** – posterior media; **CuA** – anterior cubitus. Scale bars represent 5 mm.

Figure 7. Libellulidae species A from the Upper Oligocene Sapropelite- and Diatomite-Layers of Rott.7 Photograph of GPIBo Ro-37a. Abbreviations: **N**– nodus; **RP3/4**– posterior radius; **MA**– anterior media. Scale bar represent 5 mm.

Diversity of ichnofossils

Fossil endophytic oviposition of insects on plant organs are among the rarest, but also the most revealing traces of plant-insect associations in the geological record (e.g., Labandeira 2002; Béthoux et al. 2004; Vasilenko and Rasnitsyn 2007) but only late Cretaceous and Cenozoic oviposition scars can be reliably assigned to several insect groups, mainly Odonata (e.g., Hellmund and Hellmund 1991, 1993, 1996a, b, c, 2002a; Labandeira 2002; Labandeira et al. 2002; Vasilenko and Rasnitsyn 2007; Sarzetti et al. 2009). Hellmund (1986, 1987, 1988) was the first to mention oviposition scar pattern from the Upper Oligocene of Rott but he was only able to list them as undetermined oviposition scars at that time. Later, the specimens have been transferred



Figures 8–10. Coenagrionidae Kirby, 1890, subfamily and genus undetermined, species A, specimen; coll. Kastenholz **8** Photograph of GPIBo KH-1a **9** Camera lucida drawing GPIBo KH-1a **10** Photograph of GPIBo KH-1b. Abbreviations: **Ax** – costal braces; **N** – nodus; **Pt** – pterostigma; **RP** – posterior radius; **IR** – intercalated vein; **MA** – anterior media; **MP** – posterior media; **CuA** – anterior cubitus. Scale bars represent 2 mm.

by Hellmund and Hellmund (1991, 1996c, 2002a) to the Odonata, but they were described without any ichnotaxonomic analyses. Thus, they referred the scars to the most common "Coenagrionid Type", for which the arcuate and zigzag arrangements are the modal configurations, and the less common "Lestid Type", in which the files of paired oviposition scars follow the stronger veins and attribute them to oviposition habits. The linear/arcuate zigzag modal was referred to the coenagrionids but in fact could be found also in Anisoptera (Aeshnidae) and probably also in relatively more basal extinct Epiproctophora, as it is present in Recent Epiophlebiidae (Shimura 2005; Matushkina 2007). One important fact is that some Coenagrionidae, the Aeshnidae and Epiophlebidae lay their eggs in stems of aquatic plants (Shimura 2005; Matushkina 2007) and not in leaves like ichnofossils in present study. Taking apart the problem of the stem/leaf oviposition, for the moment there are not characters to distinguish the analogue (linear/arcuate zigzag modal of) oviposition of these groups to make accurate attributions in the fossil record. Possible characters could be the resulting 'drawing' (letters V, W, Z), angle and shape between the rows. In coenagrionids the angle could be open near 90º and the rows smoothly changing their direction (*vide* Sarzetti et al. 2009), in the Epiophlebiidae the angle is less opened, less than 45º, rows of eggs are more or less parallel, and change their directions abruptly (*vide* Shimura 2005). The zigzag modal of aeshnids is quite different with parallel rows each other resulting in a Z without its middle portion. Other interesting feature to take into account is the length of the egg laying. epiophlebiid females produce long egg laying in zigzag pattern (*vide* Shimura 2005) as described here for Rott (Fig. 19) and also present in Laguna del Hunco, Eocene of Argentina (Sarazetti et al. 2009: 441, fig. 5.6).

At Rott the distinguished damage occurred at least on five different host plants (Apocynaceae, Salviniaceae, Rhamnaceae, Lauraceae, Sapotaceae Hellmund 1986, 1988; present study), whereas lauraceous leaves (*Cinnamomum*- and *Laurophyllum*-type leaves) showing a marked preference for oviposition. However, the species with linear/arcuate zigzag ovipositions from the same locality seem to have been less selective, and even deposited their eggs in floating leaves of aquatic ferns (Table 1; Hellmund and Hellmund 1991). A broad spectrum of plant hosts for this ichnofossil is observed also in the Eocene of Laguna del Hunco, Argentina (Sarzetti et al. 2009; Petrulevičius pers. obs.). This fact also could be related that this trace seems to be made by different groups of Odonata as the coenagrionids and damsel-dragonflies as discussed above.

Contrary to previous statements (e.g., Müller 1976) leaf damage produced by ovipositors is relatively abundant throughout the Cenozoic (comp. Sarzetti et al. 2009). The percent of leaves with damage produced by ovipositors is significantly higher at Rott than at any other Oligocene site (unpublished data), whereas 2.78% of the damaged leaves show some kind of endophytic oviposition. They are especially rare at Aix-en-Provence, lacustrine outcrop of similar age (Nel pers. obs.). For the investigated Cenozoic localities oviposition frequency is highest at Messel, where over 3.3% of leaves show endophytic oviposition (Wappler pers. obs.).

Table 1. Odonatan endophytic oviposition from the Upper Oligocene of Rott, Germany.

[§]modified from Hellmund and Hellmund (1991)
[#]*sensu* Sarzetti et al. (2009)

Collection no	patterns of ovipositional plant damage[§]	Host plant	Ichnospecies[#]	Reference
GPIBo Rott HELL-854	"Coenagrionid/damsel-dragonfly-Type"	*Apocynophyllum* sp.	*Paleoovoidus arcuatus*	Hellmund 1986, 1987, 1988; Hellmund and Hellmund, 1991, 1996a, b
GPIBo Rott HELL-852	"Coenagrionid/damsel-dragonfly-Type"	unknown	*Paleoovoidus arcuatus*	Hellmund and Hellmund 1991
GPIBo Rott HELL-851a+b	"Coenagrionid/damsel-dragonfly-Type"	unknown	*Paleoovoidus arcuatus*	Hellmund and Hellmund 1991
SMNS 22147	"Coenagrionid/damsel-dragonfly-Type"	unknown	*Paleoovoidus arcuatus*	Hellmund and Hellmund 1991
SMNS 22148	"Coenagrionid/damsel-dragonfly-Type"	? *Salvinia* sp.	*Paleoovoidus arcuatus*	Hellmund and Hellmund 1991
SMNS 22149	"Coenagrionid/damsel-dragonfly-Type"	unknown	*Paleoovoidus arcuatus*	Hellmund and Hellmund 1991; Hellmund and Hellmund 2002a
Slg. Hellmund, ohne Nr.	"Coenagrionid/damsel-dragonfly-Type"	*Daphnogene cinnamomifolia*	*Paleoovoidus arcuatus*	Hellmund and Hellmund 1993
GPIBo_Ro_10982	"Coenagrionid/damsel-dragonfly-Type"	*Laurophyllum pseudoprinceps*	*Paleoovoidus arcuatus*	**This study**
GPIBo_Ro_10355	"Coenagrionid/damsel-dragonfly-Type"	unknown	*Paleoovoidus arcuatus*	**This study**
GPIBo_Ro_11887	"Coenagrionid/damsel-dragonfly-Type"	unknown	*Paleoovoidus arcuatus*	**This study**
HW_Ro_2.8	"Coenagrionid/damsel-dragonfly-Type"	*Sideroxylon salicites*	*Paleoovoidus rectus* / *Paleoovoidus arcuatus*	**This study**
GPIBo ohne Nr.	"Lestid-Type"	*Daphnogene cinnamomifolia*	*Paleoovoidus bifurcatus*	Hellmund 1988
SMNS 22144	"Lestid-Type"	*Daphnogene cinnamomifolia*	*Paleoovoidus bifurcatus*	Hellmund and Hellmund 1991; Hellmund and Hellmund 1996b; Hellmund and Hellmund 2002a

Collection no	patterns of ovipositional plant damage[§]	Host plant	Ichnospecies[#]	Reference
SMNS 22145	"Lestid-Type"	*Daphnogene cinnamomifolia*	*Paleoovoidus bifurcatus*	Hellmund and Hellmund 1991; Hellmund and Hellmund 1996b
SMNS 22146	"Lestid-Type"	*Daphnogene cinnamomifolia*	*Paleoovoidus bifurcatus*	Hellmund and Hellmund 1991; Hellmund and Hellmund 1996b
HW_Ro_58.2	"Lestid-Type"	*Daphnogene cinnamomifolia*	*Paleoovoidus bifurcatus*	**This study**

Systematic palaeontology

Suborder Anisoptera Selys, 1854
Family Libellulidae Leach, 1815
Libellulidae undetermined

***Libellula cassandra* Hagen, 1863**
http://species-id.net/wiki/Libellula_cassandra

Remarks. This species is based on larval stages. Hagen (1863) placed the specimens in the recent genus *Libellula* but the morphological characters are insufficient for this attribution. We have to consider it as an undetermined Libelluloidea, following Nel and Paicheler (1993b).

***Libellula ceres* Hagen, 1863**

Remarks. Same remarks as for *Libellula cassandra*.

Libellulidae species A
Fig. 7

Material examined. GPIBo Ro-37a from the locality of Rott (Upper Oligocene, Sapropelite- and Diatomite-Layers): three fragmentary preserved wings; body and appendages missing.

Description. Three wings articulated but wrinkled. Only antero-apical part of one wing is possible to be described. Nine postnodals preserved, not aligned with 10 postsubnodals. Pterostigma covering three cells. Nine posterostigmal veins.Pseudo-IR1 long born beneath posterior part of pterostigma and covering 11 cells. IR1 almost straight connected to pseudo-IR1. RP2 slightly curved. IR2 ending at more than three cells from RP2.Rspl almost straight but ending on IR2 distally, with two rows of cells between it and IR2.

Remarks. The shape of Rspl ending on IR2 and those of IR1 and pseudo-IR1, together with the weak pterostigmal brace are typical of Libellulidae. The postnodals and postsubnodals not aligned together with the broad area between RP1 and RP2 suggest possible affinities with the Trameinae. Nevertheless, this fossil differs from *Paleotramea cellulosa* from the same outcrop in the presence of only two rows of cells between Rspl and IR2. Also the patterns of cells between RP1 and IR1 are different in the two fossils. Thus it corresponds to a different unnamed species of Libellulidae.

Family Aeshnidae Leach, 1815

***Aeshna dido* Hagen, 1863**
http://species-id.net/wiki/Aeshna_dido

Remarks. This species is based on larval stages. Hagen (1863) placed the specimens in the recent genus *Aeshna* but the available characters are insufficient for this attribution and this taxon must be treated as an Aeshnidae *incertae sedis*, as already indicated in Nel et al. (1994).

Suborder Zygoptera Selys, 1854
Family Coenagrionidae Kirby, 1890

Subfamily and genus undetermined

Coenagrionidae species A
Figs 8–10

Material examined. GPIBo KH-1a, b from the locality of Rott (Upper Oligocene, sapropelite- and diatomite-layers): nearly complete forwing; body and appendages missing.

Description. A nearly complete wing, 16.0 mm long, 3.6 mm wide; distance from wing base to arculus 3.1 mm, from arculus to nodus 2.5 mm, from nodus to pterostigma 8.0 mm, from pterostigma to wing apex 1.4 mm; arculus aligned with Ax2, distance between Ax1 and Ax2 1.2 mm, CuP 0.4 mm distal of base of AA; basal side of discoidal cell 0.2 mm long, costal side 0.5 mm long, distal side 0.6 mm long, posterior side 1.0 mm long; pterostigma 1.1 mm long, 0.8 mm wide, covering one

cell, pterostigmal brace pronounced but no distinct angle on RP1 at its level; nine postnodal cross-veins; base of RP2 three cells distal of subnodus; base of IR1 two cells basal of pterostigmal brace; IR2, MA and CuA distally zigzagged, other longitudinal veins nearly straight.

Discussion. This fossil wing corresponds to that of a Coenagrionidae for the shape of pterostigma, pronounced pterostigmal brace, relative position of IR2, RP3/4 and subnodus, long petiole, alignment of cross-veins, veins IR2, MA and CuA distally zigzagged, etc. Its exact position within this family is much more delicate to establish on the sole basis of the wing characters. The subfamily divisions proposed by Fraser (1957) or Davies and Tobin (1984) have been recently rejected by O'Grady and May (2003) or Carle et al. (2008). These recent phylogenetic analyses were based on molecular and morphological characters different from the wing venation. The subfamily divisions of the Coenagrionidae are still rather uncertain and need further investigations. Nevertheless this fossil shares with the genera grouped together in the subfamily Argiinae by Fraser (1957) the following characters: CuP well distal of base of AA, discoidal cell distally widened, arculus aligned with Ax2. This wing is very similar to that of the recent genus *Palaiargia* Foerster, 1903 in the position of base of RP2, but it differs from it in the shorter IR1 (Münz 1919). Nel and Papazian (1990) described some Coenagrionidae from the Oligocene of the South of France without naming them. Two of them 'Argiinae, genre incertae sedis, espèce A' and 'Argiinae, genre incertae sedis, espèce B' were tentatively attributed to the 'Argiinae' for the same reasons as above. The new fossil differs from both of them in the base of vein RP2 four cells distal of subnodus instead of three cells, and CuA less zigzagged in 'espèce A' and more zigzagged in 'espèce B' than in our fossil. Thus the present fossil probably corresponds to a new different species, but naming it is for the present improper. Hagen (1863) described another putative Coenagrionidae from Rott under the name '*Agrion icarus*', transferred by Scudder (1890) in *Platycnemis* but by Kirby (1890) in *Coenagrion*. Its exact affinities remain uncertain (Nel and Papazian 1990; Nel and Paicheler 1993a). It differs from the here described fossil in the greater distance between subnodus and base of RP2, with six cells between them.

Systematic palaeoichnology

Ichnofamily Paleoovoididae Vasilenko, 2005

Ichnogenus *Paleoovoidus* Vasilenko, 2005

* *Paleoovoidus* Vasilenko, 2005, p. 630, figs 1–3.
part. *Sertoveon* Krassilov, 2008, p. 69, figs 1–5.
Paleoovoidus Vasilenko, 2008, p. 516, fig. 2, pl. 7.
Paleoovoidus Sarzetti et al., 2009, p. 433, figs 2–7.
"Flea beetle egg deposition," Lewis and Carroll, 1991, p. 335, fig. 2.
"Flea beetle egg deposition," Lewis and Carroll, 1992, p. 3, fig. 2.

Type ichnospecies. *Paleoovoidus rectus* Vasilenko, 2005, by monotypy

Diagnosis (taken from Sarzetti et al. 2009). Medium-sized elongate, narrow, ovoid, or lens-shaped structures, characterized by regular arrangement in leaf lamina. These structures, defined by dark, surrounding reaction tissue, are narrow at one end, each of which often bears a dark spot.

Comments. Sarzetti et al. (2009) provided a revision of the ichnogenus *Paleoovoidus* including *P. rectus*, *P. flabellatus*, *P. arcuatus*, and *P. bifurcatus*. We have used here the narrowed concept of *Paleoovoidus* as presented by Sarzetti et al. (2009: 437). Other ichnogenera erected by Krassilov and Silantieva (2008), *Costoveon* and *Catenoveon*, are comparable with *Paleoovoidus*, although the disposition of the scars over the leaf are different (*vide* Sarzetti et al. 2009). Unfortunately, the use of nomenclature to describe fossil damage types within a fossil assemblage in the literature is unsatisfactory, not least because of the inconsistency created by different authors using their own particular schemes (e.g., Krassilov and Silantieva 2008; Vasilenko 2008).

***Paleoovoidus rectus* Vasilenko, 2005**
http://species-id.net/wiki/Paleoovoidus_rectus
Figs 11–12

* *Paleoovoidus rectus* Vasilenko, 2005, p. 631, figs 1–3, pl. 5.
"Odonata eggs" van Konijnenburg-van Cittert and Schmeißner, 1999, p. 217.
"Egg scars" Krassilov et al., 2007, p. 806, fig. 3D.
Paleoovoidus rectus Sarzetti et al., 2009, p. 437, figs 2.3–2.4.

Diagnosis (taken from Sarzetti et al. 2009: 437). Elongate to lens-shaped scars oriented in a single, linear row, with long axes of scars aligned lengthwise, mostly parallel to the long axis of the leaf and usually occurring along the midrib.

Description. The specimen of *Paleoovoidus rectus* occurs in a leaf of *Sideroxylon salicites* (Sapotaceae, Ro_2.8; Figs 11–12). This leaf has two sets of leaf scars; the inset box in Fig. 11 indicates those corresponding to *P. rectus*. There are seven scars arranged rectilinearly near the leaf apex, aligned closely adjacent along the primary vein, with the scar long axis parallel to the primary vein. The fifth scar is arranged symmetrically about the midvein. All scars show an elongate- to lens-shaped structure with an enveloping raised rim and a central depression ("elongated hole"), indicating the absence of plant tissue.The individual length of the scars ranges from 0.9 to 1.3 mm, and the width ranges from 0.4 to 0.5 mm. The distance between adjacent scars varies from 0.6 to 2.4 mm. Additionally, *Paleoovoidus arcuatus* (Fig. 13) appears basal to the *P. rectus* trace, indicating that both patterns can occur on the same leaf (*vide infra*).

Comments. The specimen of *P. rectus* (HW_Ro_2.8; on *Sideroxylon salicites* [Sapotaceae]) derives from the pelite and lignite facies of the 'Hangendschichten' at the Rott locality. The sediments belong to the younger part of the Upper Oligocene

(Chattian), based on the mammal assemblage (MP30) recorded by Mörs (1995) with an age of approximately 25 million years as accepted for the Rott Formation (von Koenigswald et al. 1996).

Patterns similar to *P. rectus* described here occur so far only in the early Eocene of Patagonia (Sarzetti et al. 2009) and have a sporadic occurrence on Mesozoic Coniferales and Ginkgoales (Vasilenko 2005; van Konijnenburg-van Cittert and Schmeißner 1999). The Rott specimen exhibits only minor differences from the Argentinian material described by Sarzetti et al. (2009), mainly in dimensions and the total amount of scars preserved. Interestingly, *P. rectus* from the Upper Oligocene occurs at the same position at the tip of the leaf as preserved from the early Eocene Laguna del Hunco floras of Patagonia, and is also associated with *P. arcuatus*.

***Paleoovoidus arcuatus* (Krassilov, 2008)**
http://species-id.net/wiki/Paleoovoidus_arcuatus
Figs 13–22

* *Sertoveon arcuatum* Krassilov, 2008, p. 69, fig. 5.
"Concentric oviposition tracks" Hellmund, 1986, p. 166 fig. 74; Hellmund, 1987, p. 154, fig. 15; Hellmund ,1988, p. 323.
"Coenagrioniden-Typ" Hellmund and Hellmund, 1991, p. 7, figs 3.1–3.4, p. 8, fig. 4, p. 9, figs 5.1–5.2; Hellmund and Hellmund, 1993, p. 349, fig. 1, p. 350, fig. 2–3; Hellmund and Hellmund, 1996a, p. 59, fig. 6.3; Hellmund and Hellmund, 1996b, p. 166, fig. 17; Hellmund and Hellmund, 1996c, p. 109, figs 1a, b; Hellmund and Hellmund, 2002c, p. 262, fig. 8a
"Coenagrioniden-Typ vom Bogenmodus" Hellmund and Hellmund, 1998, p. 282, fig. 1; Hellmund and Hellmund, 2002a, p. 3, fig. 2, p. 10, fig. 8; Hellmund and Hellmund, 2002c, p. 255, fig. 1a, p. 259, fig. 5a, p. 260, fig. 6, p. 261, fig. 7, p. 264, fig. 11a, p. 265, fig. 14, 15.
"Concentric oviposition tracks" Labandeira, 2002, p. 41.
"Radially oriented oviposition scars" Labandeira et al., 2002, p. 312, fig. 80.
"Ovoposiciones de la Familia Coenagrionidae" Peñalver and Delclòs, 2004, p. 74, fig. 2.
"Zygopteran egg sets" Krassilov et al., 2007, p. 806, fig. 3a–c.
"Endophytic oviposition probably of Calopterygina" Vasilenko and Rasnitsyn, 2007, p. 1156, figs 4–6.
Paleoovoidus arcuatus, Vasilenko 2008 (new syn.), p. 516, fig. 2c, pl. 7, figs 2, 3.[meeting the requirements of ICZN, 1999: Art. 31.2]
Paleoovoidus arcuatum, Sarzetti et al., 2009, p. 438, figs 3, 4, 5.1, 5.4–5.6, 6, 7.
Paleoovoidus arcuatum, Wappler, 2010, p. 545, figs 3k–l.

Diagnosis (taken from Sarzetti et al. 2009: 438). Elongate, lens-shaped to teardrop-shaped scars arranged with the short axes aligned horizontally to each other, either as

straight rows or as arcs. Frequently the long axes of scars are sub parallel to each other. Occasionally, successive rows are parallel or exhibit zigzag patterns.

Description. The endophytic oviposition scars of *P. arcuatus* are quite variable in shape as recognized by Hellmund and Hellmund (1991), Krassilov et al. (2007), and Sarzetti et al. (2009). They range from elongate (Figs 13, 15–17), lens-shaped (Fig. 19), teardrop-shaped (Fig. 22), to more or less irregular shapes (Fig. 20). At the first glance, the scar patterns look chaotic (Fig. 12), but in most cases the scars are arranged in concentric arches (Figs 16, 20–21), but even more or less linear oviposition arcs are realized (Fig. 18). In other cases (Figs 18–19) the arcuate rows are not parallel to each other, resulting in a zigzag pattern (Fig. 19). In general, the dimension of the scars ranges from 1.2 to 1.7 mm in length, and widths range from 0.3 to 0.5 mm. In two cases the specimens cover nearly the entire width of the leaf-blade, containing 111 and 376 scars (Fig. 1.4; comp. Hellmund and Hellmund 1991: Fig 3.1, Hellmund and Hellund 1996a: Fig. 6.3). The scars in rows are usually ranging between 2 to 15. They are variously orientated within the leaves, with the long axis parallel to sub parallel to the primary veins (Figs 16, 20). In some specimens the scars show a distinctive enlargement of the callus (Figs 17, 20, 22).

Comments. The specimens of *P. arcuatus* occur on *Laurophyllum pseudoprinceps* (Ro_10982; Lauraceae), *Apocynophyllum* sp. (GPIBo_Rott_HELL_854, Apocynaceae), *Sideroxylon salicites* (HW_Ro_2.8; Sapotaceae), and on three undetermined dicotyledon leaves (Ro_10355; Ro_11887; GPIBo_Rott_HELL_852; GPIBo_Rott_HELL_851a+b). All specimens derive from the pelite and lignite facies of the 'Hangendschichten' at the Rott locality. The sediments belong to the younger part of the Upper Oligocene (Chattian), based on the mammal assemblage (MP30) recorded by Mörs (1995) with an age of approximately 25 million years as accepted for the Rott Formation (von Koenigswald et al. 1996). This type of endophytic oviposition behav-

Figures 11–23. Endophytic oviposition from the Upper Oligocene Fossillagerstätte Rott. ***Paleoovoidus rectus***isp **11–12** On *Sideroxylon salicites* (HW_Ro_2.8; Sapotaceae). ***Paleoovoidus arcuatus*** isp **13** On *Sideroxylon salicites* (HW_Ro_2.8; Sapotaceae), showing a zigzag pattern **14–15** On *Laurophyllum pseudoprinceps* (Ro_10982; Lauraceae), entire leaf fossil showing the distributions of scars over the lamina. Lettered lines (a-j) point to individual rows or 'files' of oviposition marks. **16** Trace-fossil specimens GPIBo_Rott_HELL_852 on an indeterminate dicot leaf **17** Enlargement from rectangular template in Figure 16, showing details of an individual scar **18** Entire leaf fossil showing the distributions of scars over the lamina on an indeterminate dicot leaf (Ro_11887). Lettered lines (a-b) point to individual rows of oviposition marks **19** Enlargement from trapezoid template in Figure 18, showing a zigzag pattern **20** Specimen Ro_10355 (an indeterminate dicot leaf) a-c (lettered lines) point to individual rows with a consecutive and parallel pattern **21** Trace-fossil specimens *Apocynophyllum* sp. (GPIBo_Rott_HELL_854, Apocynaceae). Lettered lines (a-d) point to individual rows of oviposition marks oriented along the secondary venation **22** Enlargement from rectangular template in Figure 21, showing teardrop-shaped oviposition scars. ***Paleoovoidus bifurcatus*** isp **23** On *Zizyphus zizyphoides* (HW_Ro_58.2; Rhamnaceae). Arrows pointing to oviposition scars forming double rows located in an acute angle along to both sides of the veins. Scale bars: stippled bar, 1 cm; slashed bar, 2 mm; dotted bar, 1 mm.

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iour is widely distributed and known from several host plants, indicating that the species producing this ichnofossil are less selective than the Lestoidea for their angiosperm host plants. The specimen MPEF-Pb-1052 of Laguna del Hunco, is suggestive similar to the ovipositions made by *Epiophlebia superstes* and likely attributed to Frenguelliidae (both Epiproctophora) instead of Coenagrionidae as established by Sarzetti et al. (2009: 444, fig. 5.5).

Note. The ichnogenus *Paleoovoidus* Vasilenko, 2005, originally described from the Upper Jurassic–Lower Cretaceous locality of Chernovskie Kopi, Russia, typically comprises arched oviposition scars, with the eggs set in rows at a considerable distance from each other parallel to their long axes. Since then several ichnospecies have been included. However, considerable confusion persists regarding the ichnotaxonomic status and diagnostic features of the ichnospecies. The ichnospecies *Paleoovoidus arcuatus* Vasilenko, 2008 was published several weeks later than *Sertoveonarcuatum* Krassilov, 2008 (type species of ichnogenus *Sertoveon:*Krassilov and Silantieva 2008). Sarzetti et al. (2009: 438, 441) synonymized these two ichnospecies and established the combination "*Paleoovoidus arcuatum* (Krassilov, 2008)"; however, they erroneously indicated "*P. arcuatum"* as new in their abstract and figure captions. According to ICZN (1999: Art. 31.2), this species name, as a Latin adjective in the nominative singular, must agree in gender with the generic name with which it is at any time combined, therefore is here corrected to: *Paleoovoidus arcuatus* (Krassilov, 2008).

Paleoovoidus bifurcatus Sarzetti, Labandeira, Muzón, Wilf, Cúneo, Johnson & Genise, 2009

http://species-id.net/wiki/Paleoovoidus_bifurcatus
Fig. 23

* *Paleoovoidus bifurcatus* Sarzetti et al., 2009, p. 438, figs 2.1, 2.2.
"Galle *Aceria nervesqua fagina*" Straus, 1977, p. 74, fig. 2, p. 78, fig. 50.
"Oviposition damage on primary and secondary veins ("Doppelreihen Modus")" Hellmund, 1988, p. 323.
"Lestiden-Typ" Hellmund and Hellmund, 1991, p. 4–5 figs 1.1–1.3, 2; Hellmund and Hellmund, 1996a, p. 58, fig. 6.1a–b; Hellmund and Hellmund, 1996b, p. 165, fig. 16; Hellmund and Hellmund, 2002a, p. 3, fig. 2; Hellmund and Hellmund, 2002b, p. 49, figs 2–3, p. 53, fig. 12.
"Oviposition damage on secondary veins" Labandeira et al., 2007, p. 10.

Diagnosis (taken from Sarzetti et al. 2009: 438). Elongate to lens-shaped scars arranged in pairs along both sides of a primary vein, forming double rows and sometimes a V-shaped configuration, with the arms of the V parallel to secondary veins and the vertex embedded in the midvein.

Description. The oviposition scars are preserved on a nearly complete preserved lanceolate leaf. Base acute and slightly asymmetric. Venation imperfect basal acro-

dromous.Midrib moderately thick and straight. Besides the pair of stout secondary veins arising at the base, secondary and tertiary veins form a fine network. The ovoid or ellipsoidal-shaped oviposition scars occur in pairs along the midrib and oriented at a right angle with respect to the vein in the upper part of the leaf. Main cluster occurs on the secondary vein, whereas the occurrence of endophytic oviposition scars on the midrib vein is more scattered. The total amount of scars is 25. The axial length of the scars ranges from 0.5 mm to 0.8 mm, and their width ranges from 0.3 mm to 0.4 mm. The distances between consecutive scars are variable within the range of 0.5 mm to 0.7 mm.

Comments. The specimen of *P. bifurcatus* (HW_Ro_58.2, on *Zizyphus zizyphoides* [Rhamnaceae]) derives from the pelite and lignite facies of the 'Hangendschichten' at the Rott locality. The sediments belong to the younger part of the Upper Oligocene (Chattian), based on the mammal assemblage (MP30) recorded by Mörs (1995) with an age of approximately 25 million years as accepted for the Rott Formation (von Koenigswald et al. 1996). The pattern was originally mentioned by Hellmund (1986, 1987, 1988) and originally described and figured by Hellmund and Hellmund (1991, figs 1–2) but without any ichnotaxonomic analyses. A new ichnospecies, *P. bifurcatus*, was described by Sarzetti et al. (2009) from the early Eocene Laguna del Hunco floras of Patagonia. Accordingly, the ichnotaxonomic status of the ichnogenus *Paleoovoidus* was reviewed, providing a new ichnotaxonomic classification, indicating that the preservation of *P. bifurcatus* is variable across a broad range of compression/impression floras and host plants. The presense of *P. bifurcatus* on the Buckthorn family (Rhamnaceae) at Rott extending its host plant range. Previously, the ichnogenus show a marked preference for lauraceous leaves of the morphogenus *Daphnogene cinnamomifolia* (Hellmund and Hellmund 1991, 1996a, b).

Discussion

In Rott the two main modern lineages of Odonata, Zygoptera and Anisoptera, are recorded. Additionally, the Sieblosiidae, a basal and extinct epiproctophoran family (Nel et al. 2005), is also recorded there. This family is only present in the Eocene to the Miocene of Europe. The Epiproctophora nec Anisoptera are mainly Mesozoic, while the Cenozoic to Recent representatives of this grade are the Sieblosiidae, the Eocene Frenguelliidae from Patagonia (Petrulevičius and Nel 2003, 2007), plus the recent Epiophlebiidae present in Japan and Himalaya. Latter family, with two species, is the unique survivor of these damsel-dragonflies. With respect to the structure of their functional ovipositors, the Sieblosiidae were probably laying their eggs in aquatic plants and/or floating leaves but their type of oviposition remain unknown. Despite their damselfly-like habitus of the adults, the Sieblosiidae are distinctly larger than the Coenagrionoidea and Lestoidea already known from Rott, suggesting that their eggs and oviposition traces could have been also larger. Anyway, the presence

of a zigzag modal of oviposition in Rott and Laguna del Hunco similar to that of an Epiophlebiidae is suggestive but could as well have been caused by an aeshnid, also recorded in Rott.

As supposed, the diversity of traces of oviposition left on the leaves together with the presence of larvae in the fossil record from Rott indicate that many of the Odonata found as adults in this outcrop were autochthonous. This is not the case for the nearly contemporaneous outcrop of Céreste in which adult Odonata are frequent and diverse but larvae and trace of oviposition are still unrecorded (Nel pers. obs.). The impressive rarity of aquatic beetles (only one known specimen of Hydrophilidae for more than 60000 fossil insects, Nel collection) at Céreste also greatly contrasts from their diversity at Rott (Fikáček et al. 2010). These data are of interest for a better estimation and comparison of the former quality of lake water and general palaeoecological reconstructions of these localities.

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The smallest Neoptera (Baryshnyalidae fam. n.) from Hagen-Vorhalle (early Late Carboniferous: Namurian B; Germany)

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Abstract

With *Baryshnyala occulta* **gen. et sp. n.** (Baryshnyalidae **fam. n.**) we report a new small species from early Late Carboniferous (Pennsylvanian) deposits in Hagen-Vorhalle. It differs in its unique venation pattern and small size from all other Neoptera known from this Lagerstätte and other contemporaneous locations worldwide. With an estimated wing length of <10 mm it is by far the smallest species of Neoptera from Hagen-Vorhalle and is less than half as long as *Heterologopsis ruhrensis* Brauckmann & Koch, 1982 (~25 mm). The specimen shows some relations to the earliest Holometabola and may date back the first appearance of holometaboly to the Namurian B (early Bashkirian: Marsdenian). The new species increases the paleo-biodiversity and span of inter-specific variability within the early Neoptera. It shows that very small and tiny specimens and species can easily be overlooked.

Keywords

Hagen-Vorhalle, Neoptera, *Baryshnyala occulta* **gen. et sp. n.**, Namurian B, holometaboly

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Introduction

Hagen-Vorhalle is one of the most important Konservat-Lagerstätten of the early Late Carboniferous (Early Pennsylvanian) and has provided remarkable data of supra-regional importance about the evolution of the most ancient Pterygota.

An extraordinary insect fauna was discovered in 1982 and reported in a brief article by Brauckmann & Koch (1982). Over 16,000 samples were recovered in an excavation campaign in 1990–1997 and by private collectors. Insects are represented by ~310 individuals (mostly in dorsal view with part and counterpart). Hendricks (2005) published a complete list of determinable taxa whereas Brauckmann et al. (2010) presented an actual outline of the insect fauna and their relation to other locations. Most of the material is very well preserved, including basal Neoptera Martynov, 1923 with ~210 specimens in 5 species: *Kemperala hagenensis* Brauckmann, 1984, *Holasicia rasnitsyni* Brauckmann, 1984, *Kochopteron hoffmannorum* Brauckmann, 1984, *Heterologopsis ruhrensis* Brauckmann & Koch, 1982, and *Baryshnyala occulta* **gen. et sp. n.**

Kemperala Brauckmann, 1984 and *Holasicia* Kukalová, 1958 can be assigned to the family Paoliidae Handlirsch 1906. For diagnosis and included genera see Kukalová (1958), Brauckmann (1984), Brauckmann et al. (1985, 2003, 2010), Prokop and Nel (2007), Ilger and Brauckmann (2008), and Prokop et al. (in press). As shown in the historical compilation by Prokop and Nel (2007), the systematic rank of paoliids and related early Pterygota has been the subject of controversy during the last few decades: Carpenter (1992), for example, traditionally considered them as a family within the "Protorthoptera," a clearly polyphyletic "order". Kukalová-Peck and Brauckmann (1992) assigned the "paoliid line" together with other early Neoptera to the "hemipteroid stem assemblage". Grimaldi and Engel (2005) placed them as Paoliidae directly in Neoptera without indication of any order. On the other hand, Rohdendorf and Rasnitsyn (1980) and subsequently Rasnitsyn and Quicke (2002) ranked them as Paoliida on ordinal level. Prokop and Nel (2007) did the same, and additionally introduced their Katerinkidae, a closely related new family of the same order. A more general critical discussion of different views of hexapod phylogeny including the Palaeoptera/early Neoptera problem has been provided by Klass (2007, 2009). In the present contribution we avoid a precise higher systematic assignment, because we do not want to anticipate the final results of the current phylogenetic analyses.

The systematic position of the *Kochopteron* Brauckmann, 1984 and *Heterologopsis* Brauckmann & Koch, 1982—which are morphologically similar to the Paoliidae—is unclear and still under controversial discussion. Brauckmann et al. (2003) assigned them to the family ?Cacurgidae Handlirsch, 1911. In contrast, Béthoux and Nel (2002) placed *Heterologopsis* in the Archaeorthoptera.

Baryshnyala occulta **gen. et sp. n.** cannot be allocated to any of these groups and is a representative of a new family within the early Neoptera (Baryshnyalidae fam. n.)

Methods

The specimen WMf.N P.21299 is stored in the Hagen-Vorhalle collection of the LWL-Museum für Naturkunde, Westfälisches Landesmuseum mit Planetarium in Münster. It was recovered in an excavation campaign in 1990–1991.

Investigations were done using a Euromex® ZT-45 zoom trinocular with an attached camera tube. Objects were illuminated with a Euromex® EK-1 cold light lamp with polarizing filters to minimize reflections on clay minerals and mica surfaces. Imaging conditions for photo documentation were optimized by varying illumination levels and angles with polarized and non-polarized light. Photographs were taken by using a Canon PowerShot A470 digital point-and-shoot camera with Super Macro function. Digital images were edited using the computer programs IMAGEJ, COREL PHOTO-PAINT and GIMP.

The nomenclature of wing venation follows Kukalová-Peck and Willmann (1990) as well as Kukalová-Peck and Brauckmann (1992). Main vein terminology corresponds to this scheme: ScP– = Subcosta posterior, RA+ = Radius anterior, RP– = Radius posterior, Ma+ = Media anterior, MP– = Media posterior, CuA+ = Cubitus anterior, CuP– = Cubitus posterior, AA+ = Analis anterior, arc = arculus (strong cross-vein between MP– and CuA+), cmf = cubito-median fold (nomenclature follows Nel et al. (2007): convex fold between MP– and CuA+). Attached plus and minus indicate the corrugation of the wing; i.e.: + = above plane of projection, – = below plane of projection.

Systematics

Infraclass Neoptera Martynov, 1923

Family Baryshnyalidae fam. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Baryshnyalidae

Type (and only know) genus. *Baryshnyala* **gen. n.**, original designation.

Diagnosis. Wing small and well rounded, with the following venation pattern: (i) strong cross-vein between MP– and CuA+ in basal part of wing (arculus), (ii) pronounced convex fold between MP– and CuA+ (cubito-median fold), (iii) CuP– strongly convex, with 3 terminal branches, (iv) a number of straight cross-veins between main veins.

***Baryshnyala* gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Baryshnyala

Type (and only known) species. *Baryshnyala occulta* **gen. et sp. n.**, original designation.

Diagnosis. Very small (length <10 mm) and compact wing with well rounded apex. The venation pattern shows a combination of the following unique characters: (i) RP– branches far before reaching the mid-wing, (ii) well pronounced cubito-median fold, (iii) CuP_1– very strongly convex, (iv) posterior branches of MP– and CuA+ curved backwards (strongly convex), (v) no archedictyon but a number of cross-veins mainly in distal half of the wing.

Remarks. Despite the small size of the wing the regular shape precludes that it is a nymphal wing as it shows no kind of a typical strong backward flexion.

Etymology. The genus name is a combination of the Russian "baryshnya" for young, unmarried woman and Latin "ala" for wing; gender feminine.

***Baryshnyala occulta* gen. et sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Baryshnyala_occulta
Fig 1A–B, 2A–F

Holotype (and only known specimen). Specimen no. WMf.N P.212999, left metathoracic wing, with slightly damaged apex and lacking wing base. Stored in the collection of the LWL-Museum für Naturkunde, Westfälisches Landesmuseum mit Planetarium in Münster (Germany).

Type locality. Former brickyard quarry near Hagen-Vorhalle, North Rhine-Westphalia, Germany (topographic map 1 : 25,000 sheet no. 4610 Hagen/Westfalen; 51° 22.88'N; 007° 26.77'E, ~115 m a.s.l.).

Type stratum. Early Late Carboniferous (Early Pennsylvanian): early Bashkirian, late Namurian B, late Marsdenian, ammonoid zone R2c, Ziegelschiefer Formation.

Diagnosis. As for the genus (due to the temporarily monospecific status). Length ≥9.6 mm.

Preservation. The isolated wing is quite well preserved, though it lacks the proximal tenth with articulation and most of the anal area. Apical wing margin is also slightly damaged. The corrugation is easily discernible but flattened by diagenetic compression. The anterior mid-wing is slightly damaged by preparation marks which obscure the exact reconstruction of terminal ScP– and RA+ branches—especially whether they do or do not fuse.

Also visible in the apical area (Fig. 1), tiny prodissoconchs of young bivalves are attached to the dorsal wing membrane. These embryonic shells are common in basal Neoptera from Hagen-Vorhalle but are absent in all other Pterygota from the same locality. Most recently this has led to new interpretation of the taphonomy of the

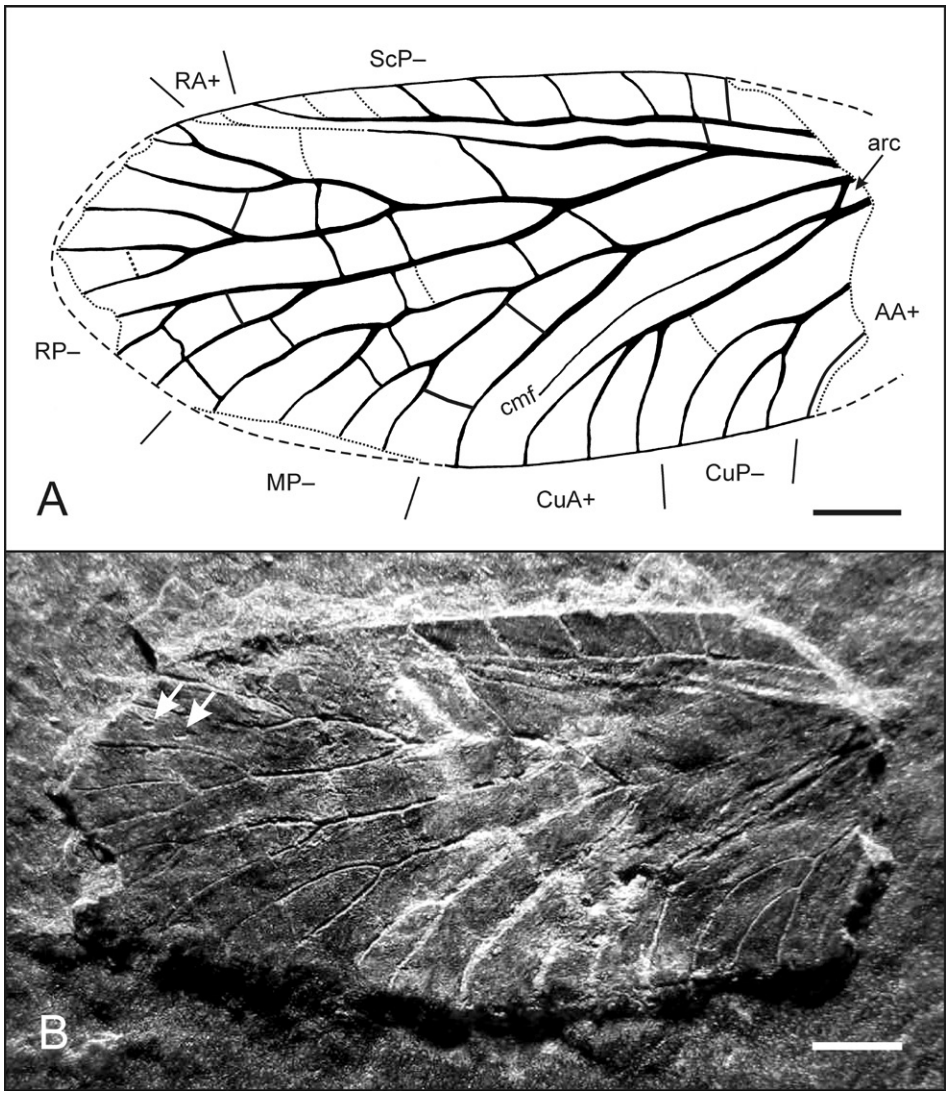

Figure 1. *Baryshnyala occulta* **gen. et sp. n.**; holotype, isolated left metathoracic wing (WMf.N P.21299); early Late Carboniferous (Early Pennsylvanian: Namurian B, Marsdenian): **A** superimposed drawing with interpretation of the wing venation pattern; black arrow indicates arculus (arc) **B** photograph under polarized light; white arrows indicate attached bivalve prodissoconchs. Scale bars: 1 mm.

Lagerstätte.—A manuscript by Ilger is currently in review, Ilger and Brauckmann (2009) gave a short overview.—The model implies a stage of drifting along a pycnocline in a well stratified water body. During this period the corpses were affected by free-swimming bivalve larvae.

Measurements. Preserved length: 8.7 mm; estimated length: ≥9.6 mm; maximum width (at most posterior branch of MP–): 4.2 mm. Approximated ratio length/width: ~2.3.

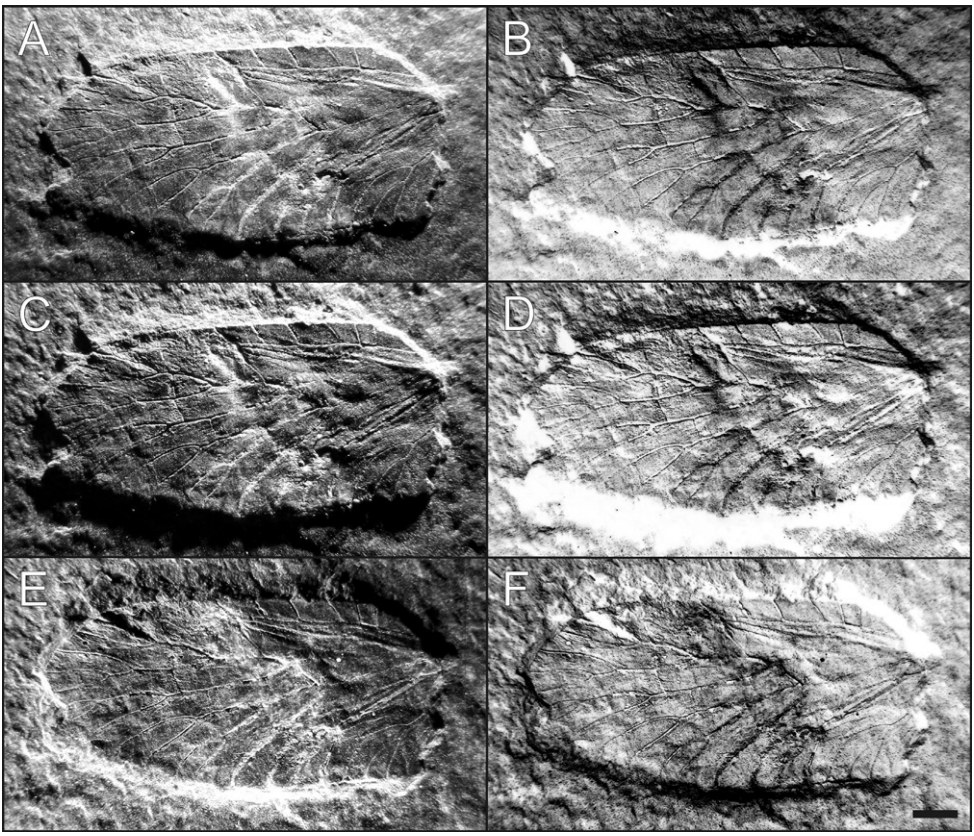

Figure 2. *Baryshnyala occulta* **gen. et sp. n.**; holotype, isolated left metathoracic wing (WMf.N P.21299); early Late Carboniferous (Early Pennsylvanian: Namurian B, Marsdenian): **A–F** The same wing in different illumination settings. Scale bar: 1 mm.

Description. There is only one isolated wing known. Due to its shape and the existence of a cubito-median fold we suppose it is a metathoracic wing (Figs 1–2). Costal margin in mid-wing straight, apex well rounded. Costal area strongly pectinate with wide-standing cross-veins. ScP– simple and most likely reaching costal margin. R stem proximally thick and strong, branching in proximal quarter of wing length. RA+ simple and generally straight, terminal development not well preserved but probably reaching costal margin in distal fifth. RP– well and strongly developed, with 9 terminal branches. MP– strong, with 5 terminal branches, first branching clearly before mid-wing and fanning at basal third of wing length, posterior branches with strongly curved backwards at posterior wing margin. Strong arculus (= cross-vein between MP– and CuA+) present in proximal eighth of the wing. CuA+ slightly reduced, slightly concave in the middle part before branching, with 3 terminal branches, all very strongly curved backwards. Well developed and probably sclerotizied cubito-median fold (between MP– and CuA+) running close to CuA+, especially in the proximal part. CuP– with 3 terminal branches, CuP_1– very strongly convex. First AA+ straight.

A number of thin and straight cross-veins mainly in the sectors of RP– and MP– and distal of mid-wing.

Etymology. Latin occultus, -a, -um (adjective) meaning arcane. The holotype specimen was stored for twenty years in the collection without being identified as a new species.

Discussion

Small basal Neoptera of the Late Carboniferous

Baryshnyala occulta **gen. et sp. n.** can be easily separated from all other Neoptera from Hagen-Vorhalle by its very small size (length: ≥9.6 mm, width: 4.2 mm). In comparison to other wings within this group the specimen is about half as long as *Heterologopsis ruhrensis* (length: ~25 mm, width: ~8 mm). *Holasicia rasnitsyni* (length: 36 mm, width: 13 mm) and *Kochopteron hoffmannorum* (length: 41 mm, width: 13 mm) are distinctly larger, and *Kemperala hagenensis* (length: 61 mm, width: 22 mm) is by far the largest species of basal Neoptera from Hagen-Vorhalle (Fig. 3). *Baryshnyala occulta* fits very well in this set of proportions: all species show a tendency towards a length/width ration about 3 (l/w = 2.8 in *B. occulta*). *K. hagenensis* and *K. hoffmannorum* seem to vary mostly in the wing length whereas the width is more consistent. In contrast, the wings of *H. rasnitsyni* vary more in their width and less in length. The variation in *H. ruhrensis* and *B. occulta* is unknown because they are monotypic.

Further small Late Carboniferous (Pennsylvanian) basal Neoptera from localities in northwestern Germany and thus close to Hagen-Vorhalle are for example (arranged by their stratigraphical age):

Metropatorites kassenbergensis Keller, 1934 (ord. et fam. inc. sed.), Namurian C (Bashkirian: Yeadonian): preserved length: 9 mm, estimated total length: ~22 mm, preserved width: 5 mm, estimated maximal width: ~9 mm.

Micropalentomum minusculum Schmidt, 1962 (Micropalentomidae), late Westphalian A (Bashkirian: Langsettian): length: ~3,5 mm [sic!], width: ~1 mm.

Eodelopterum priscum Schmidt, 1962 (Miomoptera: Archaemiopteridae), early Westphalian B (late Bashkirian: Duckmantian): length: <5 mm, width: ~2.3 mm.

Heterologellus teichmuellerae Schmidt, 1962 (Protophasmatidae), early Westphalian C (Moskovian: Bolsovian): length: ~18 mm, width: ~7 mm.

Controversala miomopteroides Brauckmann & Herd, 2005 (ord. et fam. inc. sed.), Westphalian D (late Moskovian): preserved length: 19 mm, estimated total length: ~20 mm, width: 8 mm.

Worldwide there are known many other small Neoptera from the Late Carboniferous and Permian. Especially Early Permian Protomeropidae Tillyard, 1926 are very small. For example *Westphalomerope maryvonneae* Nel et al., 2007 from the early Langsettian (Late Carboniferous: Bashkirian, Westphalian A) of France is twice smaller than *B. occulta*.

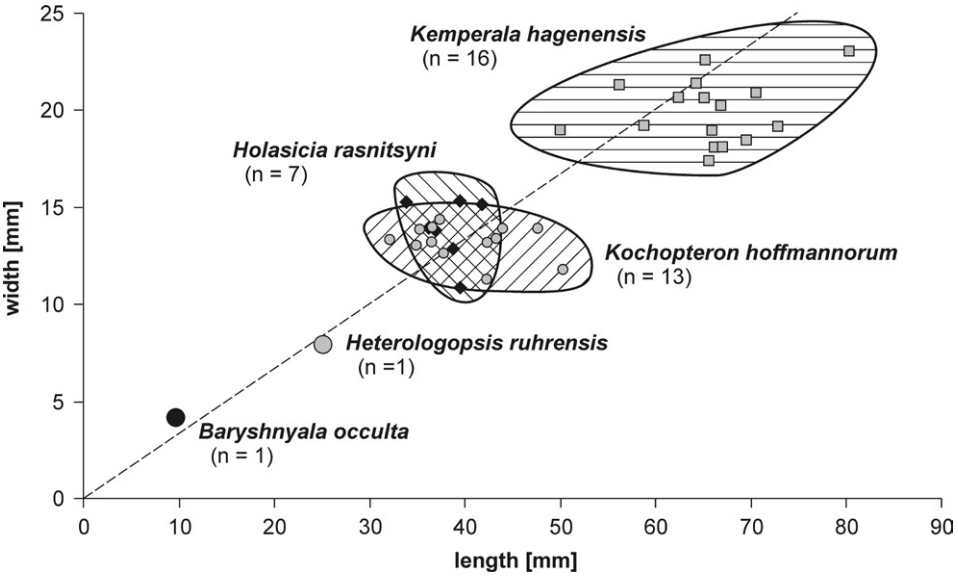

Figure 3. Synopsis of wing proportions in basal Neoptera from Hagen-Vorhalle. *Baryshnyala occulta* gen. et sp. n. fits very well in this set: all species show a tendency towards a length/width ration about 3 (dashed graph).

Most ancient representative of Holometabola?

The probably earliest evidence for holometabolous insects is a metathoracic wing of *Westphalomerope maryvonneae*. As the authors correctly pointed out, Holometabola lack a distinct synapomorphy in their wing venation pattern. The allocation to Endopterygota Sharp, 1898 is done by attribution of *W. maryvonneae* to a subgroup of this clade, e.g. the family Protomeropidae. An adapted diagnosis of the family is given by Sukatsheva (1976). The two main characters are (terminology changed to the scheme used in the present paper): (i) a brace (= arculus) between CuA+ and MP–, and (ii) a heavily sclerotizied convex fold in front of CuA+ (= cubito-median fold). Such fold is not restricted to Holometabola but can also be found e.g. in *Evenka archaica* Rasnitsyn, 1977 which is probably close related to Paoliidae. Furthermore an arculus is also widespread and can be found in Paoliidae and other groups as well.

Both species, *B. occulta* **gen. et sp. n.** and *W. maryvonneae*, share the following characters within the diagnosis by Kukalová-Peck and Willmann (1990; terminology here adapted): (i) narrow costal area, (ii) very narrow area between ScP– and RA+, (iii) arculus present (typical for Permian Protomeropidae but lacking in *W. maryvonneae*), (iv) well developed and prominent cubito-median fold, sub-parallel to $CuA_{(1)}$+, (v) branching of Cu close to wing base (this part of the wing is not preserved in *B. occulta* but can be extrapolated from the course of the preserved parts of CuA+ and CuP–), (vi) branched CuA+ (probably plesiomorphic).

W. maryvonneae is quite similar to other hindwings in Protomeropidae. *B. occulta* however differs from all Protomeropidae in the following characters: (i) ScP– reach-

ing anterior wing margin and probably distally not fused with RA+, (ii) CuA– not simple but with 3 terminal branches, and—probably most important character—(iii) CuP– branched as rich as CuA+, the first branch (CuP_1–) extremely curved backwards. The first character is regarded as an apomorphy of the Protomeropidae by Ivanov and Sukatsheva (2002), whereas Nel et al. (2007) assume it to be a plesiomorphy at the level of Holometabola or even the whole Pterygota. Other plesiomorphic characters of *B. occulta* are the rich branching of ScP– (with 8 anterior branches) and RP– (with 9 terminal branches). The rich branching of CuP– and backward-curving especially of CuP_1– is quite unique in Late Carboniferous basal Neoptera.

Therefore we conclude that *B. occulta* is vague related to the Protomeropidae but represents a separate new family of uncertain systematic placement. Both taxa might be stem group representatives of Endopterygota. In this case *B. occulta* would be the most ancient holometabolous insect.

Conclusions

The previously known species of Neoptera from Hagen-Vorhalle are of medium to rather large size. *Baryshnyala occulta* **gen. et sp. n.** shows that expanded and carefully directed prospection methods will increase the chance of also finding small insects. A similar conclusion is reached by Zessin et al. (2011).

Very small species and specimens are always in danger of being overlooked during their excavation and subsequent scientific handling. *B. occulta* **gen. et sp. n.** obviously differs from all other Neoptera and "Palaeoptera" species known from Hagen-Vorhalle by its small size and venation pattern.

Similarities in the venation pattern and the occurrence of a well developed cubitomedian fold indicate a systematic position distantly related to the family Protomeropidae but possibly within the Endopterygota. If so, this would date the first occurrence of holometaboly back to the Namurian B (early Bashkirian: Marsdenian).

B. occulta shows that the early Neoptera in general can be expected to be much more frequent and diverse than currently known. It is the fifth Neoptera species from this important paleo-ecosystem and enlarges the morphological range of this group. Up to now small Late Carboniferous Pterygota are generally rare, and each new specimen can be essentially important for the knowledge of their early evolution. Further examinations, even in already stored collections, are expected to yield surprising discoveries.

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RESEARCH ARTICLE

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Nobloedischia rasnitsyni, a new genus and species of Oedischiidae (Orthoptera) from the Lower Permian Wellington Formation of Oklahoma, USA

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Abstract

***Nobloedischia rasnitsyni* gen. et sp. n.** (Oedischiidae) is described from the Lower Permian Wellington Formation of Noble County, Oklahoma. The genus is similar to both *Petrelcana* (Oedischiidae: Mezenoedischiinae) and *Oedischia* (Oedischiidae: Oedischiinae) and is left unplaced at the subfamily level. The new species is the twelfth Orthoptera species and the fourth species of Oedischiidae from these deposits.

Keywords

Nobloedischia; fossil insect; Noble County; paleoentomology

Introduction

The Oedischiidae are considered to be the most basal family of orthopterans; they occurred from the Late Carboniferous through the Late Permian (Sharov 1971; Goro-

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chov 1987, 1995; Gorochov and Rasnitsyn 2002). For the most part, Oedischiidae are known only be their forewings; in the Carboniferous (Commentry, France) *Oedischia* Brongniart, 1885, the hind legs were saltatorial (Sharov 1971), and in the Lower Permian *Uraloedischia* Sharov, 1968 (Urals, Russia), prehensile spines on the legs and pointed denticles on the mandibles suggested oedischiids were predacious (Sharov 1971; Gorochov and Rasnitsyn 2002). The wing form and venation suggest they were active fliers (Sharov 1971). Besides *Oedischia*, a second Carboniferous genus, *Sinoedischia* Hong, 1985, is known from the Shanxi of China (Gorochov and Rasnitsyn 2002; Meng et al. 2006).

Oedischiids became more diverse in the Permian; known genera include *Afroedischia* Geertsema & van Dijk, 1999 (Middle–Upper Permian, South Africa. The Laingsburg Formation was dated as Lower Permian by Geertsema and van Dijk 1999, but is now dated as Middle–Upper Permian by Fildani et al. 2009.), *Iasvia* Zalessky, 1934 (Lower Permian, Russia, and Middle Permian, France; Béthoux et al. 2002), *Macroedischia* Sharov, 1968, *Tettoedischia* Sharov, 1968, and *Uraloedischia* Sharov, 1968 from the Lower Permian (Kungurian) of Russia, *Metoedischia* Martynov, 1928, *Elcanoedischia* Gorochov, 1987, and *Mezenoedischia* Gorochov, 1987 from the Middle Permian (Kazanian) of Russia, and, from the Lower Permian Wellington Formation of the United States, in subfamily Elcanoedischiinae Gorochov, 1987: *Kansasoedischia* Gorochov, 1987 (Kansas), and in Mezenoedischiinae Gorochov, 1987: *Petrelcana* Carpenter, 1966 (Kansas), and *Pseudoiasvia* Bethoux & Beckemeyer, 2007 (Oklahoma).

Of the more than 200 species of insects known from the Lower Permian Wellington Formation of Kansas and Oklahoma, USA (Beckemeyer and Hall 2007), eleven are in the order Orthoptera: eight from the Elmo, Kansas deposits (Tillyard 1932; 1937; Carpenter 1943, 1966; Gorochov 1987), and three from the Midco, Oklahoma (Noble County) formations. Four of the eleven species, one from Kansas and three from Oklahoma, were described only recently (Béthoux and Beckemeyer 2007; Beckemeyer 2011). The new taxon described here constitutes the tenth genus and twelfth species of Wellington Formation Orthoptera (see Beckemeyer 2011 for a list of previously described species). It seems most closely related to *Oedischia* and *Petrelcana*.

Materials and methods

This description is based on a forewing specimen (Figs 1, 2) collected by Don Arnold and Rick Grantham of Oklahoma State University (OSU). The holotype is in the K. C. Emerson Museum, Department of Plant Pathology and Entomology, OSU. The specimen comprises part and counterpart of a nearly complete wing, absent approximately the basal 20% of the wing length (including the precostal area), the anal field, and the posterior margin of the cubital field; cross veins are poorly preserved in the distal radial and medial fields.

Photomicrographs of the part and counterpart were made using a Nikon 990 digital camera with an American Optical dissecting microscope and an external strobe

flash (Nikon SB-26). Flash orientation was optimized to show details of interest. The photographed images were processed using Adobe Photoshop 6.0 and imported into a vector-graphics software program (XARA Extreme 4.0, XARA Group, Ltd., London), where they were assembled into composite images. The venation reconstruction drawing was made as an overlay (Fig. 3).

Venation interpretation and notation follow the system of Béthoux and Nel (2001, 2002). Since that system is relatively new, not uniformly accepted, and not in as wide use as the terminology of Sharov (1971), Gorochov (1987, 1995), Carpenter (1992), and Gorochov and Rasnitsyn (2002), I list here the relationship between the most common notation systems:

Béthoux and Nel	**Sharov/ Gorochov**	**Carpenter**	**Gorochov and Rasnitsyn**
ScP	Sc	SC	SC
RA	RA	R	R_1
RP	RS	RS	RS
MA1	$1MA_1$	MA1	MA_1
MA2	$2MA_1$	MA2	MA_2
MP	MA_2	MP	MP
CuA+CuPaα	$MP+CuA_1$	CuA	M_5+CuA_1
CuPaβ	CuA_2	CuA	CuA_2
CuPb	CuP	CuP	CuP

Systematic paleontology

Order Orthoptera Olivier, 1789
Family Oedischiidae Handlirsch, 1906

***Nobloedischia* Beckemeyer, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Nobloedischia

Composition. Type species *Nobloedischia rasnitsyni* Beckemeyer, sp. n.

Etymology. A combination of Noble County and the family name Oedischiidae.

Diagnosis. *Nobloedischia* is differentiated from *Oedischia* by branches of RA directed distally, first branching of RA at level of fusion of MA1 and RP; fusion of RP and MA1 (the anterior branch of MA) long rather than limited to a point of contact; field between MP and CuA+CuPaα narrower than area between MP and MA/MA2 at least in basal 2/3 of length; CuA+CuPaα and its branches reach posterior wing margin obliquely.

Differs from *Petrelcana* by width of costal and subcostal fields at level of branching of M about equal rather than costal field much wider than subcostal field; cross veins between RA and RP without secondary cross veins; branching of MA moderately remote from anastamosis with RP (as in Gorochov 1995, Fig. 142) rather than MA

branching close to fusion with RP, stem of MA1 before fusion an obvious branch of the longitudinal vein rather than this segment of MA1 very short and appearing as a thickened cross vein between MA/MA2 and RP+MA1 (as in Gorochov 1995, Fig. 144; stems of CuA and CuPaα about equal rather than stem of CuA very short.

Nobloedischia rasnitsyni **Beckemeyer, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Nobloedischia_rasnitsyni
Figs 1–3

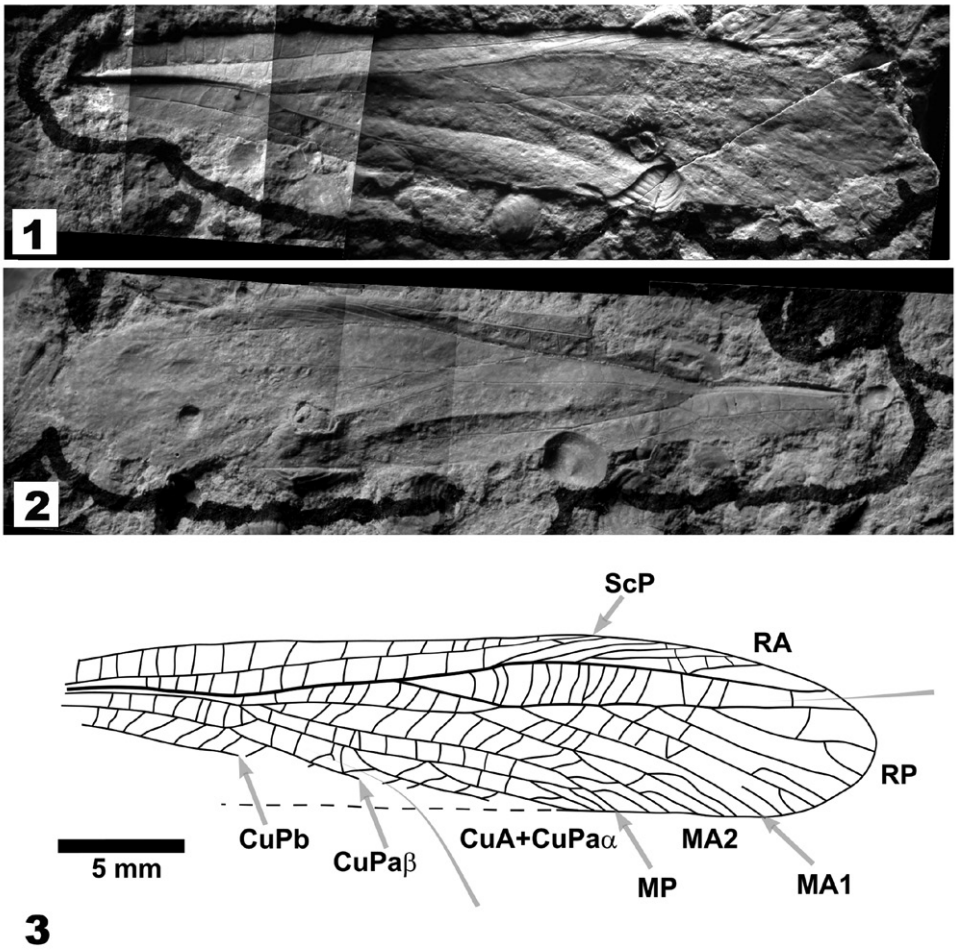
Type locality. Noble County, Oklahoma, USA; Wellington Formation, Artinskian, Lower Permian.

Type material. Holotype: Oklahoma State Museum Fossil Insect Specimen No. 826a, part (Fig. 1) and 826b, counterpart (Fig. 2), comprising the only Orthoptera fossil on slabs densely covered with multiple insect wing fragments of varied orders and with Conchostraca fossils as well. The slab containing 826a is approximately 12 by 21 cm and contains a total of 88 insect specimens (818a through 905a); the second slab (8 by 17 cm) contains 78 insect specimens (818b through 896b).

Etymology. The specific epithet, *rasnitsyni*, is an honorific for eminent scientist Dr. Alexandr P. Rasnitsyn in recognition of his long and productive career, and his invaluable and varied contributions to paleoentomology.

Diagnosis. As for genus.

Description. Forewing. Preserved length 32 mm, estimated length 39 mm (basal 20%, including precostal area, missing); width 7 mm. ScP terminates at 78% wing length, cross veins simple, moderately spaced, and oriented normal to costal margin and ScP, maximum width of costal field 1.4 mm, maximum width of subcostal field 1.0 mm, ratio width of subcostal to width of costal field 1.4:1. RA sigmoidal in form, bending anteriorly at level of separation of Cu and M (35% of wing length), bending posteriorly at level of fusion of MA and RP, where RA branches; RA branching anteriorly pectinate, six branches reaching wing margin, basal branches intersecting margin obliquely, distal branches nearly longitudinal in orientation; posterior–most branch of RA terminating at 95% wing length; cross veins between ScP and RA similar in form and spacing to those between ScP and costal margin. RP origin at 51% wing length; RP fusion with MA1 at 62% of wing length, length of fusion 0.9 mm; RP with four posteriorly pectinate branches, simple or distally twigged, first branch at 72% wing length, anterior–most branch straight and terminating near apex of wing at 98% wing length; cross veins between RA and RP with veins simple, some bowed with center of curvature basal. M+CuA branches at 35%, M branches at 37%, length of M from separation from M+CuA to branch 0.9 mm, MA branches at 59%, MA2 branches at 69% of wing length each branch with terminal twig, MA1 apparently simple, terminating at 89%, free length of MA1 before fusion with RP 1.0 mm. MP distally twigged, terminating on posterior margin at 74% and



Figures 1–3. *Nobloedischia rasnitsyni* gen. et sp. n. **1.** Holotype specimen, part, OSU826a. Forewing in dorsal aspect **2.** Holotype specimen, counterpart, OSU826b. Forewing in ventral aspect **3.** Venation reconstruction and notation following Béthoux and Nel 2002. Photographs and drawing to same scale; scale bar 5 mm.

77% wing length. CuA+CuPaα with four branches; the basal branches of CuA+CuPaα intersect the posterior margin obliquely, with the angle between the branches and the wing margin increasing distally (angles of intersection are 12°, 13°, 23°, and 32°, for the successive branches); CuPa branches at 34% of the wing length, free length of CuPaα before fusion with CuA 1.1 mm, length of CuA from separation from M+CuA to fusion with CuPaα 0.9 mm, CuPaβ straight as preserved, cross veins between CuPaβ and CuA+CuPaα normal to the longitudinal veins, becoming oblique and oriented longitudinally after the first branching of CuA+CuPaα; short segment of CuPb that is preserved (extending from 20% to 35% of wing length) is straight; anal veins not preserved.

Discussion

The combination of character states of *N. rasnitsyni* make placement in one of Gorochov's subfamilies somewhat problematic; it would perhaps come closest to fitting in Oedischiinae. *Nobloedischia* shares with *Oedischia* the characters: origin of anterior branch of MA moderately remote from its anastamosis with RP (as in Gorochov 1995: Fig. 142); distance from branching of M+CuA to branching of M subequal to distance from branching of M+CuA to fusion of CuA and CuPaα, and greater than length of cross veins between CuA+CuPaα and MP; ratio of width of costal field (anterior margin–ScP) to width of subcostal field (ScP–RA) less than 1.5; field between RA and RP with some cross veins bowed and/or sigmoidal rather than straight; CuPaα medium sized basal of its fusion with CuA (last three characters were used by Béthoux and Nel 2002, to distinguish the clade (*Gerarus bruesi* Meunier, 1909 + *O. williamsoni*)). On the other hand, *Nobloedischia* is differentiated from *Oedischia* by the characters listed in the Diagnosis (vide supra). Béthoux and Nel (2002) used a total of 74 characters in their cladistic phylogenetic analysis of the Orthoptera; I have not repeated that analysis, but did code the characters and found that of the 61 character states that could be compared (the remaining characters were not preserved in available specimens of one or the other of the taxa) between *Nobloedischia* and *Oedischia*, 52 matched and 9 did not.

For the other oedischiids, the next closest pairing was between *Nobloedischia* and *Elcanoedischia*, with 45 of 58 character states matching. However, *Nobloedischia* differs from genera in Elcanoedischiinae Gorochov 1987 by branching of MA moderately remote from anastamosis with RP (as in Gorochov 1995: Fig. 142) rather than MA branching close to fusion with RP, with this short segment of MA appearing as a thick cross vein between MA/MA2 and RP+MA1 (as in Gorochov 1995: Fig. 144). *Nobloedischia* can be differentiated from genera in Tettoedischiinae Gorochov, 1987 by costal field not greatly wider than subcostal field; base of MP well basal rather than at or distal to base of RP; branching of CuPb basal rather than distal to branching of M+CuA. *Nobloedischia* differs from genera in Mezenoedischiinae by the features listed in the Diagnosis section for *Petrelcana* (vide supra). Because of the presence of these conflicting character states, at this point I prefer to leave the subfamilial assignment undetermined.

The high number of densely distributed specimens (wings and wing fragments) present on the slabs containing this species seems to support Hall's (2004) thesis that the Oklahoma Wellington Formation insect deposit facies are derived from marginal marine lagoon sediments, with insect remains likely comprised of allochthonous material washed in by streams.

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RESEARCH ARTICLE

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Review of the Permian family Permulidae nomen novum pro Aliculidae Storozhenko, 1997 (Grylloblattida)

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Abstract

A new replacement name Permulidae **nom. n.** is proposed for the Permian family Aliculidae Storozhenko, 1997 (Insecta: Grylloblattida). A review of Permulidae is given. All genera and species are redescribed and illustrated. A key to genera of Permulidae is given. New taxa of Permulidae are described: *Permula edemskii* **sp. n.**, *Sojanopermula rasnitsyni* **sp. n.**, *Kazanalicula reducta* **gen. et sp. n.**, *Mezenalicula connata* **gen. et sp. n.**, all from the Soyana locality (Middle Permian, Kazanian Stage; Arkhangelsk Region, Russia), and *Mezenalicula conjuncta* **sp. n.** from the Isady locality (Upper Permian, Severodvinian Stage; Vologda Region, Russia). New combinations are proposed: *Sojanopermula minor* Aristov, 2004 = *Permula minor* (Aristov, 2004), **comb. n.**; *Sojanopermula tshekardensis* Aristov, 2004 = *Permula tshekardensis* (Aristov, 2004), **comb. n.** A new genus *Acropermula* **gen. n.** (type species: *Permula acra* Kukalová, 1964, from the Lower Permian of Czech Republic) is established in the family Ideliidae. *Neraphidia* Novokshonov & Novokshonova, 1997 is transferred from Aliculidae to the order Eoblattida as a genus of uncertain taxonomic position inside this order.

Keywords

Grylloblattida, Permulidae, Aliculidae, Ideliidae, Eoblattida, taxonomy, key, new taxa, Permian, Europe, North America

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Introduction

Family Aliculidae was established for two genera of the Permian Grylloblattida characterized by distinct narrowing of the costal area in the forewing base and by CuA not dividing into CuA1 and CuA2 (Storozhenko 1997). Originally it included the Lower Permian *Alicula lebachensis* Schlechtendal, 1913 from the Saar-Nahe Basin in Germany, *A. acra* (Kukalová 1964) from the Obora locality in Czech Republic, the Upper Permian *A. asiatica* Storozhenko, 1997 from the Karaungir-II locality in Kazakhstan, and the Middle Permian *Sojanopermula lucida* Storozhenko, 1992 from the Soyana locality in Russia. Aristov (2004a) described in Aliculidae two new species (*Sojanopermula minor* Aristov, 2004, *S. tshekardensis* Aristov, 2004) and one monotypic genus (*Neprotembia truncata* Aristov, 2004) from the Lower Permian Tshekarda locality in Russia, and transferred to family Aliculidae the genus *Neraphidia* Novokshonov & Novokshonova, 1997, originally described in the family Protembiidae (Novokshonov and Novokshonova 1997). At the same time he re-examined the holotype of *Alicula asiatica* and placed this species in the genus *Metidelia* Martynov, 1937 of the family Ideliidae (Aristov 2004b). *Neprotembia complicata* Aristov, 2005 was described from the Lower Permian Vorkuta locality in Russia (Rasnitsyn et al, 2005). The genus *Elmopterum* with a single species *Elmopterum rotundum* Béthoux & Beckemeyer, 2007 from the Lower Permian Elmo locality in the USA, originally described as Grylloblattida incertae sedis (Béthoux and Beckemeyer 2007), was placed in Aliculidae by Aristov (2009). Finally *Tshepanichoptera lacera* Aristov, 2008 was described from the Middle Permian Chepanikha locality in Russia (Aristov and Bashkuev 2008). Thus, the composition and conception of family Aliculidae are changed considerably during last ten years and a critical examination of this family is necessary. Moreover, the family name Aliculidae Storozhenko, 1997 was based on *Alicula* Schlechtendal, 1913, a junior homonym of *Alicula* Eichwald, 1830 in Mollusca. So, this generic name must be replaced by the synonymic name *Permula* Handlirsch, 1919, and the family name Aliculidae by Permulidae nom. n.

A review of the family Permulidae nom. n. is given below. Two new genera and five new species are described. The keys to genera and to species of each genus are given based on forewing characters. In addition the taxa previously erroneously included in Permulidae are listed, and a new genus of family Ideliidae is established.

Material

All studied material including the holotypes of new species is deposited in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN).

The vein symbols are as follows: **C** costa, **SC** subcosta, **R** stem of radius, **RA** radius anterior, **RS** radius sector (= radius posterior), **M** stem of media, **MA** media anterior, **MP** media posterior, **M5** strong oblique vein between stems of media and cubitus, **Cu** stem of cubitus, **CuA** cubitus anterior, **CuA1** first cubitus anterior (if CuA distinctly

forked into branched first and simple second veins), **CuA2** second cubitus anterior, **CuP** cubitus posterior, **A1** first anal, **A2** second anal vein.

Taxonomy

Order Grylloblattida Walker, 1914
Suborder Protoperlina Brongniart, 1885

Family Permulidae Aristov & Storozhenko, nom. n.
http://species-id.net/wiki/Permulidae

Type genus. *Permula* Handlirsch 1919.

Aliculidae Storozhenko, 1997: 8 (type genus: *Alicula* Schlechtendal, 1913); Storozhenko 1998: 97. Invalid name according to Article 39 of the Code (ICZN, 1999).

Diagnosis. In Permulidae CuA is either simple or branching distal of its middle and CuA2 not individualized. In other families of the order Grylloblattida either the first fork of CuA is situated near the base, or CuA1 and CuA2 are well individualized.

Description. Medium-sized insects. Forewing uncolored, without spots and stripes. Costal area narrow to broad. SC ending near the apical third of wing or apically. RS originates in basal third or quarter of wing. The base of M and CuA distinctly separated or fused. M forked distinctly before or near the base of RS. MA simple or branched. MP desclerotized near the middle of wing. M5 not individualized. CuA not divided into CuA1 and CuA2, CuA is branched distal of its middle, with 2–4 branches, distal branches of CuA not parallel to posterior margin of wing, rare CuA simple. CuP simple, straight or gently curved. A1 simple. Cross-veins either simple or forming two or more rows of cells in the majority of areas. Hind wing similar to forewing but anal area enlarged. Body unknown.

Composition. Seven genera are known from the Permian of Europe and North America, two of them are described as new below.

Notes. The generic name *Alicula* Schlechtendal, 1913 (Insecta) is a junior homonym of *Alicula* Eichwald, 1830 (Mollusca). The name *Alicula* Schlechtendal, 1913 must be replaced by *Permula* Handlirsch 1919 (the next oldest available name from among its synonyms). Thus, the family name Aliculidae Storozhenko, 1997 must be replaced by a new replacement name Permulidae based on the valid name of the former type genus according to Article 39 of the Code (ICZN, 1999).

Key to genera of Permulidae

1(10) The basal portion of M distinctly separated from CuA.
2(5) Costal area distinctly broader than subcostal one.
3(4) The basal portion of costal area broadly rounded, without an abrupt narrowing ..... ***Permula***

4(3) Costal area distinctly narrowing in its basal portion ..... ***Sojanopermula***
5(2) Costal area narrower than or as broad as subcostal one.
6(7) CuA simple..... ***Kazanalicula* gen. n.**
7(6) CuA with two branches.
8(9) The base of anterior branch of CuA distinctly sclerotized..... ***Elmopterum***
9(8) The base of anterior branch of CuA desclerotized..... ***Tshepanichoptera***
10(1) The basal portion of M fused with CuA completely or at certain distance.
11(12) First fork of CuA situated distinctly proximal to main fork of M. Costal area with a row of simple or bifurcated anterior branches of SC..... ..... ***Mezenalicula* gen. n.**
12(11) First fork of CuA situated near to main fork of M. Anterior branches of SC form double row of cells near the middle of costal area ..... ***Neprotembia***

***Permula* Handlirsch, 1919, nom. resurr.**
http://species-id.net/wiki/Permula

Alicula Schlechtendal 1913: Pl. 2, figs. 10a, b (type species: *Alicula lebachensis* Schlechtendal, 1913, by monotypy); Carpenter 1992: 109 (partim); Storozhenko 1998: 97 (partim). Invalid name according to Article 56 of the Code (ICZN, 1999).
Permula Handlirsch 1919: 32 (type species: *Permula lebachensis* Handlirsch, 1919, by original designation); Handlirsch 1922: 77; Kukalová 1964: 46, 47 (partim).

Description. The base of costal area in forewing broadly rounded; costal area is considerably broader than subcostal one, crossed with simple or furcated anterior branches of SC; RA simple; RS with more than two branches; the base of M distinctly separated from CuA; M forked before the base of RS; CuA with 2–4 branches, first fork of CuA is situated proximal to fork of M; the base of anterior branch of CuA sclerotized; CuP curved or straight; A1 and A2 simple.

Composition. Four species from the Lower and Middle Permian of Europe.

Notes. Apparently being unaware of Schlechtendal's paper, Handlirsch (1919) described *Permula lebachensis* as a new genus and species based on the same specimen as *Alicula lebachensis* Schlechtendal, 1913. Later Carpenter (1992) synonymized *Permula lebachensis* Handlirsch, 1919 with *Alicula lebachensis* Schlechtendal, 1913 and included *Permula acra* Kukalová, 1964 in the genus *Alicula*. But the generic name *Alicula* Schlechtendal, 1913 is a junior homonym of *Alicula* Eichwald, 1830 and must be replaced by *Permula* Handlirsch 1919. Herein two species are transferred from *Sojanopermula* to *Permula* based on the shape of costal area and one new species is described. Moreover, *Permula acra* Kukalová, 1964 is not congeneric with other species of *Permula* and is placed in a new genus of the family Ideliidae (see below).

Key to species

1(4) CuA with three or four branches.
2(3) Anterior margin of wing straight; CuA with four branches ..... ***Permula lebachensis***
3(2) Anterior margin of wing convex; CuA with three branches ..... ***Permula tshekardensis* comb. n.**
4(1) CuA with two branches.
5(6) Cross-veins simple or forming a double row of cells in the areas between RA and RS, between MP and CuA, and between CuA and CuP..... ***Permula minor* comb. n.**
6(5) Cross-veins forming numerous rows of cells in all areas..... ***Permula edemskii* sp. n.**

***Permula lebachensis* (Schlechtendal, 1913)**
http://species-id.net/wiki/Permula_lebachensis
Fig. 1

Alicula lebachensis Schlechtendal 1913: Pl. 2, figs. 10a, b (holotype – fragment of the basal portion of forewing; drawing by Schlechtendal in Handlirsch 1906–1908: 348, tab. 34, fig. 34; depositary unknown; not studied); Carpenter 1992: 109; Storozhenko 1998: 97, fig. 181.
Permula lebachensis Handlirsch 1919: 32; Handlirsch 1922: 77; Kukalová 1964: 46, 47. Synonymized by Carpenter 1992: 109.

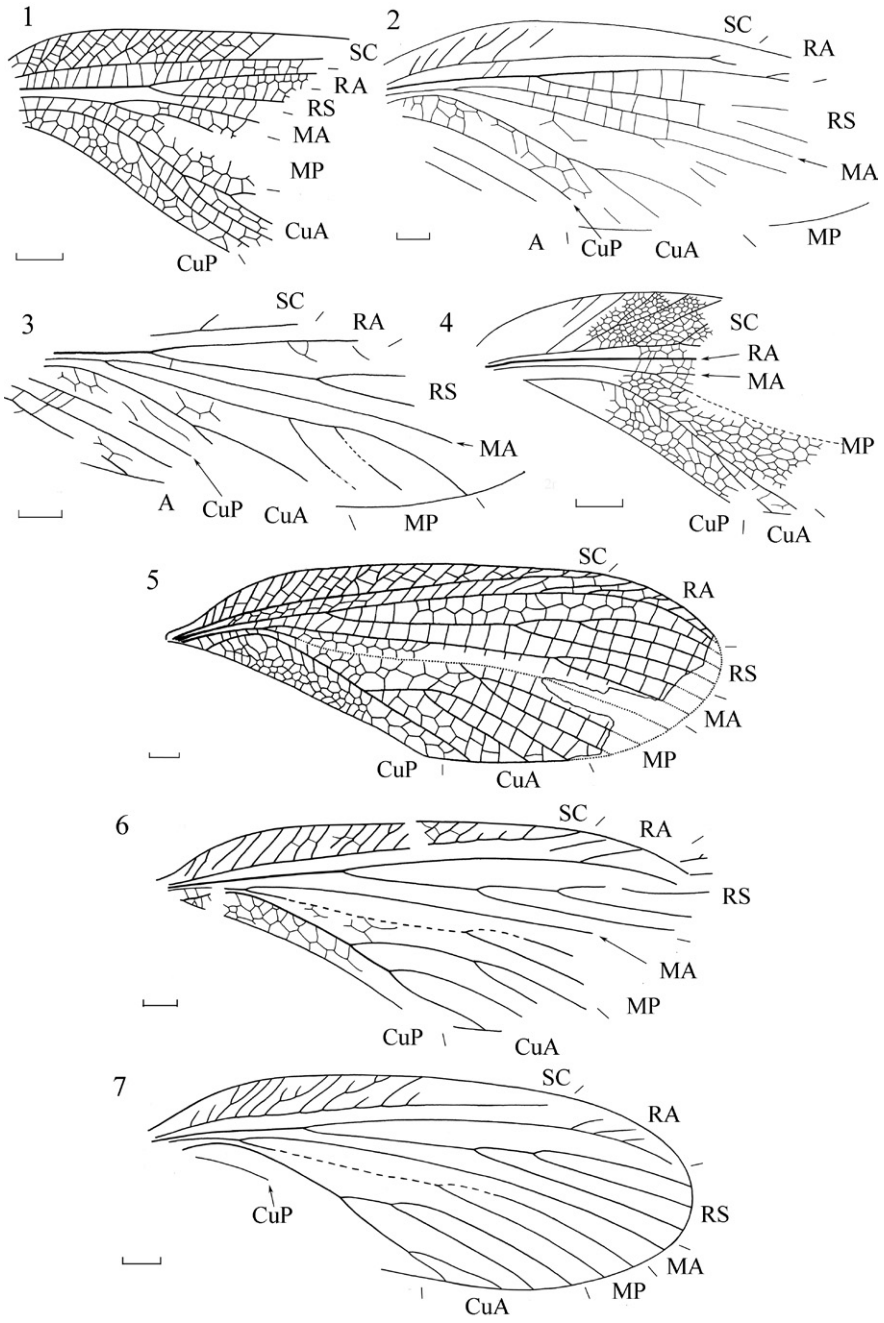
Horizon. Asselian Stage, Lebacher Schichten (the Lower Permian).

Locality. Lebach locality, Saar-Nahe Basin, Saarland, Germany.

Description. Anterior margin of forewing gently convex; costal area as broad as intercubital one; RS distinctly separated from MA; MP forked; CuA with four branches; CuP curved; cross-veins in almost all areas forming a row of two cells, cross-veins simple in the basal portion of areas between SC and R, and between M and CuA, cross-veins forming rows of three cells in the basal portion of intercubital area.

Measurements. Length of forewing about 25 mm.

Notes. *Permula lebachensis* Handlirsch 1919 is an objective synonym of *Alicula lebachensis* Schlechtendal 1913 because the descriptions of both species are based on the same specimen.



Figures 1–7. Forewings of Permulidae **1** *Permula lebachensis* Schlechtendal (after Handlirsch 1906–1908) **2** *P. tshekardensis* Aristov (holotype PIN 1700/1151, after Aristov 2004) **3** *P. minor* Aristov (holotype PIN 1700/4934, after Aristov 2004) **4** *P. edemskii* sp. n. (holotype PIN 94/1027, orig.) **5** *Sojanopermula lucida* Storozhenko (holotype PIN 94/117, after Storozhenko 1992) **6** *S. rasnitsyni* sp. n. (holotype PIN 117/301, orig.) **7** *S. rasnitsyni* sp. n. (paratype PIN 117/195, orig.). Scale bars 2 mm.

***Permula tshekardensis* (Aristov, 2004), comb. n.**
http://species-id.net/wiki/Permula_tshekardensis
Fig. 2

Sojanopermula tshekardensis Aristov 2004a: 107, fig. 10a (holotype – positive imprint of incomplete forewing; PIN 1700/1151; examined).

Material. Holotype only.

Horizon. Kungurian Stage, Koshelevka Formation (the Lower Permian).

Locality. Tshekarda locality, Krasnaya Gora Mountain on the left bank of Sylva River near the Tshekarda village, Suksun District, Perm Region, Russia.

Description. Anterior margin of forewing convex; SC reaching the apical quarter of wing; costal area distinctly broader than intercubital one; RS with more than two branches, distinctly separated from MA; MA simple or bifurcate near the apex of forewing; MP with three or four branches directed to the posterior margin of wing; CuA with three branches; CuP curved; A1 and A2 straight and simple; cross-veins are simple or forming a double row of cells in the areas between MP and CuA, and between CuA and CuP.

Measurements. Length of forewing 30 mm.

***Permula minor* (Aristov, 2004), comb. n.**
http://species-id.net/wiki/Permula_minor
Fig. 3

Sojanopermula minor Aristov 2004a: 107, fig. 10b (holotype – positive and negative imprints of incomplete forewing; PIN 1700/4934; examined).

Material. Holotype only.

Horizon. Kungurian Stage, Koshelevka Formation (the Lower Permian).

Locality. Tshekarda locality, Krasnaya Gora Mountain on the left bank of Sylva River near the Tshekarda village, Suksun District, Perm Region, Russia.

Description. RS with more than two branches, distinctly separated from MA; MA simple or probably with short terminal fork; MP with three branches sharply turning towards the posterior margin of wing; CuA with two branches; CuP straight; A1 and A2 simple and straight; cross-veins are simple or forming a double row of cells.

Measurements. Length of forewing about 23 mm.

***Permula edemskii* Aristov & Storozhenko, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Permula_edemskii
Figs 4, 15

Material. Holotype PIN 94/1027, positive and negative imprints of an incomplete forewing.

Type horizon. Kazanian Stage, Lower Kazanian Substage, Iva-Gora Beds (the Middle Permian).

Type locality. Soyana locality, right bank of the Soyana River 56–60 km upstream of the mouth, Mezen District, Arkhangelsk Region, Russia.

Description. Anterior margin of forewing distinctly convex; costal area considerably broader than intercubital one; R distinctly separated from M; CuA with two branches; CuP straight; cross-veins forming numerous rows of cells in all areas.

Measurements. Length of forewing about 30 mm.

Etymology. The new species is named in honor of the Russian geologist M.B. Edemsky, who collected the type specimen.

***Sojanopermula* Storozhenko, 1992**
http://species-id.net/wiki/Sojanopermula

Sojanopermula Storozhenko 1992: 217 (type species: *Sojanopermula lucida* Storozhenko, 1992, by original designation); Storozhenko 1998: 98.

Description. The base of costal area in forewing distinctly narrowing; costal area is broader than subcostal one, crossed with simple or furcated anterior branches of SC; RA simple; RS originated in the basal quarter of the wing, with three branches; the base of M distinctly separated from CuA; M forked before the origin of RS; CuA with three or four branches, first fork of CuA is situated distinctly proximal to fork of M; the base of anterior branch of CuA sclerotized; CuP straight.

Composition. Two species from the Middle Permian of Europe.

Key to species

1(2) CuA with three branches. Costal area as broad as intercubital area..... ***Sojanopermula lucida***

2(1) CuA with four branches. Costal area distinctly broader than intercubital one... ***Sojanopermula rasnitsyni* sp. n.**

***Sojanopermula lucida* Storozhenko, 1992**
http://species-id.net/wiki/Sojanopermula_lucida
Fig. 5

Sojanopermula lucida Storozhenko 1992: 218, fig. 18 (holotype – positive imprint of forewing without apical part and anal area; PIN 94/117; examined); Storozhenko 1998: 98, fig. 184.

Material. Holotype only.

Horizon. Kazanian Stage, Lower Kazanian Substage, Iva-Gora Beds (the Middle Permian).

Locality. Soyana locality, right bank of the Soyana River 56–60 km upstream of the mouth, Mezen District, Arkhangelsk Region, Russia.

Description. Anterior margin of forewing straight; SC reaching apical one fifth of the wing; costal area as broad as intercubital one; RS distinctly separated from MA; MA with fork; MP with three branches; CuA with three branches; cross-veins in the almost all areas simple, but forming a row of two cells in the area between RA and RS, in the basal portion of areas between MA, MP and CuA, and between branches of CuA; in the intercubital area cross-veins forming numerous rows of cells.

Measurements. Length of forewing about 34.6 mm.

***Sojanopermula rasnitsyni* Aristov & Storozhenko, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Sojanopermula_rasnitsyni
Figs 6, 7, 16, 17

Material. Holotype PIN 117/301, positive imprint of incomplete forewing. Paratype PIN 117/195, positive imprint of forewing without anal area.

Type horizon. Kazanian Stage, Lower Kazanian Substage, Iva-Gora Beds (the Middle Permian).

Type locality. Soyana locality, right bank of the Soyana River 56–60 km upstream of the mouth, Mezen District, Arkhangelsk Region, Russia.

Description. Anterior margin of forewing straight; SC reaching apical quarter or one fifth of wing; costal area distinctly broader than intercubital area; RS separated from MA; MA simple; MP with two branches; CuA with four branches; cross-veins in the almost all areas simple, but forming a row of two cells in the basal portion of area between MP and CuA; in the intercubital area cross-veins forming two or three rows of cells.

Measurements. Length of forewing about 30 mm.

Etymology. The new species is named in honor of the Russian paleoentomologist Prof. A.P. Rasnitsyn.

Kazanalicula **Aristov & Storozhenko, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Kazanalicula

Type species. *Kazanalicula reducta* Aristov & Storozhenko, **sp. n.**

Diagnosis. Similar to *Elmopterum* and *Tshepanichoptera* by the narrow costal area, but distinct from these in the simple CuA.

Description. The base of costal area in forewing gentle rounded; costal area is narrower than subcostal one, crossed with simple anterior branches of SC; RA simple; RS originated in the basal third of the wing, with two branches; the base of M distinctly separated from CuA; M forked slightly before the base of RS; CuA simple; CuP straight; A1 simple, A2 furcated.

Composition. One species from the Middle Permian of Europe.

Etymology. After the name of the Kazanian Stage and genus *Alicula*; gender feminine.

Kazanalicula reducta **Aristov & Storozhenko, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Kazanalicula_reducta
Figs 8, 18

Material. Holotype PIN 117/467, positive imprint of forewing without apical portion.

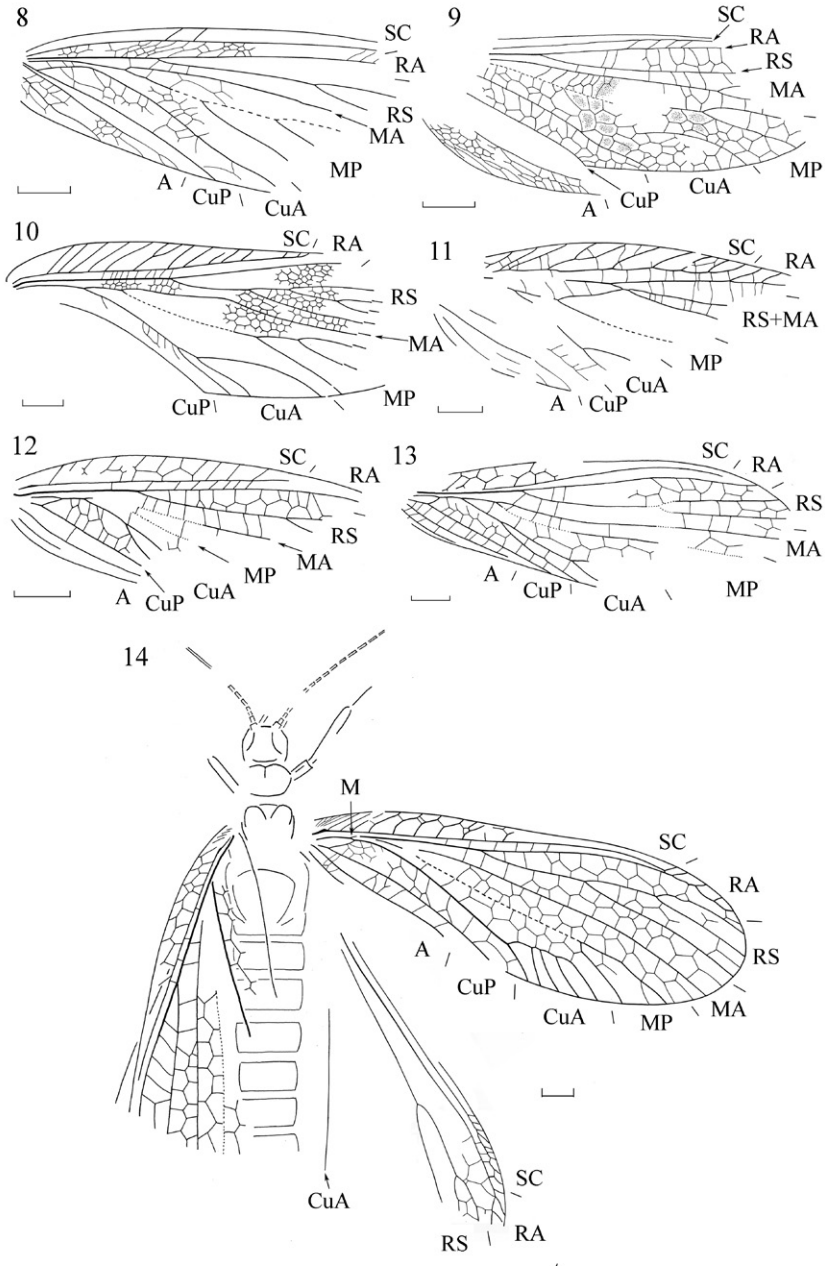
Type horizon. Kazanian Stage, Lower Kazanian Substage, Iva-Gora Beds (the Middle Permian).

Type locality. Soyana locality, right bank of the Soyana River 56–60 km upstream of the mouth, Mezen District, Arkhangelsk Region, Russia.

Description. Anterior margin of forewing weakly convex; costal area 2.5 times narrower than intercubital one; RS distinctly separated from MA; MA simple; MP with three branches directed to the posterior margin of wing; CuA simple; cross-veins in almost all areas forming a double row of cells.

Measurements. Length of forewing about 20 mm.

Etymology. From Latin *reductus* (distant).



Figures 8–14. Forewings of Permulidae and Eoblattida incertae sedis **8** *Kazanalicula reducta* sp. n. (holotype PIN 117/467, orig.) **9** *Tshepanichoptera lacera* Aristov (holotype PIN 3286/14, after Aristov and Bashkuev 2008) **10** *Mezenalicula connata* sp. n. (holotype PIN 94/883, orig.) **11** *M. conjuncta* sp. n. (holotype PIN 3840/1243, orig.) **12** *Neprotembia truncata* Aristov (holotype PIN 1700/1026, after Aristov 2004) **13** *N. complicata* Aristov (holotype PIN 1631/314, after Rasnitsyn et al. 2005) **14** *Neraphidia mitis* Novokshonov & Novokshonova (orig. reconstruction based on holotype PIN 1700/643 and spec. PIN 4987/10). Scale bars 2 mm.

Elmopterum Béthoux & Beckemeyer, 2007

http://species-id.net/wiki/Elmopterum

Elmopterum Béthoux and Beckemeyer 2007: 55 (type species: *Elmopterum rotundum* Béthoux & Beckemeyer, 2007, by monotypy); Aristov 2009: 37.

Description. In forewing costal area as broad as subcostal one, crossed with simple anterior branches of SC; RA simple; RS originated in the basal third of the wing, with three or four branches; M forked distinctly before the base of RS; CuA with two branches, fork of CuA is situated distinctly proximal to fork of M; the base of anterior branch of CuA sclerotized; CuP straight; several branches of anal veins reaching posterior wing margin. In hind wing RA simple, RS dichotomously branched, with four branches; M branched distal of the first fork of RS.

Composition. One species from the Lower Permian of North America.

Elmopterum rotundum Béthoux & Beckemeyer, 2007

http://species-id.net/wiki/Elmopterum_rotundum

Elmopterum rotundum Béthoux and Beckemeyer 2007: 55, fig. 5 (holotype – positive and negative imprints of an incomplete individual; MCZ 7468 and MCZ 7469; deposited in the Museum Comparative Zoology, Cambridge, USA; not examined).

Horizon. Leonardian Stage, Wellington Formation (the Lower Permian).

Locality. Elmo locality, Kansas, USA.

Description. Anterior margin of forewing weakly convex; SC reaching the apical one fifth of the wing; costal area as broad as intercubital one; RS distinctly separated from MA; MA simple or with two branches directed to the apex of wing; MP with three branches directed to the posterior margin of wing; CuA with two branches; crossveins in almost all areas forming a double row of cells.

Measurements. Length of forewing about 18 mm.

Tshepanichoptera Aristov, 2008

http://species-id.net/wiki/Tshepanichoptera

Tshepanichoptera Aristov in Aristov and Bashkuev 2008: 57 (type species: *Tshepanichoptera lacera* Aristov, 2008, by original designation).

Description. In forewing costal area narrow, as broad as subcostal one; anterior branches of SC absent; RA simple; RS originated in the basal third of the wing, simple; M forked distinctly basally to main fork of R; CuA with two branches, the fork of

CuA is situated distinctly proximal to fork of M; the base of anterior branch of CuA desclerotized; CuP straight; A1 simple, A2 reduced.

Composition. One species from the Middle Permian of Europe.

Tshepanichoptera lacera Aristov, 2008

http://species-id.net/wiki/Tshepanichoptera_lacera
Fig. 9

Tshepanichoptera lacera Aristov in Aristov and Bashkuev 2008: 57, fig. 2d (holotype – positive and negative imprints of forewing without apex and with anal area separated; PIN 3286/14; examined).

Material. Holotype only.

Horizon. Urzhumian Stage (the Middle Permian).

Locality. Chepanikha locality, Rossokha River 1.8 km north of the Chepanikha village, Zavyalovsk District, Udmurtia, Russia.

Description. Anterior margin of forewing straight; SC reaching the apical quarter of wing; costal area considerably narrower than intercubital one; RS distinctly separated from MA; MA forked; MP with two branches directed to the posterior margin of forewing; CuA with two branches; cross-veins in almost all areas forming a double row of cells, but in the areas between MP and CuA, between branches of CuA and in anal area, cross-veins forming numerous rows of cells.

Measurements. Length of forewing about 18 mm.

Mezenalicula Aristov & Storozhenko, gen. n.

urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Mezenalicula

Type species. *Mezenalicula connata* Aristov & Storozhenko, **sp. n.**

Diagnosis. Similar to *Neprotembia* by the base of M fused with CuA, but distinct from it in the more proximal first fork of CuA, and anterior branches of SC not forming double row of cells.

Description. The base of costal area in forewing broadly rounded; costal area broader than subcostal one, crossed with simple or furcated anterior branches of SC; RA simple; RS originated in the basal third or near the mid wing, with four or fewer branches; the base of M completely fused with CuA; M forked before the base of RS; CuA with two or three branches, first fork of CuA is situated distinctly proximal to fork of M; the base of anterior branch of CuA sclerotized; CuP straight; A1 and A2 simple.

Composition. Two species from the Middle and Upper Permian of Europe.

Etymology. After the name of the Mezen District in the Arkhangelsk Region of Russia and genus *Alicula*; gender feminine.

Key to species

1(2) Cross-veins forming a double row or numerous rows of cells. RS distinctly separated from MA ..... ***Mezenalicula connata*** **sp. n.**

2(1) Cross-veins simple. RS fused with MA at short distance near the base ..... ***Mezenalicula conjuncta*** **sp. n.**

Mezenalicula connata **Aristov & Storozhenko, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Mezenalicula_connata
Figs. 10, 19

Material. Holotype PIN 94/883, positive imprint of incomplete forewing.

Type horizon. Kazanian Stage, Lower Kazanian Substage, Iva-Gora Beds (the Middle Permian).

Type locality. Soyana locality, right bank of the Soyana River 56–60 km upstream of the mouth, Mezen District, Arkhangelsk Region, Russia.

Description. Anterior margin of forewing convex in basal portion of wing; SC reaching the apical third of wing; costal area considerably broader than intercubital one; RS distinctly separated from MA; MA simple; MP with three branches directed to the posterior margin of forewing; CuA with three branches; cross-veins forming numerous rows of cells in all areas.

Measurements. Length of forewing about 21 mm.

Etymology. From Latin *connatus* (connate).

Mezenalicula conjuncta **Aristov & Storozhenko, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Mezenalicula_conjuncta
Figs 11, 20

Material. Holotype PIN 3840/1243, positive imprint of incomplete forewing.

Type horizon. Severodvinian Stage, Upper Severodvinian Substage, Poldars Formation, Kichuga Bundle (the Upper Permian).

Type locality. Isady locality, left bank of the Sukhona River 1.8 km downstream of the Mutovino near Isady village, Veliky Ustyug District, Vologda Region, Russia.

Description. Anterior margin of forewing convex in the mid wing; SC reaching the apical third of wing; costal area as broad as the intercubital one; RS fused with MA at short distance near the base; MA and MP simple; CuA with two branches; cross-veins in all areas simple.

Measurements. Length of forewing about 20 mm.

Etymology. From Latin *conjunctus* (connected).

Neprotembia Aristov, 2004

http://species-id.net/wiki/Neprotembia

Neprotembia Aristov 2004a: 105 (type species: *Neprotembia truncata* Aristov, 2004, by original designation).

Description. The base of costal area in forewing broadly rounded; costal area about two times broader than subcostal one; the anterior branches of SC form double row of cells near the mid of costal area; RA simple; RS originated in the basal third of the wing, with two branches; the base of M fused with CuA at certain distance; M forked before the base of RS; CuA with three branches, first fork of CuA is situated near to fork of M; the base of anterior branch of CuA sclerotized; CuP straight; A1 and A2 simple.

Composition. Two species from the Lower Permian of Europe.

Key to species

1(2) Anterior margin of forewing distinctly convex; the basal part of wing broader ..... ***Neprotembia truncata***

2(1) Anterior margin of forewing gently convex; the basal part of wing narrower ..... ***Neprotembia complicata***

Neprotembia truncata Aristov, 2004

http://species-id.net/wiki/Neprotembia_truncata

Fig. 12

Neprotembia truncata Aristov 2004a: 105, fig. 9d (holotype – positive and negative imprints of incomplete forewing; PIN 1700/1026; examined).

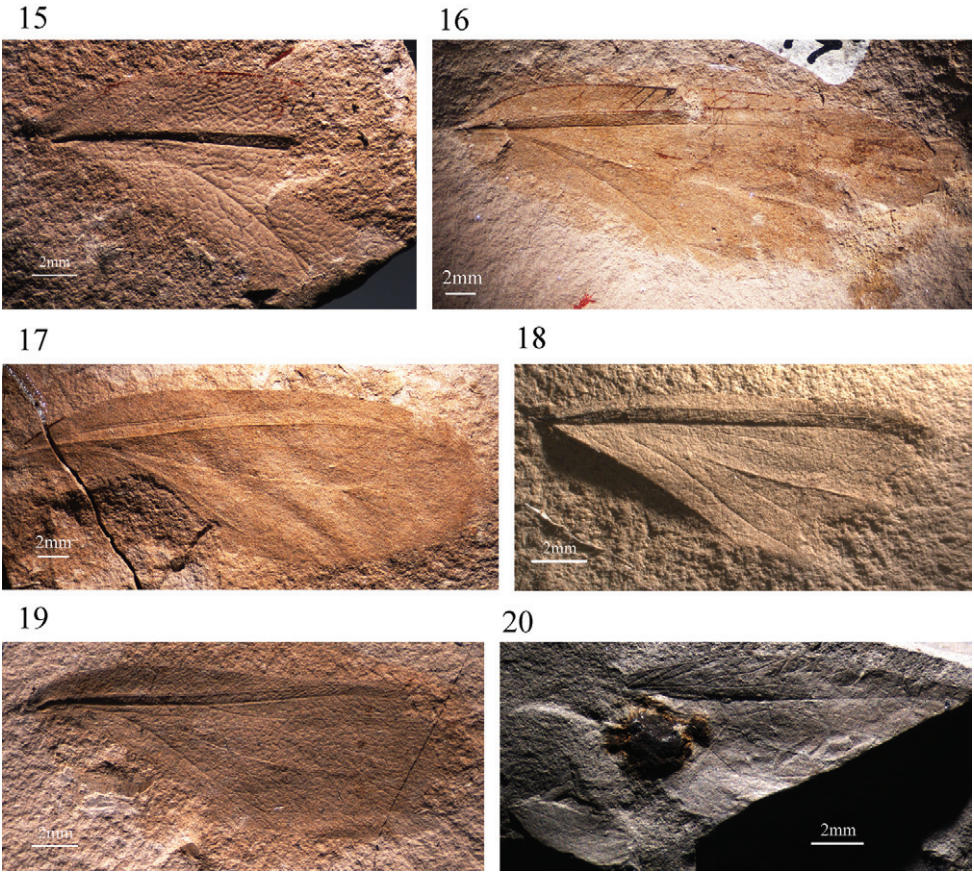
Material. Holotype only.

Horizon. Kungurian Stage, Koshelevka Formation (the Lower Permian).

Locality. Tshekarda locality, Krasnaya Gora Mountain on the left bank of Sylva River near the Tshekarda village, Suksun District, Perm Region, Russia.

Description. Anterior margin of forewing convex; SC reaching the apical quarter of wing; costal area as broad as intercubital area; RS distinctly separated from MA; MA and MP simple; CuA probably with three branches; cross-veins are simple in the subcostal area and forming double row of cells in the areas between RA and RS, and between CuA and CuP.

Measurements. Length of forewing about 15 mm.



Figures 15–20. Forewings of Permulidae **15** *Permula edemskii* sp. n. (holotype PIN 94/1027) **16** *Sojanopermula rasnitsyni* sp. n. (holotype PIN 117/301) **17** *S. rasnitsyni* sp. n. (paratype PIN 117/195) **18** *Kazanalicula reducta* sp. n. (holotype PIN 117/467) **19** *Mezenalicula connata* sp. n. (holotype PIN 94/883) **20** *M. conjuncta* sp. n. (holotype PIN 3840/1243). Scale bars 2 mm.

Neprotembia complicata Aristov, 2005

http://species-id.net/wiki/Neprotembia_complicata

Fig. 13

Neprotembia complicata Aristov in Rasnitsyn et al. 2005: 69, figs. 1g, d (holotype – positive imprint of well preserved folded forewing; PIN 1631/314; examined).

Material. Holotype only.

Horizon. Kungurian Stage, Lek-Vorkuta Formation, Rudnik Subformation (the Lower Permian).

Locality. Khalmer-Yu coalfield, borehole KhK-371, deep 88 m, Pechora Basin, Perm Region, Russia.

Description. Anterior margin of forewing weakly convex; SC almost reaching the wing tip; costal area as broad as intercubital one; RS distinctly separated from MA; MA and possibly MP are simple; CuA with three branches; cross-veins simple and forming double row of cells in the apical portion of the areas between RA, RS, MA, MP and CuA (in the subcostal area cross-veins absent).

Measurements. Length of forewing 13 mm.

Taxa erroneously included in Permulidae

Order Grylloblattida Walker, 1914
Suborder Grylloblattina Walker, 1914
Family Ideliidae Zalessky, 1928

***Acropermula* Aristov & Storozhenko, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Acropermula

Type species. *Permula acra* Kukalová, 1964, Lower Permian of Czech Republic.

Diagnosis. By shape of forewing CuA, the new genus undoubtedly belongs to family Ideliidae. It is easily distinguished from all known genera of Ideliidae in excised base of costal area.

Description. Anterior margin of forewing strongly convex; costal area broad, crossed with mostly furcated anterior branches of SC, the base of costal area distinctly excised; subcostal area very narrow; RA simple; radial area broad, with numerous slightly backwardly slanted cross-veins; RS with several branches; M dividing before the origin of RS; CuA concavely bent, with a long pectinate series of branches. CuA2 not individualized; intercubital area with single intercalary branch of CuA; cross-veins forming numerous rows of cells in almost all areas.

Composition. A type species only.

Ethymology. After the species name *acra* and genus *Permula*; feminine in gender.

Notes. The description of a new genus is based on illustrations and diagnosis of *Permula acra* (Kukalová 1964).

***Acropermula acra* (Kukalová, 1964), comb. n.**
http://species-id.net/wiki/Acropermula_acra

Permula acra Kukalová 1964: 47, fig. 2, tab. 1, fig. 1 (holotype – positive imprint of forewing, specimen no. 69/1963; deposited in the Department of Paleontology, Charles University, Prague; not studied).
Permula aera: Kukalová 1964: 47 (lapsus calami).

Alicula acra: Carpenter 1992: 109, fig. 64, 4; Storozhenko 1998: 98, fig. 182.

Horizon. Sakmarian Stage, Boskovice Graben, Letovice Formation (the Lower Permian).

Locality. Obora locality, 1 km north-west from the Obora village near Boskovice, Moravia, Czech Republic.

***Metidelia* Martynov, 1937**
***Metidelia asiatica* (Storozhenko, 1997)**

Notes. This species was described in the genus *Alicula* (Srorozhenko 1997). After examination of holotype it was transferred to the genus *Metidelia* of family Ideliidae by Aristov (2004b).

Order Eoblattida Hanlirsch, 1906
Incertae familiae
***Neraphidia* Novokshonov & Novokshonova, 1997**

Notes. The genus *Neraphidia* was described in the grylloblattid family Protembiidae (Novokshonov and Novokshonova 1997), but later it was placed in family Aliculidae (Aristov 2004a). The examination of holotype of *Neraphidia mitis* Novokshonov & Novokshonova, 1997 (Fig. 14) allows us to eliminate this taxon from order Grylloblattida. *Neraphidia* is characterized by SC terminating on RA, and by M5 stronger than the main stems of M and CuA, both characters are typical for the order Eoblattida (in order Grylloblattida SC terminating on C or disappearing in the area between C and RA; M5 usually not individualized, if present in some families, when M5 is as broad as, or narrower than stems of M and CuA). Undoubtedly *Neraphidia* is similar to genera of the family Tillyardembiidae in the shape of SC and CuA, but distinguished from the latter by most basal fork of M (in Tillyardembiidae first fork of M is situated distinctly proximal). Herein *Neraphidia* is transferred to the order Eoblattida (sensu Aristov and Rasnitsyn 2009) as a genus of uncertain taxonomic position inside this order.

Conclusion

The family Permulidae consists of thirteen species in seven genera. The oldset Lower Permian representative of the family, *Permula lebachensis*, is known from the Asselian of Central Europe. In the Leonardian Elmo locality (North America) Permulidae is represented by *Elmopterum rotundum* only. The Kungurian Chekarda locality (East Europe) is characterized by very rich fauna of Grylloblattida, but only three species of the family are described from here (*Permula tshekardensis*, *P. minor* and *Neprotembia truncata*). Another, probably younger Kungurian representative of Permulidae, *Neprotembia complicata*, is known from the Pechora Basin (East Europe). Five Middle Permian species (*Permula edemskii* sp. n., *Sojanopermula lucida*, *S. rasnitsyni* sp. n., *Ka-*

zanalicula reducta gen. et sp. n. and *Mezenalicula connata* gen. et sp. n.) are described from the Kazanian Soyana locality in East Europe. A later Middle Permian species, *Tshepanichoptera lacera*, is known from Urzhumian Chepanikha locality (East Europe). The only Upper Permian representative of family, *Mezenalicula conjuncta* sp. n., is described from Severodvinian Isady locality in East Europe. Almost all species are known solely by their holotypes, and only *S. rasnitsyni* sp. n. is known by two specimens. Thus, Permulidae was a widespread but not abundant and diverse Permian family of the order Grylloblattida.

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RESEARCH ARTICLE

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A new, enigmatic family for new genus and species of Polyneoptera from the Upper Permian of Russia

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Abstract

Alexarasniidae **fam. n.** and *Alexarasnia rossica* **gen. et sp. n.** are described from the Upper Permian of European Russia. Systematic position of this enigmatic family within the infraclass Polyneoptera is unclear.

Keywords

new taxa, possible Polyneoptera, *Alexarasnia*, Alexarasniidae, Russia, Upper Permian

Introduction

Among numerous fossil insects collected from the Upper Permian locality Isady (European Russia), there are two wings with an unusual venation which does not allow me to include these fossils in any known order of the subclass Pterygota. One of these wings (Figs 1, 2) is not deformed and has the partly parallel longitudinal venation. Wings with such venation are aerodynamically unfit for flight, therefore parallel venation may be developed only in forewings which are used as tegmina or elytra for the protection of hind wings during rest. The main organs of flight in insects with such forewings are the hind wings, and all these insects belong to

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the order Coleoptera or to the infraclass Polyneoptera (= orthopteroid insects). The above-mentioned Upper Permian wings are with the well-developed venation including crossveins, i. e., they were clearly not as sclerotized or leathery as elytra in Coleoptera. So, it is most probable that these wings are tegmina belonging to Polyneoptera.

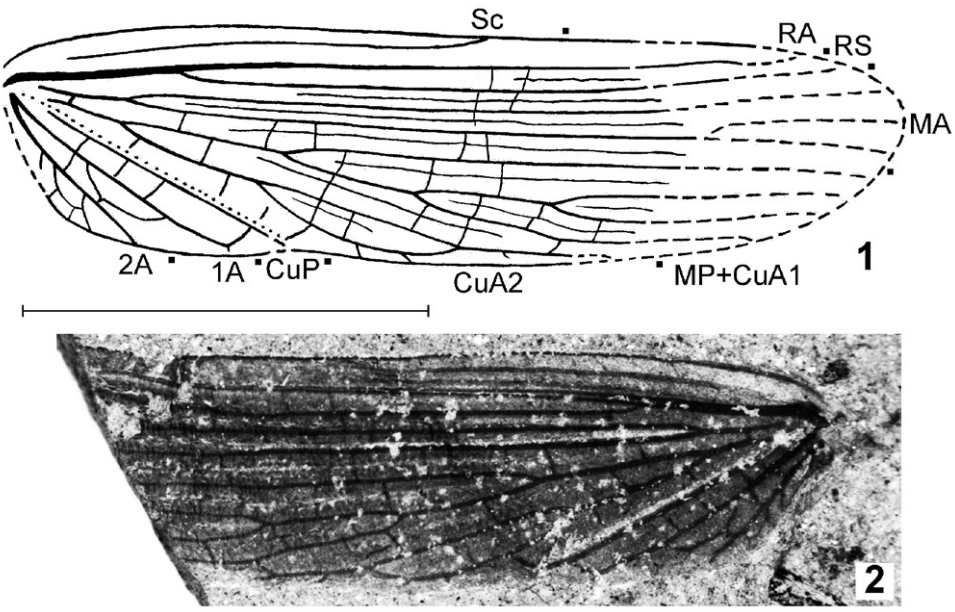
Systematic Paleontology

Family Alexarasniidae Gorochov, fam. n.
http://species-id.net/wiki/Alexarasniidae

Type genus. *Alexarasnia* gen. n.

Composition. Only the genus *Alexarasnia* gen. n.

Diagnosis. Tegmen (Figs 1–4) differs from that of Titanoptera, majority representatives of Orthoptera, and Paleozoic and Triassic Phasmatoptera in the absence of precostal area (presence of this area is a synapomorphy of all these orders). From the other representatives of two latter orders, this family differs in the reduction of Sc branches in the tegmen and/or clearly more numerous longitudinal tegminal veins (CuA has six or more branches in Alexarasniidae and four or less branches in all the other representatives of Phasmatoptera). Tegminal venation of the new family is distinguished from that of all the other orders of Polyneoptera by the partly parallel longitudinal veins in combination with the following characters: straight CuP, very narrow radial and interradial areas, and reduction of branches of RA and RS (from Dictyoptera); reduction of branches of Sc and/or RS, partial fusion of distal parts of some longitudinal veins with formation of long loop-like cells along anal edge of tegmen, and presence of intercalary veins between majority of longitudinal veins (from Grylloblattida as well as from the families Lemmatophoridae Sellards, 1909 and Atactophlebiidae Martynov, 1930 possibly belonging to the extinct order Eoblattida; Gorochov 2004); the latter characters as well as distal part of Sc not fused with RA (from Plecoptera and the other taxa of Eoblattida); tegmen not leathery with well-developed venation (from Dermaptera), and distinctly more numerous longitudinal veins (from Embioptera). Parallel venation of the tegmen is also present in the enigmatic family Chresmodidae Handlirsch, 1906 belonging to an unknown order of Polyneoptera (Delclòs et al 2008; Zhang et al 2008a, b); Alexarasniidae is distinguished from it by the distal half of tegminal CuP situated not parallel to the anal tegminal edge and more numerous branches of CuA in tegmen (6–9 instead of 3–4).

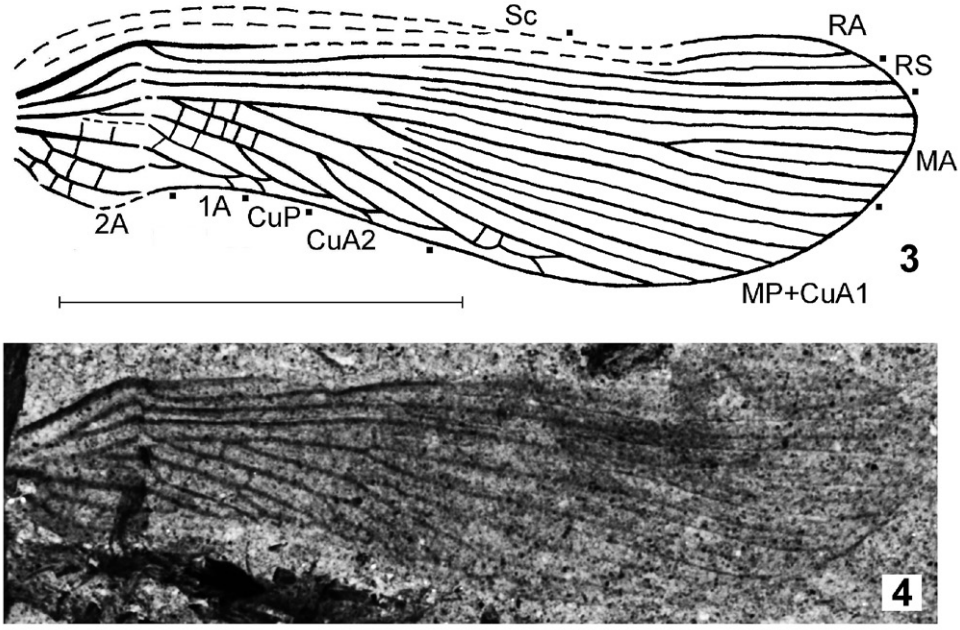


Figures 1–2. *Alexarasnia rossica* gen. et sp. n., tegmen, holotype PIN 3840/63 (part) **1** scheme of venation **2** photograph of fossil. Scale bar 5 mm.

Genus *Alexarasnia* Gorochov, gen. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Alexarasnia

Type species. *Alexarasnia rossica* sp. n.

Description. Tegmen (Figs 1, 2) moderately narrow, with parallel Sc, RA, RS, branches of MA and MP+CuA1, and short distal part of CuA2; all areas between longitudinal veins more or less narrow; majority of them with intercalary veins; Sc slightly concave, without branches and with apex situated near middle part of costal edge; R+RA slightly convex, but all longitudinal veins between this vein and CuP neutral; R and MA with proximal bifurcation situated in proximal part of tegmen; RA and RS probably simple (single); MA with only two branches in proximal and middle parts of tegmen; proximal part of MP before anastomosis with CuA1 indistinct; MP+CuA1 with four branches as minimum; CuA2 with two branches forming cell-like structure looking as a result of fusion of their distal parts; CuP concave (area near this vein with distinctly concave fold shown in Fig. 1a by dotted line), oblique and straight, but with small distal part probably looking as a result of its fusion with CuA2; 1A hardly



Figures 3–4. Alexarasniidae gen. et sp. indet., tegmen, specimen PIN 3840/1232 (part) **3** scheme of venation, **4** photograph of fossil. Scale bar 5 mm.

convex, similar to CuP in shape; 2A neutral, looking as a single, oblique, and straight vein (its branches somewhat similar to crossveins); true crossveins simple and sparse.

Included species. Only the type species.

Etymology. The genus is named in honor of the famous Russian paleoentomologist Prof. Alexandr P. Rasnitsyn.

Alexarasnia rossica Gorochov, sp. n.

urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Alexarasnia_rossica

Holotype. PIN (Paleontological Institute, Russian Academy of Sciences, Moscow) 3840/63, part and counterpart of imprint of tegmen (sex unknown) with indistinctly preserved distal area; Russia, Vologda Region, Velikij Ustyug District, left bank of Sukhona River near Isady Village (locality "Isady"); Upper Permian (Tatarian), Severodvinian Stage.

Description. Tegmen (Figs 1, 2) with all veins more-or-less dark; membranes between them slightly darkened, but with somewhat lighter subcostal area; proximal bifurcation of MP+CuA1 and that of CuA2 situated rather far distad from proximal bifurcation of R. Length of tegmen 12 mm.

Etymology. The specific epithet is adapted from "Rossia" (Latin for Russia).

Discussion

Another tegmen from the same locality (PIN 3840/1232; Figs 3, 4) has the similar size, coloration of veins, and type of venation. However this fossil is deformed (with the middle part contracted in costal-anal direction), and as a possible result of this deformation, its venation looks less parallel than it might be prior to deformation. Moreover, its MP+CuA1 has six branches (probably more numerous than in holotype of *R. rossica*), proximal bifurcation of MP+CuA1 situated near proximal bifurcation of R (compare with the description of *R. rossica*, above), CuA2 shorter, and area between 1A and 2A remarkably wider (see Figs 1 and 3). These differences do not allow me to determine this wing more exactly, because it may belong to another sex of *A. rossica*, to another species of *Alexarasnia*, or to another genus of Alexarasniidae.

Position of the new family within Polyneoptera is unclear. However, its tegminal venation looks more-or-less intermediate between the enigmatic Jurassic-Cretaceous water-striding family Chresmodidae [its very parallel tegminal venation was clearly figured by Delclòs et al (2008: Fig. 6); but in the same paper in figure 8, these authors figured the tegmen of Phasmatoptera from the superfamily Susumanioidea which was included mistakenly by them in Chresmodidae] and the Early and Middle Permian families Lemmatophoridae and Atactophlebiidae (possibly belonging to Eoblattida; Gorochov 2004). The mode of life of these Permian families was probably also connected with water (Carpenter 1935; Storozhenko 1998). In the latter publications, it was suggested that Lemmatophoridae (Carpenter 1935) and Atactophlebiidae (Storozhenko 1998) had a primitive postembryonal development, with an increase in the number of tarsal segments. This ancient type of development is absent now in all polyneopterans, but such instability of tarsal composition might be one of the prerequisites for the additional increase in the number of tarsal segments in Chresmodidae. Alexarasniidae (especially unknown body fossils) may prove to be useful in understanding this adaptive process.

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RESEARCH ARTICLE

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New earwigs in mid-Cretaceous amber from Myanmar (Dermaptera, Neodermaptera)

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Abstract

Two new earwigs (Dermaptera) recently discovered in mid-Cretaceous (latest Albian) amber from Myanmar are described and figured. *Astreptolabis ethirosomatia* **gen. et sp. n.** is represented by a peculiar pygidicranoid female, assigned to a new subfamily, Astreptolabidinae **subfam. n.**, and differs from other protodermapterans in the structure of the head, pronotum, tegmina, and cercal forceps. *Tytthodiplatys mecynocercus* **gen. et sp. n.** is a distinctive form of first-instar nymph of the Diplatyidae, the earliest record for this basal earwig family. The taxon can be distinguished from other Early Cretaceous nymphs by the structure of the head, antennae, legs, and most notably its filamentous and annulate cerci. The character affinities of these taxa among Neodermaptera are generally discussed as is the identity of an enigmatic 'earwig-like' species from the Jurassic of China.

Keywords

Albian, Amber, Mesozoic, Earwigs, Polyneoptera, Pygidicranidae, Diplatyidae

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Dedication

It is with great pleasure that I dedicate this brief contribution to my friend and colleague, Dr. Alexandr P. Rasnitsyn, one of the great statesmen of paleoentomology. For the last 52 years Alex has produced some of the most influential works in the field, fueling the interests and investigations of generations of subsequent students of both Hymenoptera and fossil insects in general. On the same day Alex marks his 75th year, I shall mark my 40th. If in the coming 35 years I can undertake merely a similar fraction of what he has achieved, then I shall consider myself pleased. It is with considerable pride that Alex may look back on a career of tremendous accomplishment, and we all look forward to many more years of such successful endeavors from him.

Introduction

Earwigs are certainly one of the lesser-studied lineages of insects, with comparatively few current investigations underway into their diversity, behavior, biology, and general natural history. This is unfortunate given the remarkable diversity of form for these often subsocial insects, with their prominent and immediately recognizeable cercal forceps which are used in aggressive/defensive interactions, courtship, and prey capture (e.g., Günther and Herter 1974; Briceño and Eberhard 1995; Haas 2003; Costa 2006; Rankin and Palmer 2009). The systematics of the group was once the concerted interest of dermapterological luminaries such as Malcolm Burr (1876–1954), Walter D. Hincks (1906–1961), and Allan Brindle (1915–2001) but has not received quite as much effort in recent years and the sizeable monographs that were once regularly flowing from earwig taxonomists has slowed. Ironically, paleontological investigation into earwigs has seen a reversed trend, with increasingly more and more accounts during the last decade (e.g., Nel et al. 2003; Wappler et al. 2005; Chatzimanolis and Engel 2010; and additional citations below). Of particular interest have been the numerous new records of Mesozoic Dermaptera which have come to light, mostly as compression fossils from Asia (e.g., Zhang 1997; Engel et al. 2002; Zhang 2002; Zhao et al. 2010a, 2010b, 2011) or South America (Engel and Chatzimanolis 2005; Haas 2007), but also including a steadily accumulating number of amber inclusions (e.g., Engel and Grimaldi 2004; Engel 2009; Perrichot et al. 2011; Engel et al. 2011).

Herein I provide the description of two newly recognized earwigs in mid-Cretaceous amber from Myanmar. The morphology and possible affinities of these taxa are discussed as is the attribution to Dermaptera of some recently described enigmatic insects from the Jurassic of China (Zhao et al. 2010a), and which have some superficial similarities to one of the species considered here.

Material and methods

The material discussed herein originates from the latest Albian amber deposits of northern Myanmar in the State of Kachin. The general paleobiota, dating, and origin

of this amber have been overviewed by Zherikhin and Ross (2000), Grimaldi et al. (2002), Cruickshank and Ko (2003), and Ross et al. (2010). All material is deposited in the Amber Fossil Collection, Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York. The classification followed herein is that of Engel and Haas (2007), while the morphological terminology and format for the descriptions generally follow those of Giles (1963), Günther and Herter (1974), Haas (1995), Engel et al. (2011), and Perrichot et al. (2011).

Systematic Paleontology

Order Dermaptera De Geer
Suborder Neodermaptera Engel
Family Pygidicranidae Verhoeff

Astreptolabidinae Engel, subfam. n.
http://species-id.net/wiki/Astreptolabidinae

Type genus. *Astreptolabis* Engel, gen. n.

Diagnosis. Female: Minute earwigs (ca. 3.5 mm in length); somewhat dorsoventrally compressed; densely setose, but not chaetulose; integument dull and matt. Head prognathous, broad, slightly broader than anterior border of pronotum (Fig. 1), apparently tumid, posterolateral corners gently curved, posterior border straight; compound eyes well developed, prominent, separated from posterior border of head by slightly less than compound eye length, setose; ocelli absent; antenna with at least 14 antennomeres (an unusually small number for basal Neodermaptera and likely autapomorphic for this subfamily), scape stout, pedicel longer than wide, flagellomeres longer than wide, progressively more elongate from flagellomere II–X, with X–IV subequal in size. Pronotum exceptionally large (Fig. 1), anterior margin relatively straight, posterior border gently convex, lateral borders slightly divergent in anterior half, flared and convex in posterior half, posteriorly broader than head, all borders ecarinate. Tegmina present, without venation, symmetrical, elongate, outer margins convex, apex gently curved and tapering to midline (not truncate), covering first four abdominal segments (Fig. 1); hind wings present, with squama slightly exposed from under tegmina. Femora apparently not carinulate; tarsi trimerous, second tarsomere shortest, not extending beneath base of third tarsomere; pretarsal ungues simple; arolium absent. Abdomen slender, elongate (eight visible segments, typical for females), lateral margins parallel-sided, most segments only slightly wider than long, apicalmost segment with straight apical margin, without tubercles. Cerci symmetrical, slightly longer than apicalmost three abdominal segments, straight, tubular, gently tapering to acute apex, densely covered in microtrichia, without tubercles, dentition, or serrations, broadly separated at base (Fig. 1); pygidium not evident; valvulae not exposed at abdominal apex.

Male: Unknown.

***Astreptolabis* Engel, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Astreptolabis

Type species. *Astreptolabis ethirosomatia* Engel, sp. n.

Diagnosis. As for the subfamily (*vide supra*).

Etymology. The new genus-group name is a combination of the Greek words *astreptos* (meaning, "not curved") and *labis* (meaning, "forceps"). The name is feminine.

***Astreptolabis ethirosomatia* Engel, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Astreptolabis_ethirosomatia
Fig. 1

Holotype. AMNH Bu-FB20; adult female; amber, mid-Cretaceous, Myanmar: Kachin State (nr. Myitkyina), ex coll. Federico Berlöcher; deposited in the Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York.

Diagnosis. As for the genus (*vide supra*).

Description. As for the subfamily and genus, with the following additions: Female: Total length as preserved (including cerci) ca. 3.5 mm; head medial length from clypeal apex to posterior border 0.38 mm, maximum width (across level of compound eyes) 0.56 mm; compound eye length 0.13 mm; length of head behind compound eye 0.11 mm. Pronotum medial length 0.45 mm, anterior width 0.47 mm, posterior width 0.70 mm; tegmen length 1.21 mm, maximum width 0.49 mm. Abdominal length as preserved (excluding cerci) 1.65 mm, maximum width 0.44 mm; cercal forceps length 0.65 mm, basal width 0.05 mm, separation between bases 0.12 mm. Integument as preserved apparently brown to dark brown, impunctate, dull, matt throughout. Legs without spines or bristle-like setae. Setae of body short and dense except more elongate setae posterolaterally on abdominal terga (Fig. 1).

Male: Unknown.

Etymology. The specific epithet is a combination of the Greek words *etheira* (meaning, "hairy") and *somation* (diminutive form of the word for, "body").

Family Diplatyidae Verhoeff

***Tytthodiplatys* Engel, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Tytthodiplatys

Type species. *Tytthodiplatys mecynocercus* Engel, sp. n.

Diagnosis. Minute earwigs (ca. 1.9 mm in length excluding cerci), with eight antennomeres (groundplan condition for first instars of Neodermaptera). Body dor-

Figure 1. Dorsal aspect photomicrograph of holotype female of *Astreptolabis ethirosomatia* gen. et sp. n. (AMNH Bu-FB20). In this orientation the head is slightly dipped forward making the postocular area appear minutely foreshortened relative to the compound eyes.

soventrally compressed (Fig. 2), with sparsely scattered setae, not chaetulose; integument dull and matt. Head prognathous, slightly broader than long (estimated as direct dorsal view of specimen not possible: Fig. 2), somewhat tumid, posterior angles rounded, posterior border relatively straight, rounded (not truncate or concave); compound eyes well developed, somewhat prominent, separated from posterior border of

head by slightly more than compound eye diameter; ocelli absent; antenna with eight articles, scape relatively slender, pedicel short, subquadrate, very slightly wider than long, meriston longer than other flagellomeres; mouthparts typical for Dermaptera (e.g., Waller et al. 1996). Pronotum and mesonotum roughly subquadrate, slightly narrower than head, with anterior and posterior angles acutely rounded, lateral borders weakly convex, all borders ecarinate; pronotal median longitudinal furrow (= sutura pronotalis longitudinalis) not evident; metanotum broader than maximum length, anterior border straight, lateral borders ecarinate and diverging posteriorly, posterior border broadly concave. Legs not greatly elongate; procoxae apparently near posterior border of prosternum; femora not carinulate or compressed; tibiae relatively short, about as long as tarsi; tarsi trimerous, second tarsomere greatly shortened, not widened apically, scarcely extending apically beneath third tarsomere; pretarsal ungues simple, arolium absent. Abdominal terga sculptured as on thoracic nota; segments transverse, apicalmost segment much smaller than penultimate segment; cerci greatly elongate, about as long as combined lengths of abdomen and thorax, filamentous, annulated (as in nymphs of Diplatyidae and Karschiellidae) (Fig. 2), with bases broadly separated.

Etymology. The new genus-group name is a combination of the Greek word *tytthos*, meaning "small" or "young", and *Diplatys*, type genus of the family (itself a combination of the Greek words *di* and *platys*, meaning "two" and "broad", respectively). The name is masculine.

***Tytthodiplatys mecynocercus* Engel, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Tytthodiplatys_mecynocercus
Fig. 2

Holotype. AMNH Bu-FB75; female nymph (first instar); amber, mid-Cretaceous, Myanmar: Kachin State (nr. Myitkyina), ex coll. Federico Berlöcher; deposited in the Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York.

Diagnosis. As for the genus (*vide supra*).

Description. As for the genus with the following minor additions: First-instar nymph: Total length as preserved (including cerci) ca. 1.9 mm; head medial length from clypeal apex to posterior border 0.46 mm; compound eye length 0.08 mm; length of head behind compound eye 0.10 mm. Pronotum medial length 0.25 mm; mesonotum medial length 0.22 mm; metanotum medial length 0.12 mm. Abdominal length as preserved (excluding cerci) 0.83 mm; cerci length 1.58 mm. Integument as preserved apparently brown, impunctate, strongly imbricate, dull, matt throughout. Legs without spines or bristle-like setae except for a few stiff setae on dorsal surface of profemora. Cerci separated at base by about cercal basal width. Setae of body sparse, where present setae stiff and erect to suberect, particularly those apicolaterally on abdominal terga; cerci with numerous, elongate, stiff, erect setae scattered along cercomeres.

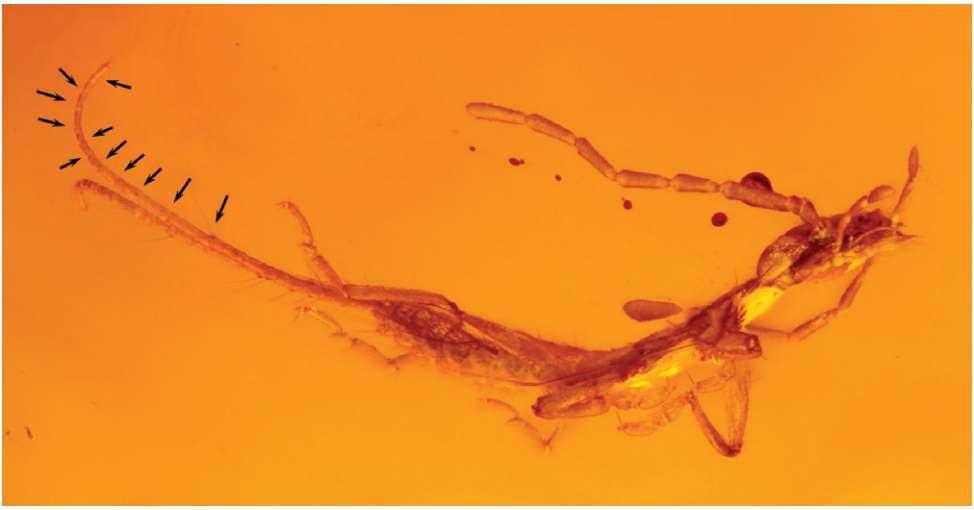

Figure 2. Photomicrograph of holotype nymph of *Tytthodiplatys mecynocercus* gen. et sp. n. (AMNH Bu-FB75) (arrows indicate most easily discernible cercomere joints).

Etymology. The specific epithet is a combination of the Greek words *mekyno* (meaning, "prolong") and *kerkos* (meaning, "tail").

Discussion

Discovery of these two specimens brings the diversity of earwigs in Burmese amber to four species – *Myrrholabia electrina* (Cockerell 1920), *Burmapygia resinata* Engel and Grimaldi (2004), *Atreptolabis ethirosomatia* gen. et sp. n., and *Tytthodiplatys mecynocercus* gen. et sp. n., none of which are of the Eudermaptera furthering the notion that Eudermaptera are of later Cretaceous or Early Tertiary origin. This is also true if we look at other Cretaceous amber earwigs, namely *Rhadinolabis phoenicica* Engel et al. and an unnamed nymph in Lebanese amber (Engel et al. 2011), and the unnamed nymphs and *Gallinympha walleri* Perrichot and Engel in French amber (Engel 2009; Perrichot et al. 2011). There are earwigs in New Jersey amber but these are too poorly preserved to permit conclusive assignment beyond Neodermaptera (Engel pers. obs.) and it is hoped that better material eventually shall be discovered.

Astreptolabis is easily placed among the Neodermaptera owing to the absence of ocelli, the trimerous tarsi, unsegmented cerci, vestigial ovipositor, and absence of venation in the tegmina (Willmann 1990; Haas and Klass 2003; Grimaldi and Engel 2005). The mouthparts with small mandibles concealed under the labrum and the galea and lacinia prominent are also of typical dermapteran form (Giles 1963; Waller et al. 1996). The presence of only eight visible abdominal tergites is indicative of a female. While the cerci are immediately distinctive for this female, males are likely to have had significantly different cercal forms (as is typically the case between males

and females of the same species among living Dermaptera). As such, males of *A. ethirosomatia* would not be recognized on the basis of similarly straight, tapering, and tubular cerci but more likely have similar setation, integumental sculpturing, and head, pronotal, tarsal, and tegminal structure. The dense setation of the body, small size and dorsoventrally compressed body, broad head, symmetrical cercal forceps, and the non-transverse antennomeres IV–VI are all indicative of a pygidicranid among primitive neodermapteran families. Unfortunately, the arrangement and structure of the ventral cervical sclerites cannot be discerned in the holotype. Interestingly, there is some superficial similarity between *Astreptolabis* and the epizoic Hemimeridae most prominently the straight, broadly separated and setose cerci, exceptionally broad head, large pronotum, and posterolateral patches of elongate setae on the abdominal terga (e.g., Giles 1963; Günther and Herter 1974; Nakata and Maa 1974). However, each of these characters is variable enough across dermapteran families such that they cannot be considered synapomorphic and these taxa differ in innumerable other characters such as the absence of tegmina and wings, absence of eyes, shape of the abdomen, and the strikingly modified legs and tarsi in hemimerids.

Astreptolabidinae can be readily differentiated from other pygidicranid subfamilies by the peculiar form of the female cercal forceps, as well as the combination of a broad, somewhat truncate head, large pronotum, and densely and finely setose body. From Burmapygiinae, also in Burmese amber, the new subfamily further differs in the stout scape, the absence of the arolium, and the shorter valvulae which do not apparently extend beyond the apex of the subgenital plate. In some respects, the head and pronotal structure of *Astreptolabis* are reminiscent of Echinosomatinae (head broad, transverse, somewhat truncate posteriorly; pronotum large, subquadrate or transverse; scape stout), but the absence of chaetae on the integument (instead dense, fine setae), particularly the head, pronotum, and tegmina, excludes inclusion therein. Echinosomatines are also rather large, broad, and stout (ca. 8–30 mm in length), never as minute as Astreptolabidinae, and although the cercal forceps are simple (i.e., lacking dentition or serrations) and generally widely separated as in the latter, they are distinctly arcuate and more stout in the former. In addition, the female valvulae of echinosomatines typically extend slightly beyond the apex of the subgenital plate. Astreptolabidinae may represent an early ally of the Echinosomatinae.

It is interesting to note that the tegminal form and minute body size are reminiscent of the recently described *Atopderma ellipta* Zhao et al. (2010a) from the Jurassic-age Daohugou deposits of Inner Mongolia (a junior synonym of *Leicarabus parvus* Hong), although the abdominal form (and thusly the cercal or other terminal structures) remains unknown for this enigmatic insect (although it may be misplaced in Dermaptera, *vide infra*). From the superficial shape of the tegmina (note that these may be elytra in *A. ellipta*, *vide infra*) alone it is tantalizing to speculate that these species might be related. However, most observable features are not shared between the two taxa as *Astreptolabis* was clearly very setose while *A. ellipta* apparently was not, and more importantly the overall morphology of the head, pronotum, and tarsi are dramatically different. Indeed, there is reason to question the assignment of *A. ellipta* to

Dermaptera at all, and certainly within Neodermaptera, a placement considered likely by the original authors (Zhao et al. 2010a). Unlike all Neodermaptera, *A. ellipta* apparently had pentamerous tarsi (or at least more tarsomeres than the trimerous condition of all living and fossil Neodermaptera). Similarly non-dermapteran in character is the assertion that the tarsus of *A. ellipta* is as long as the tibia, a feature more similar to that among some Staphyliniformia than many adult, non-epizoic Dermaptera (although the condition certainly can be found). The statement that the "ventral cervical sclerites of equal size" (p. 463) does not match with the condition for *A. ellipta* is enigmatic in that these structures are neither described nor figured in the account of the genus or species, and from the photographs of the specimens would not be discernible in the series either (these are often difficult to discern in living and amber-preserved specimens and their recognition on a few-millimeter-long compression fossil is unlikely). In Diplatyidae, Karschiellidae, and Pygidicranidae the ventral cervical sclerites are of equal size, with the posterior sclerite well separated or only very medially bordering the prosternum (i.e., the 'blattoid' neck of Popham 1959, 1965, 1985). Zhao et al. (2010a) pinned their attribution onto five features which they considered conclusively earwig in form. I must respectfully disagree with my colleagues here as I see nothing supporting placement in Dermaptera among their arguments. To be more precise (taking their points in the order with which they were presented):

1. Head shape: The assertion that in Staphyliniformia the head is much narrower than the pronotum is incorrect, and triangular heads are very common in Staphylinidae (as well as numerous other beetle families). Yes, there are many staphylinids in which the pronotum is narrower than the head, but there are similarly many in which the head is as broad as or broader than the pronotum (e.g., many Oxytelinae, Staphylininae, Scydmaeninae, &c.), not to mention this similar condition among other families such as Hydraenidae, Hydrophilidae, &c. The head shape of *A. ellipta* certainly does not exclude placement in Coleoptera. Moreover, the total antennal number (unknown for the holotype and unreported for the paratypes which have more completely preserved antennae), seems to be approximately 11 in some specimens (momentarily overlooking the concern that some of the paratypes do not appear to be conspecific with the holotype; some of the paratypes look more dermapteran-like while the holotype looks awfully coleopteran), a distinctly polyphagan, if not also staphyliniform, groundplan condition. What is known of the head and antenna in *A. ellipta* neither supports nor refutes a placement in Coleoptera or Dermaptera.

2. Prothorax without pleural sulcus separating pronotum and propleuron: This is an enigmatic character for 'distinguishing' between these orders, and it is not entirely clear what difference the authors are really referring to as both Staphyliniformia and Dermaptera have a sulcal separation between the pronotum and propleuron (e.g., Blackwelder 1936; Giles 1963; Günther and Herter 1974; Naomi 1988; Waller et al. 1999). As briefly described by Zhao et al. (2010a) this does not separate Coleoptera from Dermaptera, and it is unlikely that such a feature would have been visible based on the orientation of the available specimens.

3. 'Tegmina' purportedly long and thin, and with curved outer (costal) margins: Certainly most staphylinids do have short, more rectangular elytra, but many Staphyliniformia may also have more elongate elytra, and definitely of the form appearing in *A. ellipta*. For example, some Scydmaeninae, Omaliinae, and Scaphidiinae have more fully-developed elytra, particularly of the latter subfamily. Lastly, the assertion that Coleoptera should have more heavily sclerotized elytra than the condition observed in *A. ellipta* is both *ad hoc* and erroneous. No one could argue that the reduced elytra of many Ripiphoridae, or those of Meloidae, Melyridae, Phengodidae, Pyrochroidae, or even some Coccinellidae are more heavily sclerotized than those of *A. ellipta*. There is certainly a considerable range of cuticle thickness and development across beetle elytra (e.g., Kamp and Greven 2010). This is not to say *A. ellipta* belongs to any of these families (not by any stretch of the imagination), but simply serves to demonstrate that the *ad hoc* assertion that the elytra of *A. ellipta* are not strong enough to be coleopteran is not factually based.

4. Carinated and spined femora: Although the authors of *A. ellipta* state that it has carinulate femora, this is not the case in any of their figures. Some primitive earwigs have femora with visible lamelliform edges dorsally but the presumed carina referred to by Zhao et al. (2010a) appears to be a ventral ridge demarcating the under surface of the profemur, a feature common of many insect femora. I believe the authors have misinterpreted the condition in earwigs. Similarly, none of their figures show spines on the femora, nor do the descriptions mention any such features, and so it is unclear what Zhao et al. (2010a) are referring to. Regardless, femoral spines are not diagnostic of Dermaptera and many earwigs lack such structures. In addition, the close position of the procoxae in *A. ellipta* (Zhao et al. 2010a) is much more like a coleopteran (e.g., Staphylinidae) than an earwig in which the procoxae are almost always separated by a sizeable portion of the prosternum (e.g., Giles 1963; Waller et al. 1999).

5. Abdominal shape: That the abdominal terga in Dermaptera are always transverse and the implicit assumption from the account of Zhao et al. (2010) that parallel lateral abdominal margins is indicative of Staphylinidae and not Dermaptera is simply false. The form of the terga is quite variable across Dermaptera, many are truly transverse, but some can be nearly quadrate and elongate in form. Similarly, the lateral margins of the abdomen can be convex or parallel-sided, particularly so among the more proximal segments (e.g., Hincks 1955; Günther and Herter 1974; Steinmann 1986). Lastly, it is presumably the presence of laterotergites that Zhao et al. (2010a) are referring to when they mention that the "tergum is slightly narrower than the sternum" in staphylinids, with the laterotergites being confused for upturned sternal margins. Regardless, the described condition is not universally true for Staphylinidae, and most certainly not the case for Staphyliniformia (e.g., Blackwelder 1936; Naomi 1989). Moreover, the abdomen is not preserved in the holotype of *A. ellipta* and at most by 2–3 segments in some of the paratypes. From these basal portions alone nothing can be derived that is strictly dermapteran in character, although these segments are not necessarily 'staphylinid-like' either.

The purpose here is not to assert that *A. ellipta* is a beetle, and more precisely a staphyliniform beetle, but to demonstrate instead that a coleopteran attribution cannot be so readily dismissed by the stated characters. Naturally, dramatically autapomorphic taxa can appear in any period of time and such may be the case with *A. ellipta* should more complete material reveal definitive dermapteran synapomorphies. Thorough redescriptions of the type series are needed but more critical will be the discovery of more complete and finely-preserved specimens. Only then will accurate conclusions on the phylogenetic affinities of these wonderful animals be permitted. For the time being, however, I conservatively consider *A. ellipta* to be of uncertain ordinal assignment.

On the surface the phylogenetic affinities of *Tytthodiplatys mecynocercus* would appear more challenging than those of *Astreptolabis* given that the morphology and systematics of immature Dermaptera has not received as much attention as that of the adults. Indeed, many challenges remain for making conclusive statements about fossil earwig nymphs (e.g., Engel 2009; Engel et al. 2011; Perrichot et al. 2011). Some of the most important works are Günther and Herter (1974), Brindle (1987), and Matzke and Klass (2005), but concentrated efforts are still needed in the study of nymphal Dermaptera. Nonetheless, among all of the fossil nymphs *T. mecynocercus* is perhaps the easiest to assign to family. Firstly, the epizoic families Hemimeridae and Arixeniidae can be excluded on the basis of their numerous peculiar modifications associated with their life histories (e.g., Giles 1961, 1963; Davies 1966; Günther and Herter 1974; Nakata and Maa 1974; Waller et al. 1999; Klass 2001), leaving only the non-parasitic families of the Neodermaptera. The elongate, filamentous and annulate cerci are a plesiomorphic trait known only in the basal families Diplatyidae and Karschiellidae. In these families the adult cercal forceps develop from the basalmost cercomere of the nymph (Green 1896, 1898) and it is likely that the loss of annulations (resulting from the loss of all but the basalmost cercomere) represents a synapomorphy for Neodermaptera exclusive of Karschiellidae and Diplatyidae (as clade Cercodermaptera). The annulations are difficult to discern in the holotype but are most easily observed toward the upturned apical portion of the right cercus, where at least four distinct subunits are observable. The lack of carinulate femora and the large compound eyes are indicative of a diplatyid rather than a karschiellid. Accordingly, *T. mecynocercus* is considered the earliest representative of the ancient earwig family Diplatyidae. Staging the nymph as a first instar is based on the exceptionally small size coupled with the undeveloped antenna with only eight antennomeres, the condition typical to first-instar nymphs in Neodermaptera (where known). The count of eight antennomeres only extends into the second instar among the Eudermaptera, seemingly reflective of the generally lower number of adult antennomeres in this clade relative to other neodermapteran families (e.g., Matzke and Klass 2005).

The Cretaceous amber record of Dermaptera is steadily growing and it is only a matter of time before informative new specimens are discovered in the deposits of Spain, Canada, and elsewhere (e.g., Peñalver and Delclòs 2010; McKellar and Wolfe 2010), alongside new material from Tertiary sources such as Mexico, India, or Australia (e.g., Solórzano-Kraemer 2007, 2010; Rust et al. 2010; Hand et al. 2010). As

the wealth of available material continues to grow it is likely that the amber record for earwigs will become as informative for dermapteran phylogeny as have the treasures of fossil ants, bees, and termites that have amassed during the last 15 years for understanding their respective genealogies (e.g., Grimaldi et al. 1997; Grimaldi and Agosti 2000; Engel 2001, 2011; Grimaldi and Engel 2005; Perrichot et al. 2008a, 2008b; Grimaldi et al. 2008; Engel et al. 2007, 2009). As has been the case for these other lineages, our knowledge of Mesozoic earwigs has shifted considerably in these same 15 years and will undoubtedly continue to do so. Remarkable discoveries certainly await us.

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RESEARCH ARTICLE

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The oldest psyllipsocid booklice, in Lower Cretaceous amber from Lebanon (Psocodea, Trogiomorpha, Psocathropetae, Psyllipsocidae)

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Abstract

Libanopsyllipsocus alexanderasnitsyni **gen. et sp. n.,** of Psyllipsocidae is described and figured from the Lower Cretaceous amber of Lebanon. The position of the new taxon is discussed and the fossil is compared to other psyllipsocids. The species represents the earliest record of the family Psyllipsocidae.

Keywords

New genus, new species, Psyllipsocidae, Lower Cretaceous, Lebanese amber

Introduction

The Psocodea (Psocoptera + Phthiraptera) is a rather small order with about 10,000 valid extant species. Earlier, fossils from the Permian were assigned to the Psocodea but the attribution of these is uncertain. The first unquestionable records of psocodeans are from the middle Jurassic of China (Huang et al. 2008). The Psyllipsocidae are a relatively small family of trogiomorphan psocathropetan Psocodea, including about 50

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extant species in five genera distributed worldwide. Psyllipsocids live in caves, on rock surfaces, and among dead leaves. To date four fossils have been assigned to Psyllipsocidae: *Psyllipsocus eocenicus* Nel et al., 2005 (lowermost Eocene French Oise amber), ?*Psyllipsocus banksi* Cockerell, 1916 (mid-Cretaceous Burmese amber), a "*Psyllipsocus* sp. (nymph)" from Lower Miocene Mexican amber (Mockford 1969), and *Khatangia inclusa* Vishniakova, 1975 (Late Cretaceous Taimyr amber) but the last three attributions to Psyllipsocidae are dubious and require revision.

The Lower Cretaceous Lebanese amber is so far the oldest (Neocomian) with complete macroscopic biological inclusions (Azar 2007). Its formation corresponds to the epoch of the origin and rise of flowering plants, a critical period for the study of the evolution, with extinction of many ancient insect groups and emergence of effectively modern lineages. Up to now nine species of psocids have been described from Lebanese amber (Perrichot et al. 2003; Azar and Nel 2004; Grimaldi and Engel 2006; Azar et al. 2008, 2010).

Herein a new psyllipsocid genus and species is described from the Lower Cretaceous amber of Lebanon, representing the earliest record of this family.

Material and methods

The amber piece containing the inclusion was cut, shaped, and polished, before preparations between two coverslips and in a Canada balsam medium, as described in Azar et al. (2003). The specimen was examined with a Nikon SZ10 stereomicroscope and a Leitz Laborlux-12 compound microscope, both equipped with camera lucida for line drawings. Photographs were made with an Olympus FE-5000 digital camera.

The works of Smithers (1972, 1990), Lienhard (1998) and Mockford (1993) are followed herein for the systematics of Psocodea. The wing venation nomenclature and terminology of body structures of Smithers (1972) and Lienhard (1998) were adopted.

Systematic Paleontology

Suborder Trogiomorpha Roesler, 1944
Infraorder Psocathropetae Pearman, 1936
Family Psyllipsocidae Enderlein, 1911

***Libanopsyllipsocus* gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Libanopsyllipsocus

Type species. *Libanopsyllipsocus alexanderasnitsyni* sp. n.

Etymology. After "Libano" (Lebanese in Latin), and "*Psyllipsocus*", type genus of the family Psyllipsocidae; gender masculine.

Diagnosis. Hypopharynx with two distinct filaments. Macropterous; forewing without pterostigma; M two-branched; areola postica elongate and free; Cu2 and A ending together forming a nodulus. Hindwing with R1 absent; Rs two-branched; M simple; basal cell present. Distal end of tibia with two inner spines; tarsi three-segmented; distal pretarsi with claw with preapical tooth, and without pulvillus and microtrichia.

***Libanopsyllipsocus alexanderasnitsyni,* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Libanopsyllipsocus_alexanderasnitsyni
Figs 1–12

Holotype. Specimen n° 30 (male, coll. Azar); provisionally deposited in the Muséum National d'Histoire Naturelle, Paris, France.

Locality and horizon. Lower Cretaceous, Upper Barremian – Lower Aptian, amber of Hammana-Mdeyrij, Caza, Baabda, Mohafazat Jabal Loubnan, central Lebanon.

Etymology. In honor of our friend Prof. Alexandr P. Rasnitsyn, a world authority in entomology and palaeoentomology.

Diagnosis. As for the genus (*vide supra*).

Description. Dorsal parts of head and body not preserved. Body and wings without scales (Figs 1–2). Head elongate (but cannot be measured accurately due to state of preservation), sublingual sclerite and hypopharynx with two distinct filaments (Fig. 3). Forewing transparent (Fig. 4), with infrequent small setae, 0.96 mm long, 0.35 mm broad; apex rounded; Sc badly preserved, not reaching C nor R; R1 reaching costal margin 0.73 mm from wing base; pterostigma absent; Rs separating from R 0.46 mm from wing base; Rs bifurcating into R2+3 and R4+5 at 0.76 mm; R2+3 curved, reaching wing margin 0.83 mm distally; R4+5 curved, reaching wing margin at 0.95 mm distally; a transverse crossvein between Rs and M; fork of M into M1 and M2 0.8 mm from wing base, but one wing is aberrant in having M simple [a frequent teratology in Psyllipsocidae as noted by Lienhard (1998)]; Cu1 bifurcating into Cu1a and Cu1b 0.36 mm from wing base forming a free elongate and narrow areola postica; Cu1a much longer than Cu1b; Cu2 (badly preserved) joining anal vein at posterior wing margin in a nodulus 0.28 mm from wing base (Fig. 5); A strongly convex. Wing margin glabrous (Fig. 6), similar in structure to that illustrated by Lienhard (1998: 111, fig. 31b). Hind wing transparent (Fig. 4), bare and smaller than forewing, about 0.75 mm long, 0.24 mm broad; free or individualized and distinct arm of R1 missing; Rs forked into R2+3 and R4+5 0.16 mm from wing apex; basal cell present; simple M reaching wing margin apically; basal part of wing badly preserved. Hind leg with tibia + tarsi slightly longer than abdomen. Coxal rasp of Pearman's organ present on hind leg (Fig. 7), but without tympanum (the coxal rasp is preserved on one leg as the coxal area is missing on the other leg). Tibiae with two apical spurs on inner sides; all tarsi three-segmented with first tarsomere longer than others; pretarsal claws with a preapi-

cal tooth, without microtrichia nor pulvillus (Fig. 8). Abdomen 0.52 mm long, 0.32 mm broad; telson with epiproct and paraproct as represented in Figs 9–12, paraproct with a rounded hemispherical sensory area of trichobotria, and a spine in its ventral inner side; male genitalia with simple hypandrium, aedeagus with phallosome presenting parameres with curved arms not fused anteriorly as represented in Fig. 9 (it can be seen owing to transparency of sclerites and is comparable in structure to what occurs in other Psyllipsocidae (cf. Lienhard 1998: 112, fig. 32b).

Discussion

Following the keys of Smithers (1972), Mockford (1993), and Lienhard (1998), *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n. would fall into Trogiomorpha and can be placed in Psyllipsocidae owing to the following combination of characters, considered diagnostic of the family (Smithers 1972, 1990; Mockford 1993; Lienhard 1998), and present in the current fossil: head elongate; hypopharynx with two distinct sclerotized filaments; presence of nodulus; posterior legs with tibia + tarsi longer than abdomen; tarsi three-segmented; distal pretarsi with claw bearing preapical tooth, without pulvillus; paraproct with anal spine; phallosome with two curved arms not fused anteriorly. Other diagnostic characters of the family Psyllipsocidae could be present but cannot be seen in the specimen owing to the state of preservation, i.e., some parts of the animal are missing.

Our fossil presents a striking and astonishing similarity in some of the wing features (like elongate areola postica and M 2-branched in forewing) with the psocids belonging to the troctomorphan family Pachytroctidae, to the point that any psocidologist at first glance to the specimen would assign it to this family, and as in Pachytroctidae only females could be winged, he would tell directly that this is a female! A minute examination of the specimen shows that the fossil is a male with genitalia structure comparable to those of Psyllipsocidae as figured by Lienhard (1998: 112, fig. 32b) with the very particular conical phallosome directed forwards. Moreover, our fossil could not belong to the Pachytroctidae for several reasons: (1) in the forewing Cu2 and A are meeting together on the wing margin thus forming a nodulus, the absence of this feature being characteristic for Pachytroctidae; (2) presence of Pearman's coxal organ in hind legs, here too the absence of this feature is characteristic of the Pachytroctidae (Yoshizawa and Lienhard, 2010), and even for the whole Nanopsocetae that include this family; (3) presence of distinct separated sclerotized filaments of hypopharynx characteristic of all Trogiomorpha, whereas in Troctomorpha (that enclose Pachytroctidae) these filaments are fused.

Our fossil shows a derived character for its hind wing with M simple, though the majority of the fully-winged extant species of Psyllipsocidae, like most of the trogiomorphan psocids, have hind wings with M forked (a feature considered plesiomorphic in general for the Psocodea).

Libanopsyllipsocus gen. n. differs from all modern genera by several features of its wings; i.e., from the genera *Dorypteryx* Aaron, 1899 and *Psocathropos* Ribaga, 1899 by the glabrous anterior margin of the forewing; from *Pseudodorypteryx* García-Aldrete, 1984 and *Dorypteryx* Aaron, 1899 by the broad forewing. *Libanopsyllipsocus* gen. n. resembles mostly the genus *Psyllipsocus* Sélys-Longchamps, 1872 but differs from it in its forewing without a pterostigma and M two-branched, and in its hind wing with R1 absent and M simple. *Libanopsyllipsocus* gen. n. differs from the genus *Khatangia* Vishniakova, 1975 in the absence of a pterostigma and an elongate areola postica in the forewing. All these differences and many others lead us to the proposal of a new genus.

The monophyly of the family Psyllipsocidae is supported by one character of the female genitalia: the spermathecal sac with complex scleritizations at the origin and usually with an accessory vesicle. Molecular analysis also supports the monophyly of the family (Yoshizawa et al. 2006). *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n. represents the oldest record of the Psyllipsocidae and demonstrates that this family is at least as old as the lowermost Cretaceous, if not older. Unexpectedly some features of this very old fossil are probably derived, viz., the absence of a pterostigma in the forewing and M simple in the hind wing. The discovery of new fossils belonging to this family could bring more information on the polarity and potential homoplasy of some characters in use for the classification, and increase as such our knowledge of the evolutionary history of this lineage.

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Plates

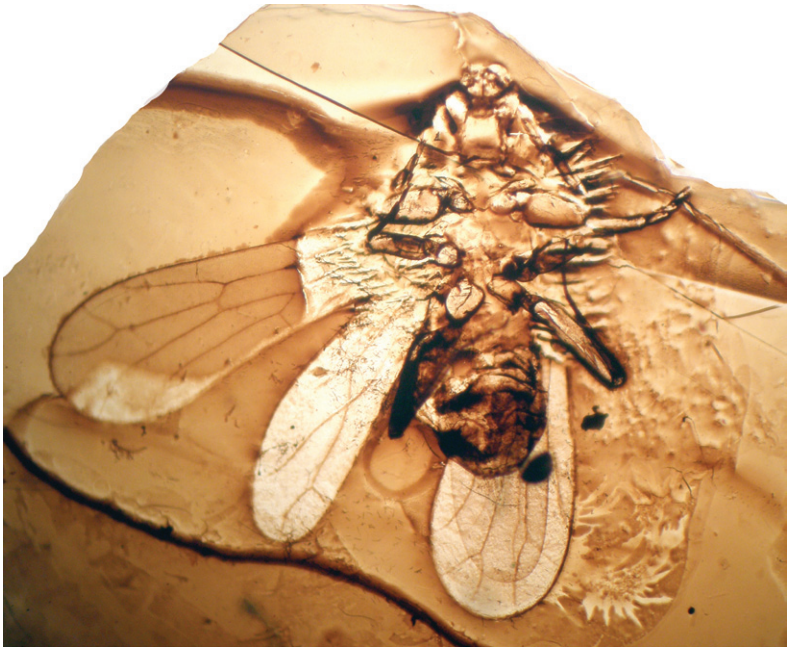

Figure 1. Photograph of habitus of *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n., holotype, male, specimen number 30.

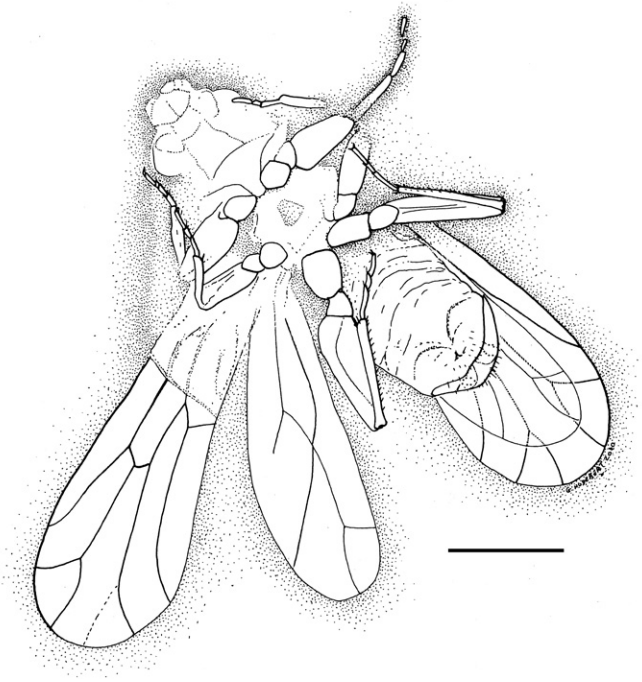

Figure 2. Drawing of habitus of *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n., holotype, male, scale bar = 0.3 mm.

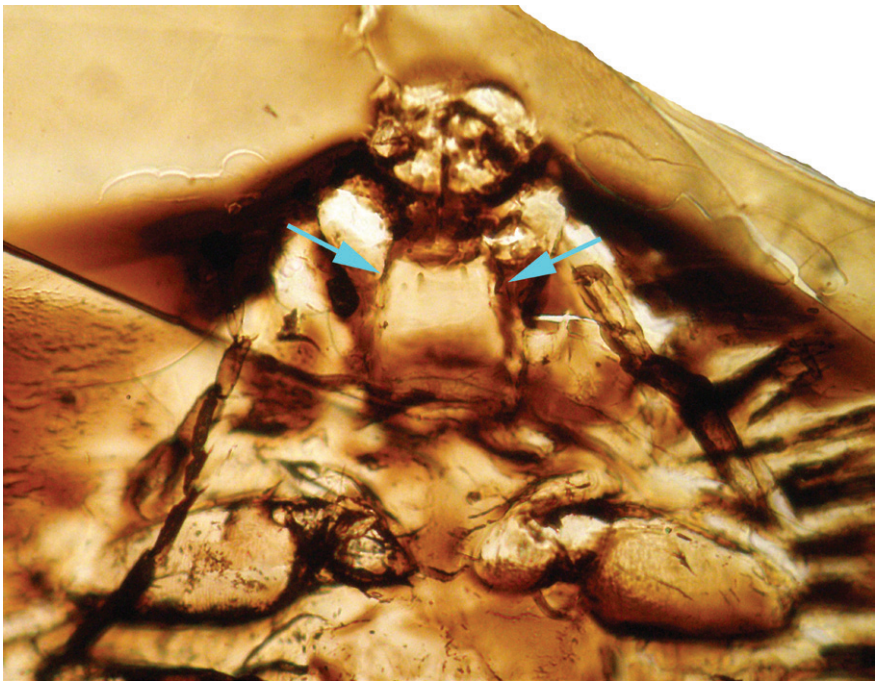

Figure 3. Photograph of hypopharynx filaments (arrows) of *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n., holotype, male.

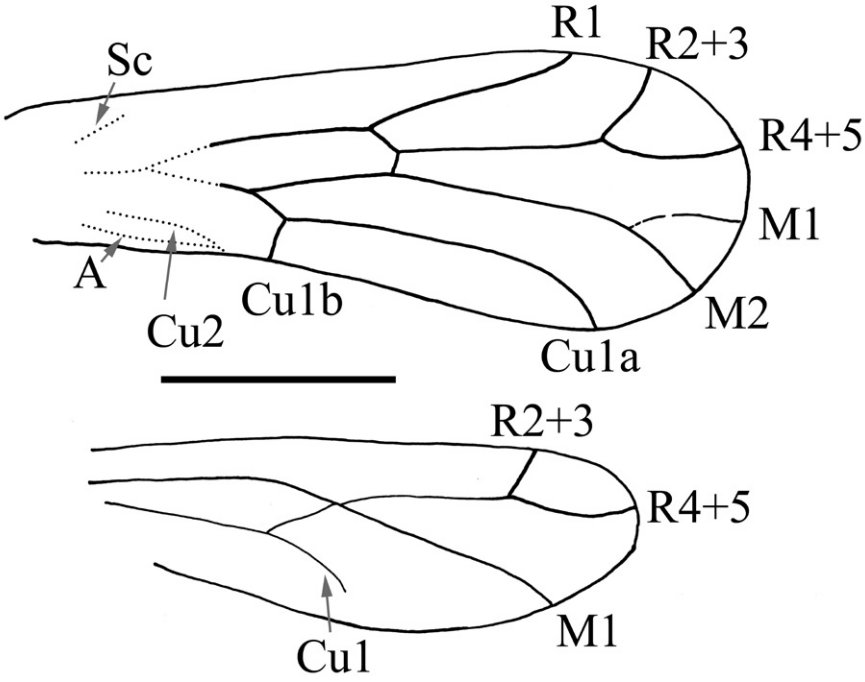

Figure 4. Drawing of wings of *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n., holotype, male, scale bar = 0.3 mm.

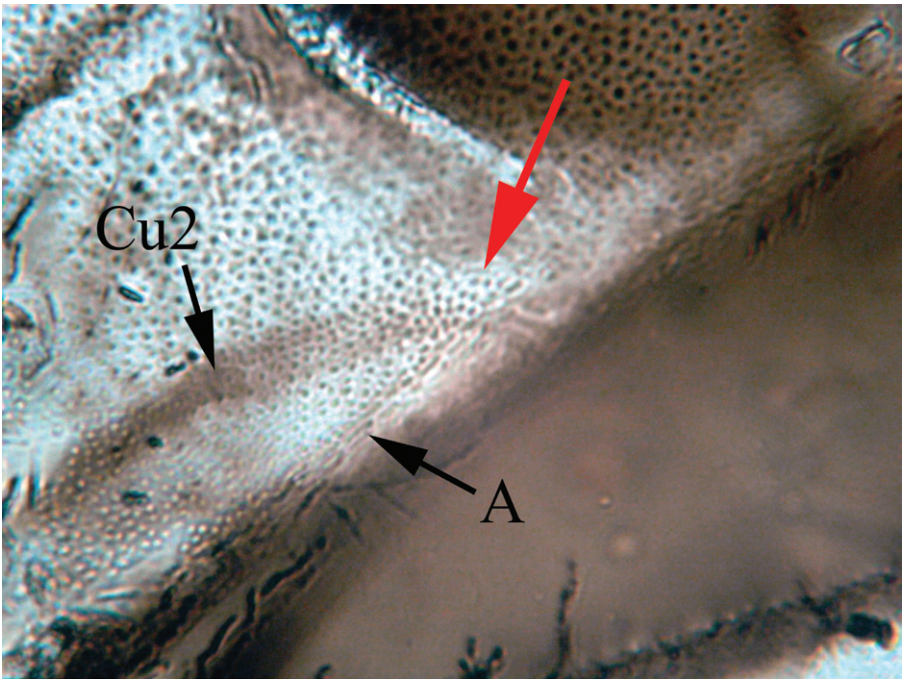

Figure 5. Microphotograph of nodulus, arrow showing the meeting area of Cu2 and A.

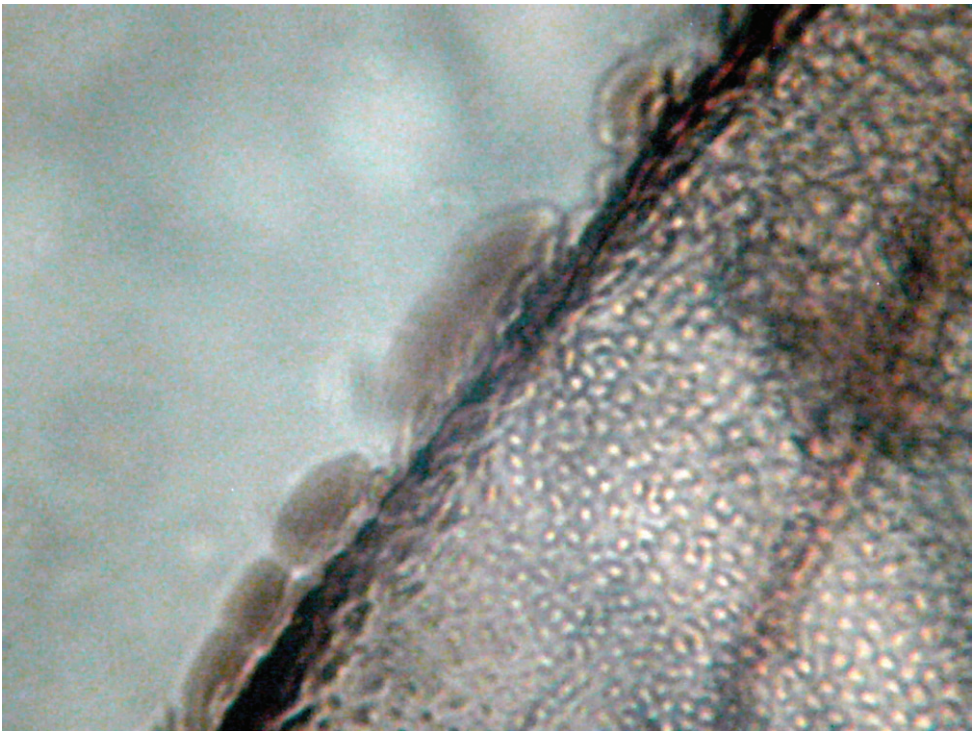

Figure 6. Microphotograph of structure of forewing margin.

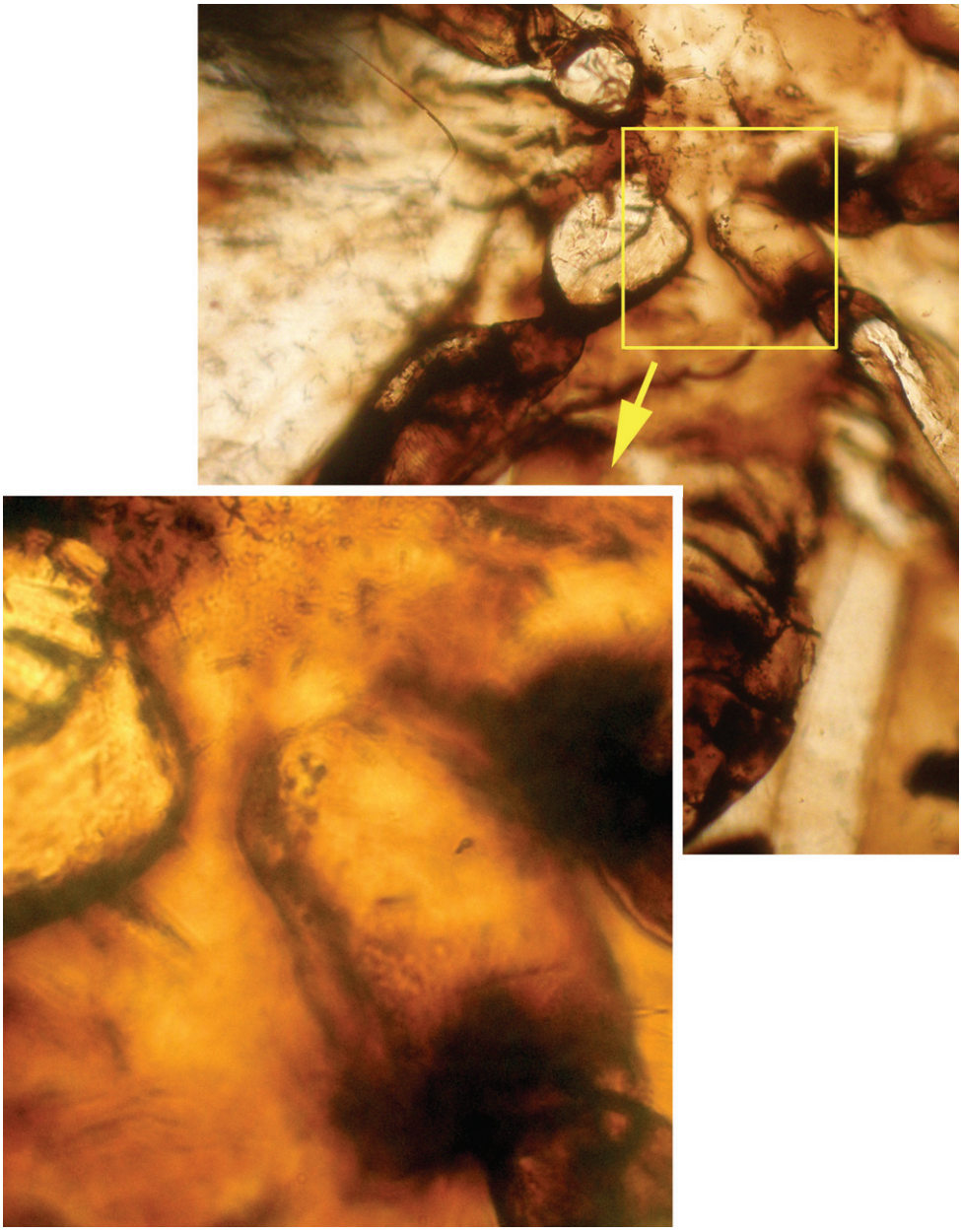

Figure 7. Microphotograph of hind leg coxal rasp (Pearman's organ).

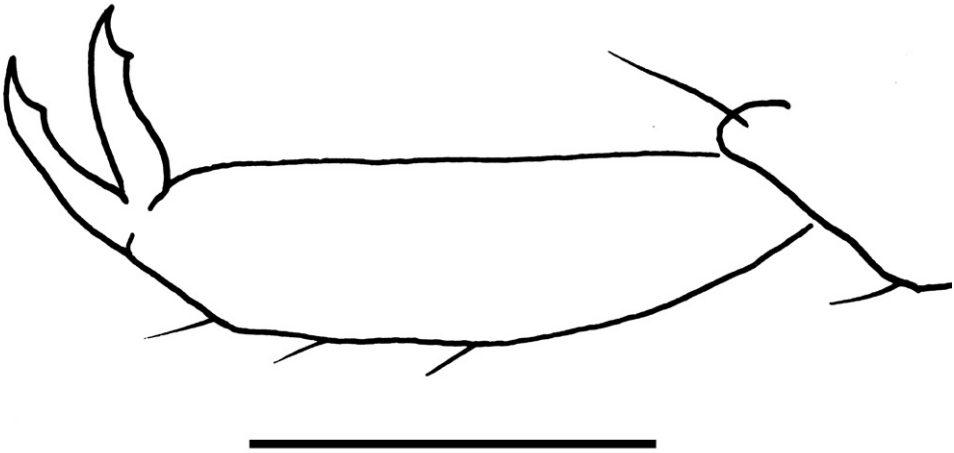

Figure 8. Drawing of pretarsal claw of *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n., holotype, male, scale bar = 0.03 mm.

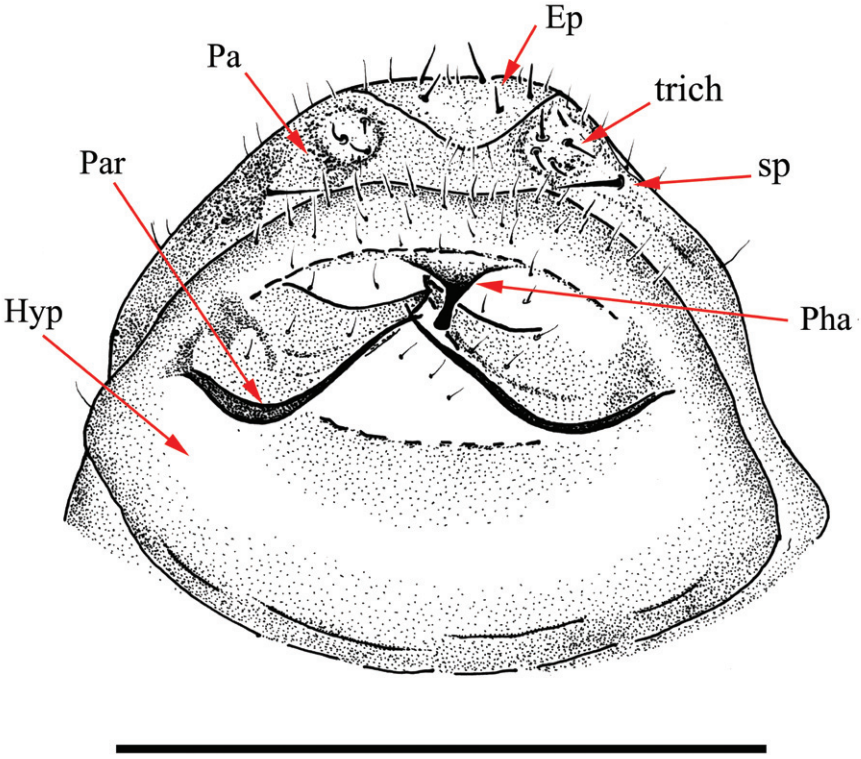

Figure 9. Drawing of aedeagus of *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n., holotype, male; Ep = epiproct, Hyp = hypandrium, Par = paraproct, par = paramers, Pha = phallosome, sp = anal spine, trich = trichobothria; scale bar = 0.3 mm.

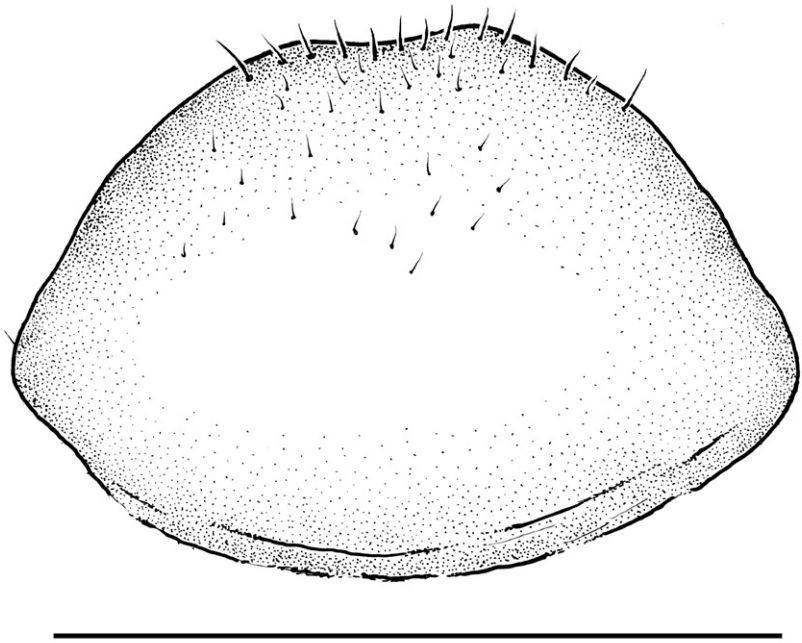

Figure 10. Drawing of hypandrium of *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n., holotype, male; par = paraproct, ep = epiproct, trich = trichobothria; scale bar = 0.3 mm.

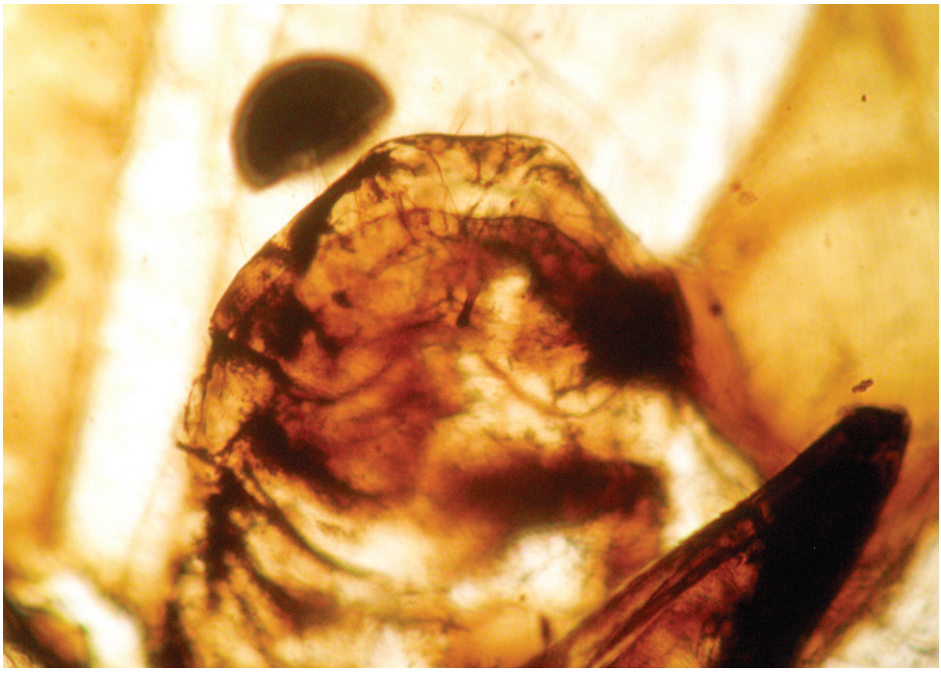

Figure 11. Photograph of hypandrium and aedeagus of *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n., holotype, male.

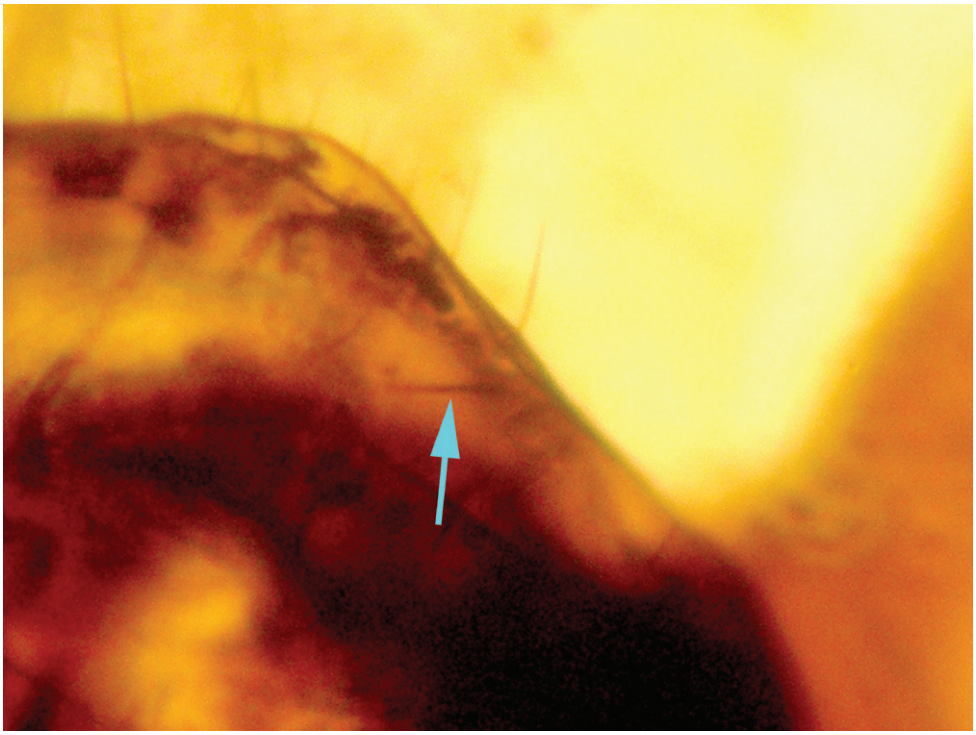

Figure 12. Photograph of paraproct of *Libanopsyllipsocus alexanderasnitsyni* gen. et sp. n., holotype, male; arrow shows the anal spine.

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A new family of aphids (Hemiptera, Sternorrhyncha) from the Lower Cretaceous of Baissa, Transbaikalia

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Abstract

The family Rasnitsynaphididae **fam. n.** has a unique combination of characters: 9-segmented antennae; rhinaria arranged in many transverse rows, surrounding the antennal segments; segment IX narrower than other segments of flagellum, always without rhinaria; cubitus branches separated; ovipositor present; siphuncular pores absent. The new family comprises the genus *Rasnitsynaphis* **gen. n.** with three species, *R. ennearticulata* **sp. n.**, *R. coniuncta* **sp. n.**, and *R. quadrata* **sp. n.,** all from the Lower Cretaceous of Transbaikalia.

Keywords

Hemiptera, aphids, fossil insects, Lower Cretaceous, Baissa, new family, new genus, new species

Introduction

Baissa is one of the most important Lower Cretaceous insect fossil sites. The outcrop is located in the Asian part of Russia, in western Transbaikalia, on the left bank of the Vitim River. The exact age of lacustrine sediments of the Zaza Formation at Baissa is

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disputable, usually estimated as Early Cretaceous (Neocomian–Aptian), however most paleoentomologists date them as Valanginian–Hauterivian (Zherikhin et al. 1999).

More than 20 000 fossil insects (including above 2 500 aphid specimens), often of excellent preservation state, have been collected there. Nearly all aphids from Baissa belong to three families: Ellinaphididae Kania & Wegierek, 2008, Szelegiewicziidae Wegierek, 1989 (both in Palaeoaphidoidea), and Oviparosiphidae Shaposhnikov, 1979 (Aphidoidea). The new taxa described below show an even higher morphological diversity of aphids in the Lower Cretaceous.

Material and methods

The material comes from the collection of the Laboratory of Arthropods, Paleontological Institute (PIN), Russian Academy of Sciences, Moscow, where it is currently stored. The research methods did not differ substantially from those widely used in paleoentomological research (Rasnitsyn 2002). The imprints were photographed under the stereoscopic and the light microscope. The graphics tablet was applied to make the drawings on the photographic layer in Adobe Photoshop. In case when the specimen was represented by two imprints, the drawings are based on both reverse and obverse, while the photograph presents only one imprint. The number of rhinaria given in the descriptions always relates only to the one side of the antenna. It results from the lack or the weak preservation of one of the imprints. All measurements are given in mm.

Taxonomy

Hemiptera Linnaeus, 1758
Sternorrhyncha Amyoy & Serville,1843
Aphidomorpha Becker-Migdisova & Aizenberg, 1962

Rasnitsynaphididae fam. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Rasnitsynaphididae

Type genus. *Rasnitsynaphis* gen. n.

Diagnosis. Antennae 9-segmented, shorter than hind tibia. Rhinaria arranged in many transverse rows, surrounding antennal segments. Segment IX narrower than other segments of flagellum, blunt at apex, always without rhinaria. Cubitus branches separated. Vein Rs separates from pterostigma in one third of its length. Media originates below the base of pterostigma. Ovipositor present. Siphuncular pores absent.

***Rasnitsynaphis* gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Rasnitsynaphis

Type species. *Rasnitsynaphis ennearticulata* sp. n.

Etymology. Named to honour Alexandr P. Rasnitsyn, who is not only eminent researcher, but also a teacher of many paleoentomologists. P.W. is honoured to be one of his students.

Diagnosis. As for family.

Description. Body massive. Front edge of head convex. Head with epicranial suture. Rostrum shorter than body, reaching to the middle of abdomen. Antennae longer than one third of the body length but shorter than its half. Antennal segment III 2–4 times as long as wide; segments IV-VIII of the same length or nearly so. Surface of all segments of flagellum sculptured in form of transverse ribs. Rhinaria ellipsoidal, arranged in more or less dense rows which are sometimes joined. Cubital vein CuA_1 2.5 times longer than CuA_2. Pterostigma big, spindle-shaped, pointed, 3–3.5 times as long as wide. Vein Rs slightly bent at base. Media with two or three branches. Bifurcation of vein M into M_1 and M_2 or into M_{1+2} and M_3 just beyond the base of vein Rs.

Key to species of *Rasnitsynaphis*

1 Antennae short, about 1/2 of thorax height, segment III two times as long as wide, with ca. 9 rows of rhinaria; segments IV–VIII as long as wide; M with 2 branches ..... ***R. quadrata* sp. n.**

– Antennae longer, segment III three to four times as long as wide; segments IV–VIII longer than wide **2**

2 Segment III four times as long as wide, with ca. 11 rows of rhinaria .... ***R. coniuncta* sp. n.**

– Segment III three times as long as wide, with ca. 17 rows of rhinaria; M with 3 branches ..... ***R. ennearticulata* sp. n.**

***Rasnitsynaphis ennearticulata* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Rasnitsynaphis_ennearticulata
Fig. 1

Material. Holotype: PIN 3064/2109(2211); Baissa, Transbaikalia; Zaza Formation, bed 31.

Etymology. From the Greek term *ennea* for "nine" and from the Latin term *articulum* for "segment" in reference to the 9-segmented antennae.

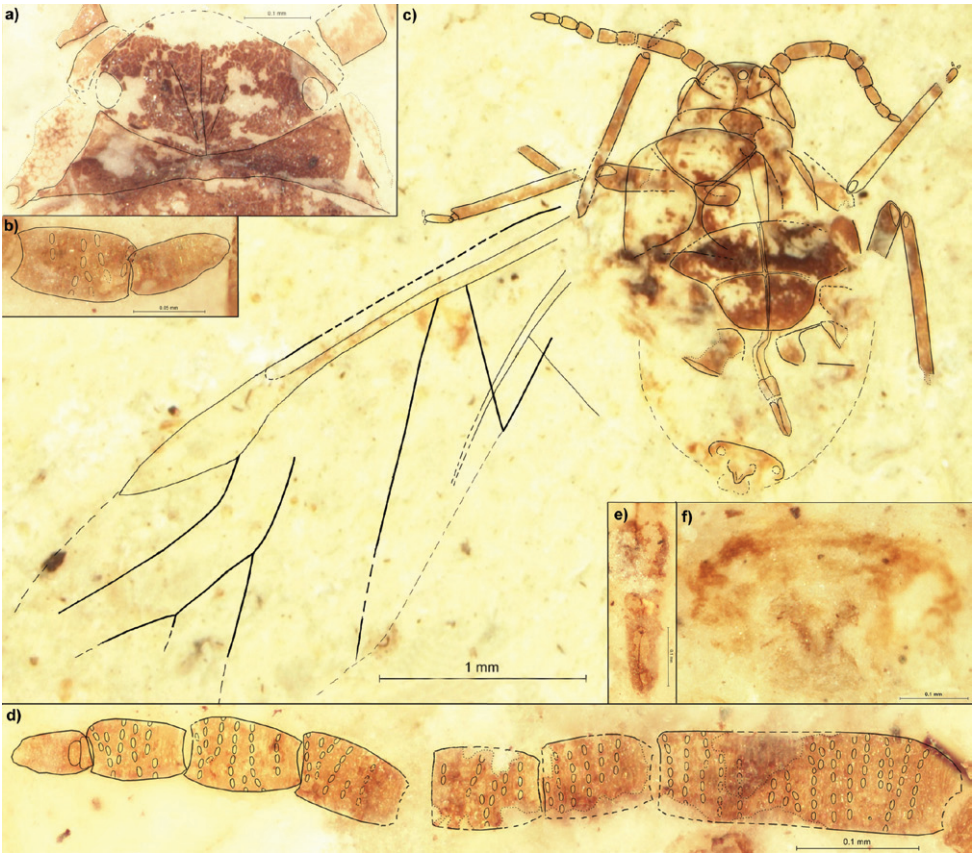

Figure 1. *Rasnitsynaphis ennearticulata* sp. n., PIN 3064/2109(2211) (holotype): **a** head, dorsal view **b** VIII and IX segment of right antenna, ventral view **c** body, ventral view **d** flagellum of left antenna, ventral view **e** apical segment of rostrum, ventral view **f** apical part of abdomen with ovipositor, ventral view.

Diagnosis. Antennae rather long; segment III three times as long as wide; segments IV–VIII of about the same length, rectangular, longer than wide. Media with three branches.

Description. Length of the body 2.1 (Fig. 1c). Width of head 0.43 (Fig. 1a). Lateral sutures join in the middle of epicranium in the four fifth of the head length. On the dorsal side of head capsule there are three diagonal strips, running from the middle part of epicranium to the frontolateral edge of head. The distance between ocelli (situated on the back of head) 0.27. Length of the apical segment of rostrum 0.18 (Fig 1e). Antennae 0.93 long, ca. 0.8 of thorax width (Figs 1b, d). Length of antennal segments: I 0.06; II 0.08; III 0.23; each of IV–VII 0.09; VIII 0.08; IX 0.07. Antennal segment III with about 17 rows of rhinaria, with at most 8 rhinaria arranged in one row. Segments IV–VIII at most with 7 rows of rhinaria. Tibia of fore legs 0.75 long, middle tibiae 0.83 to 0.86. Mesothoracic sternite 0.93 wide, 0.53 long. Fore wings about 3.8 long. The distance from the base of the wing to the end of pterostigma 2.8. Distance

between bases of cubital veins CuA_1 & CuA_2 0.14. The length of M_{1+2} more or less equals the length of the common stem of M. The posterior part of abdomen strongly sclerotized (Fig. 1f).

***Rasnitsynaphis coniuncta* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Rasnitsynaphis_coniuncta
Fig. 2

Material. Holotype: PIN 3064/2209; Baissa, Transbaikalia; Zaza Formation, bed 31.

Etymology. From the Latin term *coniunctus* for "joined" in reference to the joined rows of rhinaria.

Diagnosis. Antenna rather long; segment III four times as long as wide; segments IV–VIII of about the same length, rectangular, longer than wide.

Description. Length of the body about 2.4 (Fig. 2b). Head with epicranial suture. Antennae 0.88 long, about 2/3 of thorax height (Figs 2a, c). Length of antennal segments:

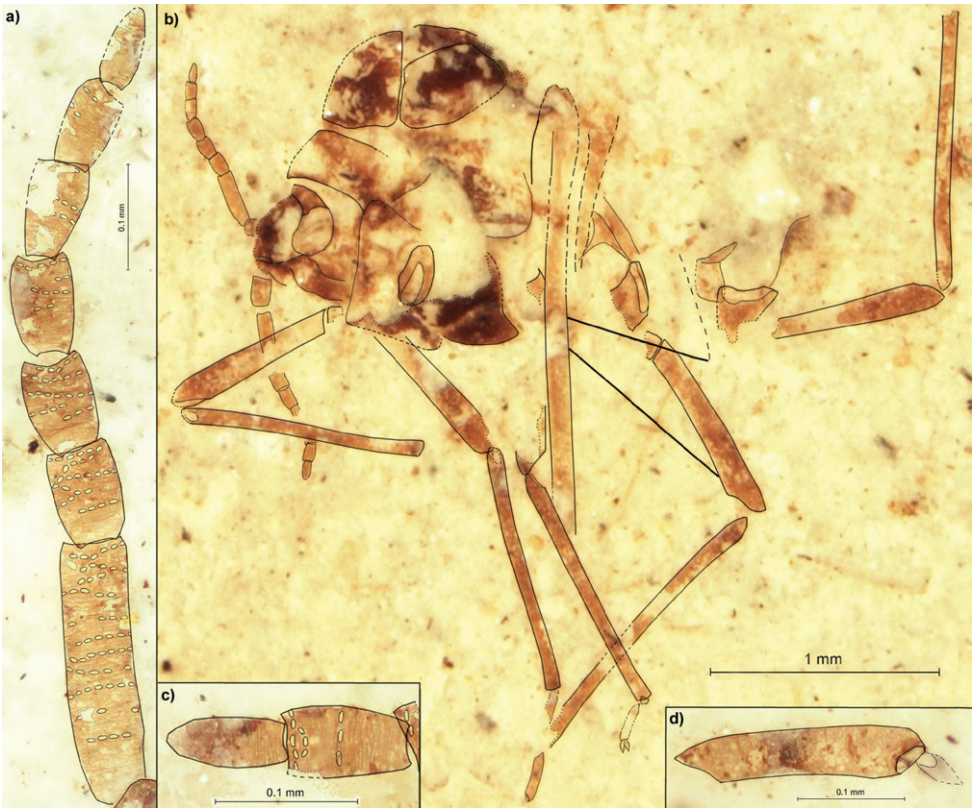

Figure 2. *Rasnitsynaphis coniuncta* sp. n., PIN 3064/2209 (holotype): **a** flagellum of right antenna **b** body, lateral view **c** VIII and IX segment of left antenna **d** second segment of hind tarsus.

II 0.12; III 0.24; IV 0.09; V 0.08; each of VI–VII 0.09; VIII 0.08; IX 0.07 to 0.08. Antennal segment III with 11 rows of rhinaria, with at most 7 rhinaria arranged in one row. Segments IV–VIII at most with 6 rows of rhinaria. Femur of fore legs 0.74 long, tibia 1.06. Middle tibia 1.14 long. Hind femur 0.87 long, tibia 1.34. The second segment of hind leg tarsus 0.24 (Fig. 2d). The distance between bases of cubital veins CuA_1 & CuA_2 0.13.

***Rasnitsynaphis quadrata* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Rasnitsynaphis_quadrata
Fig. 3

Material. Holotype: 3064/2279; Baissa, Transbaikalia; Zaza Formation, bed 31.

Etymology. From the Latin term *quadratus* for "square" in reference to the square shape of antennal segments IV–VII.

Diagnosis. Antennae quite short; segment III two times as long as wide; segments IV–VII of the same length, square, as long as wide. Media with two branches.

Description. Length of the body 2.0 (Fig. 3b). Length of head 0.28. Head with lateral sutures. Length of the apical segment of rostrum 0.14 (Fig. 3c). Antennae 0.71

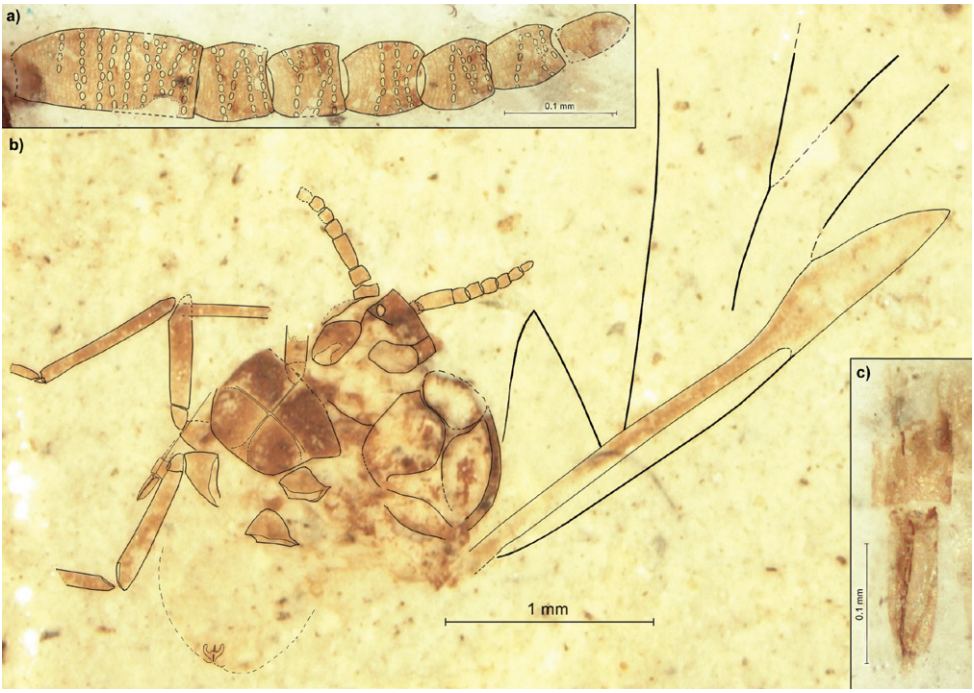

Figure 3. *Rasnitsynaphis quadrata* sp. n., PIN 3064/2279 (holotype): **a** flagellum of right antenna, dorsal view **b** body, ventral view **c** apical segment of rostrum.

long, about 1/2 of thorax height (Fig. 3a, b). Length of antennal segments: I 0.06; II 0.07; III 0.16; each of IV–IX 0.06. Antennal segment III with about 9 rows of rhinaria, with at most 8 rhinaria arranged in one row. Segments IV–VIII at most with 4 rows of rhinaria. Femur of middle legs 0.54 long, tibia 0.73. Hind femur 0.57 long. Mesothoracic sternite 0.49 long. The distance from the base of the wing to the end of pterostigma 2.7. The distance between bases of cubital veins CuA_1 & CuA_2 0.11. The posterior part of abdomen weakly sclerotized.

Discussion

The family Rasnitsynaphididae fam. n. on the one hand possesses primitive features of Jurassic Sinojuraphididae Huang & Nel, 2008 and Genaphididae Handlirsch, 1907, but on the other hand the features typical for Early Cretaceous Oviparosiphidae and Ellinaphididae, and also certain features of recent Aphididae and Drepanosiphidae (Heie & Wegierek 2009).

The body morphology and wing venation of the new family are typical for Lower Cretaceous aphids. The 9-segmented antennae recorded in Rasnitsynaphididae is the plesiomorphic feature and proves the presence of forms intermediate between Middle Jurassic Sinojuraphididae with 12-segmented antennae (Huang & Nel 2008) and Mesozoic and modern aphids with 7-, 6- or 5-segmented antennae. In the general structure of antenna, which is relatively short and massive, it resembles many representatives of Oviparosiphidae. Due to the arrangement of numerous small, ellipsoidal rhinaria in transverse rows, Rasnitsynaphididae is similar to Ellinaphididae and *Jurocallis* Shaposhnikov, 1979, however the length ratio of flagellum segments is different.

In the shape of pterostigma and place of Rs separation *Rasnitsynaphis* is similar to the species of *Oviparosiphum* Shaposhnikov & Wegierek, 1989. In the structure of CuA and M veins *Rasnitsynaphis* resembles *Bajsaphis* Shaposhnikov 1985, *Acanthotrichaphis* Shaposhnikov & Wegierek 1989, *Vitimaphis* Shaposhnikov & Wegierek 1989, and other genera of the family Oviparosiphidae (Zhang et al. 1989). In the course of the M vein *Rasnitsynaphis enneaticulata* sp. n. is similar also to *Penaphis* Lin, 1980 (Jarzembowski 1989, Lin 1995) and some species of the families Aphididae and Drepanosiphidae (Shaposhnikov 1980).

Having so many features in common with the family Oviparosiphidae, the new family differs from it by the 9-segmented antennae and lack of siphunculi.

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RESEARCH ARTICLE

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A new genus and species of Dictyopharidae (Homoptera) from Rovno and Baltic amber based on nymphs

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Abstract

Alicodoxa rasnitsyni **gen. et sp. n.** (Dictyopharinae: Orthopagini) is described based on a nymph from Rovno amber; it also occurs in Baltic amber. A small additional wax plate dorsal to the large wax plate of abdominal tergites VI–VIII is first reported in this and other genera of Dictyopharidae. A lectotype is designated for *Pseudophana reticulata* Germar & Berendt, 1856 transferred to *Protepiptera* (Achilidae): *Protepiptera reticulata* (Germar & Berendt, 1856), **comb. n.**

Keywords

Fulgoroidea, planthoppers, Dictyopharinae, Orthopagini, Achilidae, fossil, Baltic amber, Eocene, morphology, wax plates

Introduction

The family Dictyopharidae is poorly represented in the fossil record. Its oldest member, described from the Upper Cretaceous (Santonian) of Taimyr, has been assigned to the

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extinct tribe Netutelini (Emeljanov 1983). Several Cenozoic genera have been attributed to the family, but most of them need re-examination to determine their systematic position in more detail (see Szwedo et al. 2004, Szwedo 2008). Recently, Szwedo (2008) described a new monotypic genus from Baltic amber and placed it in a tribe of its own, Worskaitini, which he considered closely related to Netutelini.

Two nymphs from Late Eocene Baltic amber were described by Germar and Berendt (1856) as *Pseudophana reticulata*, i.e. as Dictyopharidae in the modern sense (*Dictyophara* Germar = *Pseudophana* Burmeister). Based on the original illustrations, these two specimens have been reinterpreted by Emeljanov (1983), the 3rd instar as resembling Tropiduchidae, and the late instar ("pupa") as belonging to Achilidae, most probably to the extant genus *Cixidia* Fieber. The late instar nymph (designated below as the lectotype of *P. reticulata*) indeed seems to be an achilid and presumably belongs to the extinct genus *Protepiptera* Usinger, which is similar to *Cixidia*, whereas the 3rd instar nymph is a dictyopharid. A photograph of yet another 3rd instar nymph of Dictyopharidae from Baltic amber has been published by Weitschat and Wichard (1998: pl. 46a). These two dictyopharid nymphs are conspecific with an excellently preserved nymph from Rovno amber, described below as a new genus and species and placed with substantial certainty into the extant tribe Orthopagini.

The Rovno amber from NW Ukraine is roughly contemporaneous to Baltic amber, both Late Eocene in age and containing similar but distinct insect faunas with many species in common (Perkovsky et al. 2010). The second planthopper species shared between the two ambers is *Protepiptera kaweckii* Usinger, 1939 (Achilini s.l.), the commonest Baltic amber achilid (redescribed by Emeljanov and Shcherbakov 2009). Other planthopper families recorded from Rovno amber are Tropiduchidae (Perkovsky and Bodgasarov 2009) and Cixiidae.

Material and methods

The specimen was collected in Klesov, Rovno Region, Ukraine, and deposited in the amber collection of the Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev (SIZK). Morphological terminology follows Emeljanov (1993, 1994). Photographs were taken with Leica MZ9.5 stereomicroscope and Leica DFC420 camera and post-processed using Helicon Focus software.

Taxonomy

Superfamily Fulgoroidea Latreille, 1807
Family Achilidae Stål, 1866
Tribe Achilini Stål, 1866, s.l.
Genus *Protepiptera* Usinger, 1939

***Protepiptera reticulata* (Germar & Berendt, 1856), comb. n.**
http://species-id.net/wiki/Protepiptera_reticulata

Pseudophana reticulata Germar & Berendt, 1856: 16, pl. II, fig. 4b (pars)
Dictyophara reticulata (Germar & Berendt, 1856): Metcalf and Wade 1966: 126
Cixidia reticulata (Germar & Berendt, 1856): Szwedo et al. 2004: 85

Lectotype. Late instar nymph ("pupa") in Baltic amber, former East Prussia (Germar and Berendt 1856: 16, pl. II, fig. 4b), designated here.

Remarks. Of the two syntype nymphs, the late instar is selected as a lectotype. The 3rd instar nymph, belonging to Dictyopharinae, is discussed under the new genus and species below. According to Szwedo et al. (2004), the type material was probably lost during World War II.

This species is possibly a senior synonym of *P. kaweckii* Usinger, 1939 based on adults and very common in Baltic amber. Other possible senior synonyms of *P. kaweckii* are *"Cixius" longirostris* Germar et Berendt, 1856 and *"Oliarus" oligocenus* Cockerell, 1910 (Emeljanov and Shcherbakov 2009).

Family Dictyopharidae Spinola, 1839
Subfamily Dictyopharinae Spinola, 1839
Tribe Orthopagini Emeljanov, 1983

Genus *Alicodoxa* gen. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Alicodoxa

Type species. *Alicodoxa rasnitsyni* sp. n.

Etymology. The genus and the type species are named in honour of our friend and colleague Prof. Alexandr Rasnitsyn. The grammatical gender is feminine.

Diagnosis. Metope not visible in dorsal aspect. Coryphe 1/3 longer than pronotal disc along midline. Pronotum deeply angulately emarginate posteriorly. Lateral carinae of mesonotal disc anteriorly converging at acute angle. Fore femur without subapical tooth. Abdominal tergites IV–V with 1–2 sensory pits displaced forwards from the row of pits. Tergites VI–VII with 2 medial and 2–3 lateral pits. Tergites VI–VIII with large lower and small upper wax plates, upper plate of tergite VII subdivided.

Remarks. Similar to the extant genera *Orthopagus* Uhler and *Saigona* Matsumura, but in the nymphs of these latter the metope is visible from above, coryphe longer relative to pronotal disc, pronotum less emarginate posteriorly, and tergites VI–VII with 4 medial and 1–0 lateral pits. Subdivided upper wax plate of tergite VII is unknown in other Dictyopharidae. Other characters listed under Diagnosis assign the new genus to Orthopagini within Dictyopharinae (see Discussion).

***Alicodoxa rasnitsyni* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Alicodoxa_rasnitsyni
Figs 1–5

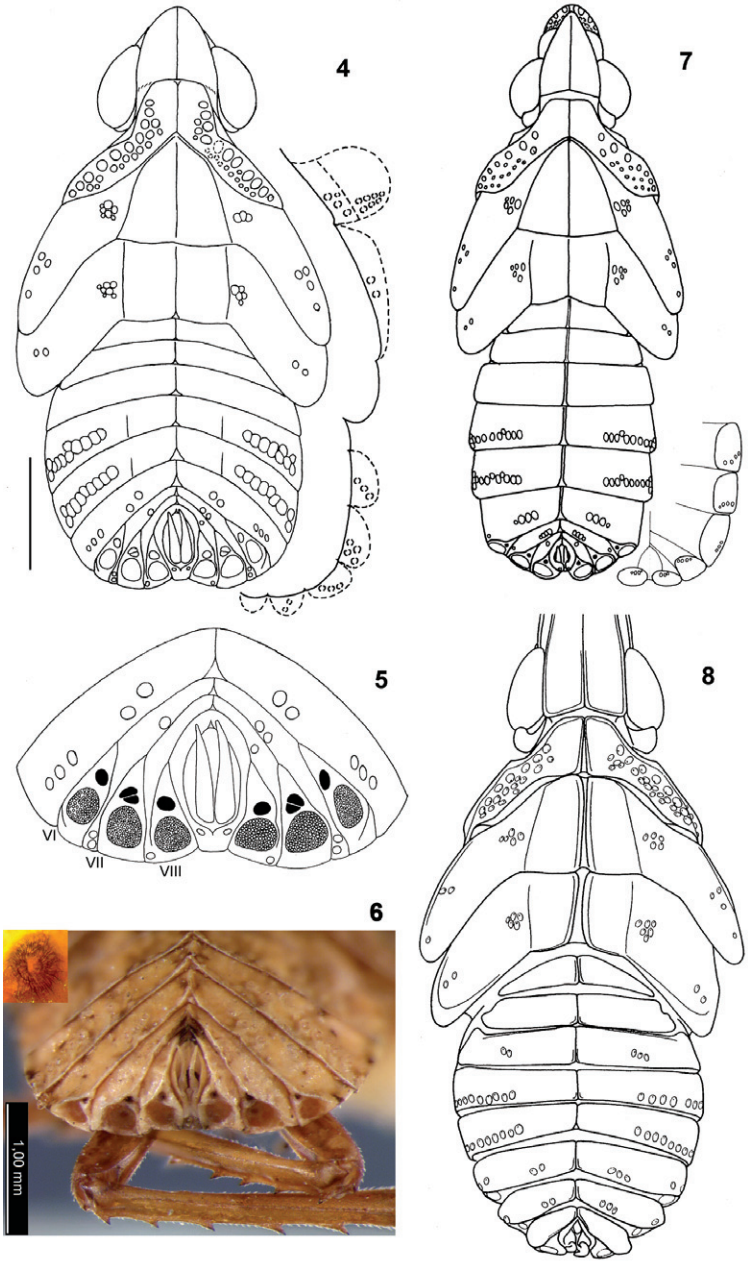
Material. Holotype, 4th instar nymph, SIZK K-3719, Klesov, Rovno amber, Ukraine; Late Eocene. Syninclusions: Mycetophilidae, Sciaroidea, Symphypleona, Acari, stellate hairs. Petaloid blind fissures arising all around lateral margins of the nymph and directed nearly laterad completely separate its dorsal and ventral sides so that only parts of its mid and hind legs are visible from above. The ventral aspect is mostly masked with variously directed fissures and in some places with milky impurities.

Description. Nymph dark brown, ovoid, moderately elongate, 4.1 mm long, 2.2 mm wide; head projecting forwards beyond oval contour; dorsum finely transversely shagreened. Coryphe somewhat longer than wide; its lateral and anterior margins forming regular parabola; its posterior margin very shallowly concave, situated at about eye midlength in dorsal aspect. All carinae of coryphe, including posterior one and medial one, well developed. Metope (only partly visible) with medial areas somewhat widened at head apex; lateral areas with two rows of sensory pits, with an additional row of four smaller pits in between the two rows. Rostrum reaching beyond hind coxae, apical segment shorter than subapical one.

Pronotal disc strongly projecting forwards (2/3 of its median length situated anterior to level of posterior eye margins), its anterior margin truncate, almost straight, anterolateral angles rounded, lateral margins moderately diverging backwards. Posterior margin of pronotum with deep right-angled emargination reaching almost 1/3 of pronotal disc length. Pronotal disc slightly narrower and 1/4 shorter along midline than coryphe, bordered with distinct carinae along all free margins, medial carina also distinct, but posterolateral carinae undeveloped, and boundary between disc and lateral lobes traceable only as flexure of surface plane (posterior ends of these flexures close to points where lateral carinae of mesonotal disc approach pronotal margin). Sensory pits of pronotal disc and paradiscal areas forming one entity: disc with row of 4 large pits along lateral margin and 3 smaller pits in second, more medial row; paradiscal area with 6 large pits in marginal row (indistinctly subdivided into two groups, each with 3 pits) and 8–10 smaller pits in second row. Humeral area with 3 pits in main row and 1 additional pit; pectoral group of pits (about 7 in two tangled rows) situated as is usual in the family near posterior margin of paranotal lobe. Lateral and collateral carinae distinct. Mesonotal disc

Figures 1–3. *Alicodoxa rasnitsyni* gen. et sp. n. (Orthopagini), 4th instar nymph, Rovno amber: **1** dorsal view **2** anteroventral view **3** lateral view (all to same scale); inset, wax plates of the right side, enlarged.

arrow-shaped anteriorly (its lateral carinae anteriorly converging at nearly acute angle, running parallel to posterior pronotal margin). Group of 6–7 pits (3 medial pits larger) situated laterad of lateral carinae. Fore wing pads mediad of subcostal carina with 3 pits (in triangle) in middle part and 1 pit near apex, and in costal area with 2 pits in middle



Figures 4–8. 4–5 *Alicodoxa rasnitsyni* gen. et sp. n., 4th instar nymph, Rovno amber: **4** dorsal view, slightly corrected and schematized; on the right, arrangement of sensory pits on the lateral body parts facing ventrad (scale bar, 1 mm) **5** posterior part of the abdomen, arrangement of wax plates and sensory pits; **6–7** *Saigona ussuriensis* (Lethierry) (Orthopagini), nymphs, recent: **6** 5th instar, posterior part of the abdomen with wax plates; inset, upper wax plate of segment VIII, enlarged **7** 4th instar, dorsal view; on the right, arrangement of sensory pits on ventrolateral parts of the tergites; **8** *Dictyophara pannonica* (Germar), 4th instar nymph, recent, dorsal view (apical part of the head not shown; after Emeljanov 1994).

part (against group of 3 pits). Posterior margins of fore and hind wing pads subparallel, directed obliquely posterolaterad. Metanotal disc rectangular, about 1.3 times as wide as long, with all carinae distinct. Medial group of pits laterad of disc similar to that on mesonotum; hind wing pad subapically with 2 pits in oblique row subparallel to posterior pad margin. Fore legs slightly widened, as long as mid legs. Fore femora without subapical tooth on posteroventral carina. Fore tibiae slightly flattened, lanceolate, widest about midlength. Mid tibiae not widened, relatively slender. Hind tibiae with 5 lateral spines including knee spine; apical teeth not possible to count. Hind tarsus three-segmented.

Abdomen with well developed middorsal carina, indistinct intermediate carinae on tergites IV–V, without sublateral carinae. Tergites I–III without pits; tergites IV–V with long (complete) rows of 8–10 pits, 5th or 6th pit (from body midline) displaced anteriad (sometimes there are 2 such pits, forming rudimentary second row anteriorly – see Fig. 1). Lateral areas of tergites IV–V with 3–4 pits in row or group. Tergites VI–VIII with several pits displaced medially (2 pits on VI, 2 pits on VII, 0–1 pit on VIII – absent at one side) and several pits laterally (ventrally: 3 pits on VI, 2 pits on VII, 1 pit on VIII). Lateral area with 3 pits on tergite VI, 2 pits on tergite VII, and 1 pit on tergite VIII. Tergite IX ventrally with pair of pits (1 pit at each side).

Wax plates situated in subtriangular posterolateral areas of tergites VI–VIII, separated from rest of tergite by carina and facing posteriad. Wax plates of uniform structure: large rounded lower (lateral) plate with discernible circular wax gland pores and small adjacent upper (medial) plate. Small upper wax plate on tergite VII subdivided, crossed by narrow chitinous bridge nearly perpendicular to body sagittal plane.

Remarks. The three-segmented hind tarsus in the holotype of *A. rasnitsyni* sp. n. indicates the 4th or 5th instar, while the fore wing pads not nearly reaching the apices of hind wing pads suggest the 4th instar (or 5th instar of a brachypterous planthopper, but the latter is not consistent with the presence of well developed abdominal wax plates).

In the nymphs of Dictyopharinae posterolateral carinae of the pronotal disc are usually absent, as in the new genus, and sensory pits of the second row are arranged more or less evenly across the imaginary boundary between pronotal disc and paradiscal area, though their number is not the same at the left and right sides.

The 3rd instar nymph from Baltic amber illustrated by Weitschat and Wichard (1998: pl. 46a) agrees with the holotype of *A. rasnitsyni* sp. n. in all diagnostic characters. The original drawing of the 3rd instar nymph of „*Pseudophana reticulata*" (Germar and Berendt 1856: pl. II, fig. 4a) is inaccurate, e.g. the legs are shown too short and the sensory pits on the fore wing pad too numerous. Nevertheless, several salient features allow recognizing it as conspecific with the holotype of the new species. Therefore, *A. rasnitsyni* sp. n. is recorded from both Baltic and Rovno amber.

Discussion

Alicodoxa gen. n. is a typical member of Dictyopharinae in its general habitus and basic structural features. The subfamily assignment is confirmed by the presence of typical

wax plates on the VI–VIII abdominal tergites (wax plates are undeveloped in another subfamily, Orgeriinae).

Nymphs of Dictyopharinae are rather uniform and difficult to identify, except for some aberrant forms. Nymphal characters to diagnose all the tribes have not been revealed yet, but there is a certain amount of morphological descriptions of varying accuracy and credibility (Wilson and McPherson 1981, Emeljanov 1993, 1994, Yang and Yeh 1994, McPherson and Wilson 1995). Several figures of nymphs in earlier papers (e.g. Sirrine and Fulton 1914, Logvinenko 1971) are not informative enough.

The descriptions scattered in the literature include those of nymphs (mainly of the last, 5th instar) from the tribes Dictyopharini, Orthopagini, Nersiini, Taosini, Phylloscelini, and Scoloptini. With the exception of Phylloscelini (genus *Phylloscelis* Germar), we examined nymphs from all these tribes plus the nymphs (yet undescribed) of the tribe Aluntiini, available in the collection of the Zoological Institute RAS. The nymphs of Lappidini, Capenini, Cleotychini, and Hastini remain unknown.

The wax plates of planthopper nymphs are originally confined to the abdominal tergites VI–VIII. The presence of 5 primary wax plates at each side of the tergites VI–VIII is characteristic of all Fulgoroidea nymphs except the primitive family Cixiidae (Emeljanov 2009). In many families these plates are greatly modified and variously reduced, but in some Fulgoridae, Nogodinidae, Ricaniidae, Flatidae, and Hypochthonellidae a complete set of wax plates is retained on at least one segment.

Within Dictyopharidae (Dictyopharinae) the structure of wax plates is quite uniform, except for the wax plates of segment VI often being small (*Dictyophara multireticulata* Mulsant & Rey) or absent (*Nersia* Stål*, Scolops* Schaum), but apparently only in the late instars (traced through developmental stages in *Nersia:* Wilson and McPherson 1981). In the holotype nymph of *Alicodoxa rasnitsyni* sp. n. a second, small, upper (medial) wax plate was discovered for the first time above the large, lower (lateral) one that was described in many genera (Wilson and McPherson 1981, Emeljanov 1990, 1993, Yang and Yeh 1994, McPherson and Wilson 1995). Subsequent examination has revealed the presence of the upper wax plates in nearly all the studied extant 5th instar nymphs from various tribes of Dictyopharinae, especially large ones in the nymphs of *Saigona ussuriensis* (Lethierry) (Figs 6–7). In these latter, at high magnification the upper wax plates show numerous dark striae radiating from the pale centre (Fig. 6, inset), the fine structure very different from that of the lower wax plates covered with densely packed circular wax gland pores.

In *Zanna tenebrosa* (Fabricius) of the subfamily Zanninae, considered the least advanced in the family Fulgoridae (Emeljanov 1979, Urban and Cryan 2009), there is a complete set of 5 wax plates at each side of segments VI–VIII, and the lower (lateral) plates differ in their structure from the remaining, uniformly built ones. In other Fulgoridae studied there are only 2 wax plates and only on the segments VII–VIII (Wilson and Wheeler 1992, Yang and Yeh 1994; in the former paper, the "dark brown sclerite" dorsal to the wax plate is apparently the upper wax plate). The lower wax plate is apparently homologous in Fulgoridae and Dictyopharidae, whereas the upper wax plate could be homologized to the row of 4 upper wax plates reduced to a single plate. This suggestion is corroborated by the upper wax plate of segment VII being subdivided in *A. rasnitsyni* sp. n.

The new genus is assigned to the tribe Orthopagini based on the arrow-shaped anterior convergence of the lateral carinae of the mesonotal disc, combined with one or two sensory pits being displaced forwards from rows on the abdominal tergites IV–V; the latter character is found only in Orthopagini, the former also in Nersiini. The subapical tooth at the fore femur is characteristic of most Orthopagini but absent in several species of *Centromeria* Stål and in the new genus.

The tribe Orthopagini is presently distributed mainly in the Oriental and eastern Palearctic regions, plus three or four genera in the tropical Africa. The tribe Nersiini is Neotropical by origin and is confined to the New World (with only one subendemic genus, *Rhynchomitra* Fennah, in the Nearctic). Only the tribe Dictyopharini occurs now in Europe; in the nymphs of this tribe lateral carinae of the mesonotal disc are straight, not curved mediad, terminating separately at the anterior segment margin, and several pits on the abdominal tergites are displaced posteriad (not anteriad) from the row (Fig. 8).

The nymphs of Worskaitini are unknown; the adult of *Worskaito stenexi* Szwedo from Baltic amber differs from *Alicodoxa* gen. n. by the narrower, more elongate head. Because elongation of the head in Dictyopharinae, if it occurs, proceeds gradually from instar to instar, the head proportions of the 4th instar suggest that the head of adult *A. rasnitsyni* sp. n. must be short and broad.

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RESEARCH ARTICLE

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New shore bug (Hemiptera, Heteroptera, Saldidae) from the Early Cretaceous of China with phylogenetic analyses

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Abstract

A new genus with a new species of Saldidae, *Brevrimatus pulchalifer* **gen. et sp. n.**, is described and illustrated. The fossil specimen was found from the Early Cretaceous Yixian Formation of Duolun County, Inner Mongolia, China. Phylogenetic analyses within Saldidae were performed, and the results indicate *B. pulchalifer* **gen. et sp. n.** should be assigned to the subfamily Chiloxanthinae.

Keywords

Saldidae, fossil, phylogeny, Early Cretaceous, China

Introduction

The Saldidae is a small family of insects belonging to Heteroptera. About 335 extant species have been described in this cosmopolitan family (Schuh and Polhemus 2009). Most saldids are littoral, inhabiting lake shores, beaches and stream banks and they

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are predaceous, feeding on small insects and decaying animal materials (Brooks and Kelton 1967).

Cobben (1959) proposed a classification of Saldidae, and divided Saldidae into three subfamilies: Aepophilinae, Chiloxanthinae and Saldinae. Schuh and Polhemus (1980) later considered the Aepophilinae to be of family rank based on their cladistic and phenetic analysis of the infraorder Leptopodomorpha. At present, Saldidae is divided into two subfamilies, Chiloxanthinae and Saldinae (Schuh and Slater 1995). The phylogenetic analyses concerning relationships within Saldidae (Polhemus 1977, Schuh and Polhemus 2009) present valuable information and conclusions.

To date, 6 incontrovertible fossil species in 3 genera have been reported: *Oligosaldina* Statz & Wagner, 1950 with three species, *O. rottensis*, *O. rhenana* and *O. aquatilis*, found from Upper Oligocene deposits in Germany; *Propentacora froeschneri* (= *Oreokora froeschneri*) found in Miocene Latah Formation in USA (Lewis 1969); *Salda exigua* Germar & Berendt, 1856 found in Eocene Baltic amber, and *Salda littoralis* found in Recent Late Glacial clay (Jessen 1923).

However, 2 genera assigned to this group previously are not saldids. *Leptosalda chiapensis* (Cobben, 1971) from Mexico amber was assigned to the subfamily Leptosaldinae within Saldidae first, but was later transferred to Leptopodidae by Schuh and Polhemus (1980). Popov (1973) erected a subfamily Saldoniinae in Saldidae with one genus *Saldonia* and one species *S. rasnitsyni* Popov, 1973, but later (Popov 1985) transferred the genus to Archegocimicidae, synonymized Saldoniinae under Archegocimicidae, and added two more species *S. sibirica* Popov, 1985 and *S. maculata* Popov, 1985, all from the Lower or Middle Jurassic of Transbaikalia, Russia. Archegocimicidae is similar to Saldidae, and it was assigned to the infraorder Leptopodomorpha (Popov 1985, 1989, Popov et al. 1994). Polhemus (1977) thought *Saldonia* probably should be classified into Dipsocoridae based on its wing venation. Cobben (1987) didn't consider this genus as a member of the infraorder Leptopodomorpha, but he didn't give detailed explanation.

In this paper, we described a new fossil shore bug, *Brevrimatus pulchalifer* gen. et sp. n., from the Yixian Formation, Baitugou, Nanyingpan Village, Sanbeigou Town, Duolun County, Inner Mongolia, China. Xing et al. (2005) and Zhang et al. (2004), respectively, based on isotope data and abundant statistical analysis of fossils data came to the consistent opinion that the age of the Yixian Formation is Early Cretaceous. And this opinion has been accepted widely (Swisher et al. 1999, Lu 2000, Zhou et al. 2003, Fürsich et al. 2007). Here we consider the age of the Yixian Formation as the Early Cretaceous (about 125 Ma).

Material and methods

Our fossil specimen is deposited in the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China. It was examined with the LEICA MZ 12.5 dissecting microscope. The specimens were examined without al-

cohol and under alcohol. Photos were taken by a Nikon Digital Camera DXM1200C. Line drawings were made with Photoshop graphic software. Morphological terminology used here follows that of Schuh and Slater (1995).

The body length was measured from the apex of head to the apex of abdomen; body width, at the maximal width of body; pronotum length, along the midline; pronotum width, across the broadest part at its posterior angles; wing length, from the basal to the apex of anterior margin; wing width, at the maximal width of the wing. All measurements are in millimeters (mm).

Systematic paleontology

Order Hemiptera Linnaeus, 1758
Suborder Heteroptera Latreille, 1810
Infraorder Leptopodomorpha Popov, 1971
Family Saldidae Amyot & Serville, 1843
Subfamily Chiloxanthinae Cobben, 1959

***Brevrimatus* gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Brevrimatus

Type species. *Brevrimatus pulchalifer* sp. n.

Diagnosis. Body ovate, moderate in size, macropterous. Head relatively short. Rostrum reaching to the base of hind coxae. Corium with large pale spots, medial fracture short, costal fracture of hemelytra very long, hypocostal ridge and associated secondary hypocostal ridge present on hemelytra, membrane with five closed cells. Posterior margin of female sternum VII concave along the midline. Base of ovipositor exposed.

Etymology. The generic name is a combination of the Latin prefix "*brev-*" (short) and Latin word "*rimatus*" (fracture), which indicated the genus with short medial fracture. Gender masculine.

Distribution. China.

***Brevrimatus pulchalifer* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Brevrimatus_pulchalifer
Figs 1, 2

Type material. Holotype, ♀, CNU-HET-ND2010334 p/c (part and counterpart).

Type locality and horizon. Baitugou, Nanyingpan Village, Sanbeigou Town, Duolun County, Inner Mongolia, China, Yixian Formation. Early Cretaceous.

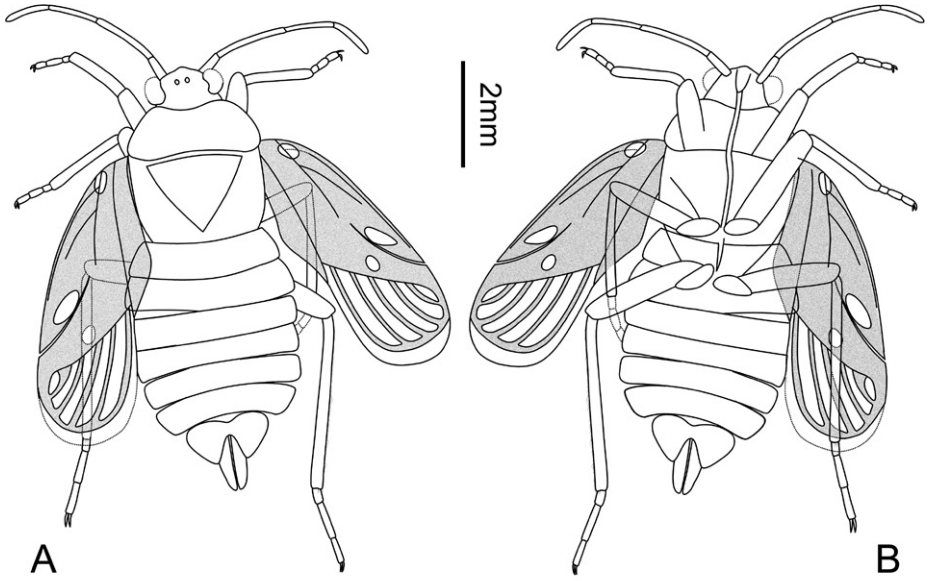

Figure 1. *Brevrimatus pulchalifer* gen. et sp. n., line drawings. Holotype, CNU-HET-ND2010334 p/c. **A** dorsal view **B** ventral view. Scale bar=2 mm.

Diagnosis. Head relatively short. The last segment of antennae slightly swollen. Corium with three large pale spots, medial fracture short, costal fracture of hemelytra very long; membrane with five cells, apex of innermost cell of membrane extending past apex of outermost cell. Posterior margin of female sternum VII extremely concave along the midline.

Description. Body ovate, about 2.4 times as long as wide.

Head 1.4 times as wide as long. Antennae slender, 4-segmented, first segment shortest, second segment longest, 1.47 times as long as the third segment, fourth segment slightly shorter than third segment. Eyes reniform, moderately protrusive, located at the posterolateral angles of the head. Ocelli round, raised slightly, ocelli separated by 1.3 times the width of an ocellus, ocelli closer to each other than to margins of eyes. Rostrum reaching to the hind coxae. Length of head subequal to the length of pronotum on midline.

Pronotum transverse, 3.2 times as wide as long, Anterior and posterior margins of pronotum concave, lateral margins straight, anterior and posterior angles feebly rounded. Scutellum distinctly longer than pronotum on midline, triangular, 1.3 times as wide as long. Tarsal formula: 3–3–3. Fore tibiae about 2.0 times as long as corresponding tarsi, fore tarsomere I shortest, tarsomeres II and III almost subequal in length; mid femora 1.3 times as long as tibiae, tibiae 2.3 times as long as tarsi, tarsomere I shortest, tarsomere II slightly longer than tarsomere III; hind tibiae long, almost 1.5 times as long as hind femora, and 2.3 times as long as tarsi. Fore wing macropterous, 0.6 times as long as body; corium and membrane clearly delimited; corium with embolium;

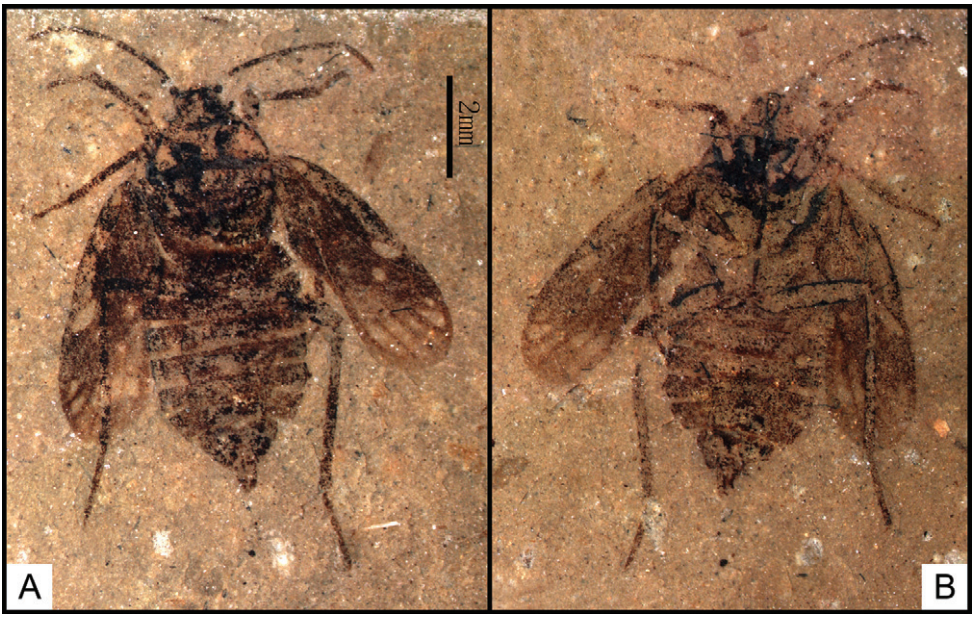

Figure 2. *Brevrimatus pulchalifer* gen. et sp. n., photographs. Holotype, CNU-HET-ND2010334 p/c. **A** part and **B** counterpart. Scale bar=2 mm.

medial fracture short, 0.3 times as long as fore wing; costal fracture of hemelytra very long, reaching to the middle of the corium; venation of corium weakly indicated; membrane large, with five closed cells, cells reduced gradually from the inner to the outer. Claval commissure shorter than scutellum length at median line. Hemelytra with only slight modification for mating, the embolar region slightly thickened.

Anterior margin of female sternum VII curve; posterior margin of female sternum VII extremely concave along the midline. Base of ovipositor exposed ventrally.

Measurements (in mm). Body length 8.00, width 3.18. Head length 0.84, width 1.24. Antennal measurements I–IV: 0.56, 1.30, 0.92, 0.85. Interocular space of ocelli 0.12. Interocular space of eyes 0.84. Pronotum length 0.78, width 2.52. Scutellum length 1.43, width 1.78. Length fore leg: tibia 1.22, tarsomeres I–III: 0.13, 0.23, 0.23; length mid leg: femur 1.91, tibia 1.57, tarsomeres I–III: 0.18, 0.27, 0.23; length hind leg: femur 2.14, tibia 3.15, tarsomeres I–III: 0.22, 0.69, 0.52. Hemelytron length 5.14, width 1.73.

Etymology. The species name is a combination of the Latin prefix "*pulch-*" (beautiful) and Latin word "*alifer*" (wing), meaning beautiful wing. Gender masculine.

Discussion

The Leptopodomorpha consists of four extant families (Saldidae, Aepophilidae, Leptopodidae, Omaniidae) and three extinct families (Archegocimicidae, Mesolygaeidae, Palaeoleptidae). Popov et al. (1994) synonymized Mesolygaeidae to Archegocimicidae.

But herein we think it is better to treat them as two separated families, because of their distinct difference in forewing. We compared our fossil with all the families in Leptopodomorpha. The body sizes of aepophilids and omaniids are less than 2mm, while the new species reaches to 8mm, much larger than aepophilids and omaniids. In Leptopodidae, rostrum at most reaches to the base of the fore coxae, while rostrum of the new species reaches to the base of the hind coxae. Besides that, anterior margin of pronotum is distinctly narrower than head in Leptopodidae, but anterior margin of pronotum of the new species is almost as wide as head. All the extinct families from Mesozoic are contemporaneous with the new fossil species. But they are different in some characters. Nine cells present in Archegocimicidae (Handlirsch 1906–1908), and the arrangement of the cells (Popov 1985) are totally different from the new species. Fore wing of Palaeoleptidae is nearly completely coriaceous except for small membrane (Poinar and Buckley 2009), which is different from the new species with large membrane. And wing venation consists of eight cells in Palaeoleptidae, which differs from the new species with five cells. The pronotum of Mesolygaeidae is divided into two parts (Zhang 1991), but in the new species no groove present on pronotum. The structure of end of abdomen is also different between the new species and mesolygaeids. So we classified our fossil into Saldidae based on the combined characters: compound eyes large and reniform, rostrum long, posterior margin of pronotum indented, hemelytra with costal fracture, medial fracture well developed and membrane with five cells.

Phylogenetic analysis

The new genus possesses some typical Chiloxanthinae characters, such as costal fracture very long, female sternum VII truncate with mesal concavity and base of ovipositor exposed. On the other hand, it possesses short medial fracture as Saldinae. Therefore, we carried out phylogenetic analyses to determine the placement of our new genus.

For the phylogenetic analyses, we selected three extant genera from Chiloxanthinae, five extant genera from Saldinae, our new fossil genus, and an unambiguous fossil species *Oligosaldina aquatilis* as in-group. Following previous studies (Polhemus 1977, Schuh and Polhemus 1980, 2009), we chose representatives from the family Leptopodidae (*Patapius thaiensis* Cobben, 1968) and Aepophilidae (*Aepophilus bonnairei* Signoret, 1879) as our out-group taxa. The 12 taxa that we chose for these phylogenetic analyses are listed in Table 1. We carried out phylogenetic analyses respectively with the fossil taxon *O. aquatilis* and without this fossil taxon.

Most character information of the extent taxa was extracted from literatures (Cobben 1959, 1969, Drake 1961, Cobben and Polhemus 1966, Polhemus and Evans 1969, Polhemus 1972, 1977, 1991, Cobben 1980, King and Fordy 1984, Chen and Zheng 1987, Vinokurov 2005, 2009, Schuh and Polhemus 2009). The descriptions for the 17 characters and character states are listed in the Appendix. All characters were treated as unordered and weighted equally. A maximum parsimony analysis of the character matrix (Table 2) edited by NDE (Nexus Data Editor) version 0.5.0 (Page 2001), was

Table 1. Taxa included in the phylogenetic analysis (*: only included when we carried out phylogenetic analysis with *Oligosaldina aquatilis*)

	Family	**Subfamily**	**Tribe**	**Species**
out-group	Leptopodidae			*Patapius thaiensis* Cobben, 1968
	Aepophilidae			*Aepophilus bonnairei* Signoret, 1879
in-group	Saldidae	Saldinae	Saldini	*Salda lugubris* (Say, 1832)
				Teloleuca altaica Vinokurov, 2009
			Saldoidini	*Saldula montana* Cobben, 1966
				Calacanthia sichuanicus Chen & Zheng, 1987
			Salduncullini	*Salduncula swezeyi* (Usinger, 1946)
		Chiloxanthinae		*Chiloxanthus pilosus* (Fallén, 1807)
				Pentacora ligata (Say, 1832)
				Paralosalda innova Polhemus & Evans, 1969
				**Oligosaldina aquatilis* Statz & Wagner, 1950
				Brevrimatus pulchalifer gen. et sp. n.

performed on NONA (Goloboff 1998), using the Multiple TBR+TBR search strategy, options set to hold 10000 trees, 1000 replications with 100 starting tree replication. The unambiguous characters were mapped by WinClada (Nixon 2000).

Phylogenetic results

For the phylogenetic analyses excluding fossil species *O. aquatilis*, we got two equally most parsimonious trees (Fig. 3A, B), with the following main characteristics: tree

Table 2. Matrix of 17 characters and the 12 taxa used for phylogenetic analysis (*: only included when we carried out phylogenetic analysis with *Oligosaldina aquatilis*)

										1	1	1	1	1	1	1	1
Taxon/Character	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
Patapius thaiensis	0	0	1	0	0	0	0	1	0	–	1	0	?	0	0	0	–
Aepophilus bonnairei	–	2	0	0	2	–	0	0	0	–	0	0	0	0	0	0	–
Salda lugubris	1	?	1	1	0	0	1	1	1	0	1	0	1	1	1	0	–
Teloleuca altaica	1	1	1	1	0	0	1	1	1	0	1	0	1	1	1	0	–
Saldula montana	0	1	1	1	0	0	1	1	1	0	1	0	1	1	1	1	0
Calacanthia sichuanicus	1	2	1	1	1	0	1	1	1	0	1	0	1	1	1	1	0
Salduncula swezeyi	2	?	0	1	0	0	1	1	1	0	1	0	1	1	1	1	0
Chiloxanthus pilosus	2	?	0	1	0	1	2	2	1	1	2	1	0	0	1	1	1
Pentacora ligata	1	2	0	1	0	1	2	2	1	1	2	1	0	0	1	1	1
Paralosalda innova	2	2	0	1	0	0	2	2	1	1	2	1	0	0	1	1	1
Brevrimatus pulchalifer gen. et sp. n.	2	2	?	1	0	1	2	1	?	?	2	1	?	?	?	?	?
**Oligosaldina aquatilis*	?	2	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?

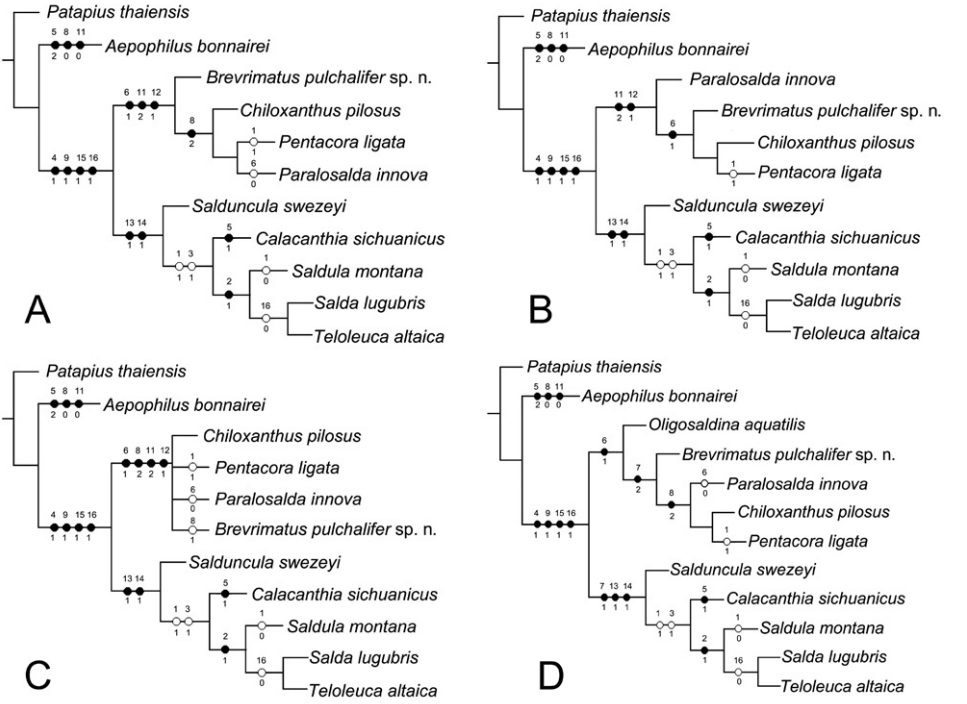

Figure 3. Phylogeny of Saldidae. **A, B** the most parsimonious trees based on 11 taxa and 17 characters. **C** the strict consensus tree based on 11 taxa and 17 characters **D** the most parsimonious trees based on 12 taxa and 17 characters. (●) non-homoplasious; (○) homoplasious.

length = 28, consistency index (CI) = 82, retention index (RI) = 87. The strict consensus tree is shown in Figure 3C. Phylogenetic results indicate Saldidae is a monophyletic group, which is supported by four synapomorphies: posterior pronotal margin indented distinctly (Character 4:1); eversible glands present posterolaterally between sterna VI and VII (Character 9:1); eggs with aeropyles (Character 15:1); larval organ present (Character 16:1). Some synapomorphic characters, such as apicolateral sclerotized structures of penis present (Character 13:1) and filum gonopori coiled one to four times, like a watch-spring (Character 14:1) supported the monophyly of the subfamily Saldinae. Chiloxanthinae with our fossil species included is a monophyletic group, which is supported by four synapomorphies: five well defined cells in membrane (Character 6:1); medial fracture long (Character 8:2); female subgenital plate truncate with concavity along the midline (Character 11:2); base of ovipositor exposed (Character 12:1). In summary, phylogenetic results suggest our new fossil genus is in Chiloxanthinae and short medial fracture was treated as a reversal character.

For the phylogenetic analysis including fossil species *O. aquatilis*, we got one most parsimonious tree (Fig. 3D), tree length = 28, CI = 82, RI = 88. The monophyly of Saldidae is supported by four synapomorphies (Character 4:1, 9:1, 15:1 and 16:1) as the results above. In this phylogenetic result, besides Character 13:1 and Character

14:1, short costal fracture of hemelytra (Character 7:1) supports the monophyly of the subfamily Saldinae. Five well defined cells in membrane (Character 6:1) indicate that our new genus should be in the branch of Chiloxanthinae. Therefore, both of the phylogenetic analyses suggest our fossil species should be classified into Chiloxanthinae.

Comparison with Chiloxanthinae indicates the new fossil species differs from other extant chiloxanthines in its short medial fracture. Besides this character, the boundary between corium and membrane is not clear in *Enalosalda*, which is different from *Brevrimatus* gen. n. with clear boundary. *Paralosalda* has four membrane cells, which is different from *Brevrimatus* gen. n. with five cells. Embolar modification of female is well developed in *Pentacora*, but in *Brevrimatus* gen. n. the embolar region is slightly thickened. Sublateral cell of membrane is shortest in *Chiloxanthus*, which differs from *Brevrimatus* gen. n. with the lateralmost cell is shortest. We further compared it with other fossil Saldidae. The arrangement of the cells of *Brevrimatus* gen. n. is similar to that of *Oligosaldina*, but lateralmost cell of membrane is distinctly smaller than that of *Oligosaldina*. Long costal fracture is present on *Brevrimatus* gen. n., but absent on *Oligosaldina.* A deep furrow is present in the pronotum of *Oligosaldina,* while it is absent in our new genus. *Propentacora* contains five closed cells in the wing membrane, but the corial vein of *Propentacora* appears to continue between the third and fourth membrane cells, which is different from the new genus. *Brevrimatus* gen. n. is distinctly different from *Salda*, which can be seen in phylogenetic result. Comparing our fossils with the fossil species *Salda exigua*, we can separate them in the following characters: *Brevrimatus* gen. n. possesses five closed cells in the forewing membrane, while *S. exigua* has three closed cells and rostrum of *Brevrimatus* gen. n. reaches to the base of hind coxae, while in *S. exigua*, rostrum just reaches to the fore coxae. Therefore *Brevrimatus* gen. n. is different from all other fossil genera. In geological age, all of the previously recorded fossil saldids are from Cenozoic. So far, *Brevrimatus* gen. n. found in the Lower Cretaceous sedimentary stratum is the oldest saldid.

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ages and correlation. Geology and resources 13 (4): 193–201 [in Chinese with English abstract].

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Appendix

List of characters and character states used in phylogenetic analysis

Distance between ocelli: equal to width of ocellus (0); less than width of ocellus (1); more than width of ocellus (2). [We treat this character inapplicable in Aepophilidae that doesn't have ocellus.]

Rostrum reaches to: fore coxae (0); middle coxae (1); hind coxae (2). [Rostrum of Leptopodidae is very short, reaching to fore coxae at most. Rostrum of Saldidae is relatively long, reaching to middle coxae or hind coxae. Rostrum of *B. pulchalifer* sp. n. and *O. aquatilis* reaches to hind coxae. Long rostrum is the primitive character (Popov 1971).]

Postclypeus: absent (0); present (1). [Postclypeus present in *S. lugubris*, *T. altaica*, *S. montana*, *C. sichuanicus.* This character cannot be identified in our fossil specimen. In other groups postclypeus is absent.]

Posterior pronotal margin: non-indented (0); indented distinctly (1). [Posterior pronotal margin nearly straight in Aepophilidae, so we threat this character in Aepophilidae as non-indented. Posterior pronotal margin of Saldidae is demonstrated briefly in Figure 4A showing the indented posterior pronotal margin and Leptopodidae in Figure 4B showing the non-indented posterior pronotal margin. This character is considered as the synapomorphy for Saldidae.]

Forewing: macroptery or submacroptery (0); semibrachypterous moderately or strongly (1); brachyptery (2). [Wing polymorphism occurs in Saldidae. Wing pattern can be separated into five categories based on the reduction of the membrane of fore wing (Cobben 1980). The membrane of Aepophilidae completely reduced, so it is brachyptery. *C. sichuanicus* with the semibrachypterous forewing.]

Cells: Four well defined cells in membrane (0); five well defined cells in membrane (1). [In Aepophilidae, forewing greatly reduced, in form of pads without membrane, so we treated this character inapplicable in this family. Usually, Saldinae have four cells and Chiloxanthinae have five cells, but the distinction in hemelytral cells between the Saldinae and Chiloxanthinae is not constant (Polhemus and Chapman 1979). The fossil species, *B. pulchalifer* sp. n. and *O. aquatilis* have five cells.]

Costal fracture of hemelytra: absent (0); present, short (1); present, very long (2). [Costal fracture length is a stable character within subfamily. Saldinae usually possesses short costal fracture and Chiloxanthinae usually possesses long costal fracture. Polhemus (1977) consider the long costal fracture in Chiloxanthinae to be a derived character providing a synapomorphy for the group. Costal fracture is absent

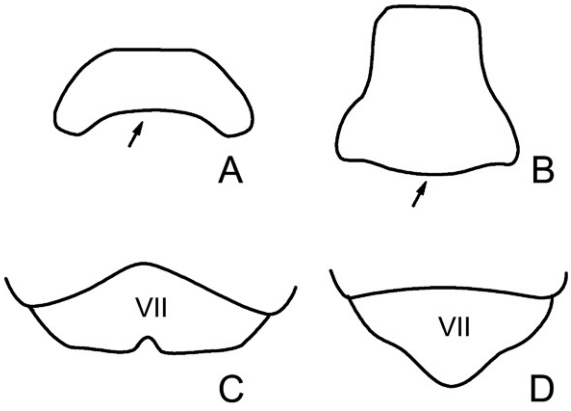

Figure 4. A, B pronotum **A** posterior pronotal margin indented **B** posterior pronotal margin non-indented **C, D** female subgenital plate **C** truncate with concave along the midline **D** posterior margin of produced caudad along the midline (modified from Polhemus and Chapman 1979).

in *P. thaiensis*, *A. bonnairei* and *O. aquatilis*. Costal fracture in our fossil species, *B. pulchalifer* sp. n., is long.]

Medial fracture: absent (0); present, short (1); present, very long (2). [Long medial fracture reaches at least to level of posterior end of claval suture, and short medial fracture not reaches anteriorly more than half the distance from costal fracture to posterior end of claval suture (Schuh and Slater 1995). Medial fracture is absent in *A. bonnairei*. In *P. thaiensis*, *B. pulchalifer* sp. n. and members of Saldinae, medial fracture is short. *C. pilosus*, *P. ligata* and *P. innova* have long medial fracture.]

Eversible glands: absent (0); present posterolaterally between sterna VI and VII (1). [Saldidae has paired abdominal eversible glands with their openings locating between sterna VI and VII. Eversible glands is absent in Leptopodidae and Aepophilidae. This structure is unknown in *B. pulchalifer* sp. n. and *O. aquatilis*. Eversible glands is considered to be a apomorphic character in Saldidae (Polhemus 1977).]

Sclerite adjacent to eversible gland: present (0); absent (1). [This sclerite is present in Saldinae, but absent in Chiloxanthinae.]

Female subgenital plate: truncate without concavity along the midline (0); triangular, posterior margin of produced caudad along the midline (1); truncate with concave along the midline (2). [In *A. bonnairei* female subgenital plate just like a normal abdominal sternite. Subgenital plate is truncate with concave along the midline is found in the members of Chiloxanthinae and *B. pulchalifer* sp. n. as Figure 4C. Subgenital plate is triangular in Saldinae as Figure 4D.]

Base of ovipositor: hidden by posterior medial prolongation of subgenital plate (0); exposed (1). [The base of ovipositor is hidden in Aepophilidae and Saldinae, but exposed in Chiloxanthinae and *B. pulchalifer* sp. n. The exposed ovipositor is considered a derived character (Polhemus 1977)]

Apicolateral sclerotized structures of penis: absent (0), present (1). [This structure absent in Aepophilidae and Chiloxanthinae, but present in Saldinae.]

Filum gonopori: base of penis-filum not curled or at most forming one closed ring (0); filum gonopori coiled one to four times, like a watch-spring (1). [Base of penis-filum not curled in Leptopodidae and Aepophilidae, and coiled less than one ring in Chiloxanthinae. In Saldinae, base of penis-filum like a watch-spring.]

Eggs: without aeropyles (0); with aeropyles (1). [Eggs with aeropyles is regarded as a synapomorphy for Saldidae.]

Larval organ: absent (0); present (1). [Larval organ is absent in Leptopodidae and Aepophilidae, *S. lugubris* and *T. altaica*. Larval organ present in *S. montana*, *C. sichuanicus*, *C. pilosus, P. ligata*, *P. innova*. Larval organ present in most members of Saldidae. The absence condition in Saldini is presumed to be the secondary lost (Polhemus 1977).]

Larval organ: larval organ lateral, adjacent to spiracle (0); larval organ located medially, some distance from the spiracle (1). [In Saldinae, larval organ when present adjacent to spiracle, while the later condition occurred in Chiloxanthinae.]

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Two new species of *Sinosmylites* Hong (Neuroptera, Berothidae) from the Middle Jurassic of China, with notes on Mesoberothidae

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Abstract

Two new species of the genus *Sinosmylites* Hong are described from the Middle Jurassic locality at Daohugou (Inner Mongolia, China): *S. fumosus* **sp. n.** and *S. rasnitsyni* **sp. n.** This is the oldest known occurrence of the family Berothidae. The berothid affinity of this genus is confirmed by examination of the hind wing venation characteristic of the family. The Late Triassic family Mesoberothidae may represent an early group of Berothidae.

Keywords

Neuroptera, Berothidae, Mesoberothidae, Daohugou, China, Middle Jurassic

Introduction

Today, the Berothidae (including Rhachiberothinae) is a small neuropteran family comprised of about 100 species discontinuously distributed mainly across tropical and

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warm-temperate regions of the world (Aspöck 1986; Aspöck and Aspöck 1997; Aspöck and Nemeschkal 1998). Their larvae are thought to be associated with termite nests, where they feed on termites (e.g., Tauber et al. 2003); however, this habit is only documented in the North American genus *Lomamyia* Banks (Johnson and Hagen 1981; Faulkner 1992).

Currently, 34 fossil berothid species have been described from various localities (listed in Table 1; others are described but unnamed, only illustrated or represented by larvae). The family was previously only known tentatively from the Jurassic: Grimaldi and Engel (2005) and Engel and Grimaldi (2008) considered the Jurassic / Early Cretaceous Mesithonidae as possible primitive Berothidae or 'stem-group berothids'. Formerly, berothids were believed to be a very ancient family, even when it almost entirely lacked a known fossil record. Tillyard (1932) stated, characteristically: "on the totality of characters, it would now appear as if the Berothidae are the oldest existing family of Planipennia [=Neuroptera]." (p. 29). Here, we describe two new species of the genus *Sinosmylites* Hong, 1983 from the Middle Jurassic of China, which we confidently assign to the family Berothidae based on characters of the hind wing. We compare the forewing venation of this genus and those of the Late Triassic Mesoberothidae, and by their similarities confirm the great antiquity of the berothid lineage.

Material and methods

This study is based on three specimens collected from Daohugou Village (Shantou Township, Ningcheng County, Inner Mongolia, China) and housed in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, curator). These insect-bearing beds are here considered as belonging to the Jiulongshan Formation and are dated Bathonian, Middle Jurassic (Gao and Ren 2006).

Specimens were examined using a Leica MZ12.5 dissecting microscope; line drawings were prepared with CorelDraw 12 graphics software with the aid of Adobe Photoshop; photographed by a Nikon SMZ1000 stereomicroscope.

Venational terminology principally follows Comstock (1918) as modified by Oswald (1993) and Archibald and Makarkin (2006). Berothid wings possess crossvenation basically similar to that of Hemerobiidae, arranged in four (incomplete) gradate series in both families. Consequently, we adopt Oswald's (1993) designation of crossveins: principal crossveins are designated by the longitudinal veins which they connect and numbered by the gradate series to which they belong in sequence from the wing base, e.g., 1a1-a2, the crossvein connecting 1A and 2A in the first gradate series; 2m-cu, the crossvein connecting M and Cu in the second gradate series; 2icu, the intracubital crossvein (i.e., between CuA and CuP) in the second gradate series; and 4rs1-rs2, the crossvein between Rs1 and Rs2 in the fourth gradate series. Terminology of wing spaces mainly follows Oswald (1993).

Table 1. A list of known fossil Berothidae.

	Species	Age	Locality	References
1	Berothidae gen. et sp. n.	Early Cretaceous (Early Berriasian)	Durlston Bay, England (Lulworth Formation)	Jepson et al. submitted
2	*Banoberotha enigmatica* Whalley, 1980	Early Cretaceous (Valanginian/ Hauterivian)	Lebanese amber (Jezzine)	Whalley 1980
3	*Paraberotha acra* Whalley, 1980	Early Cretaceous (Valanginian/ Hauterivian)	Lebanese amber (Jezzine)	Whalley 1980; Nel et al. 2005
4	Berothidae indet. (larva)	Early Cretaceous (Valanginian/ Hauterivian)	Lebanese amber (Jezzine)	Whalley 1980: figs 9, 10
5	*Chimerhachiberotha acrasarii* Nel et al., 2005	Early Cretaceous (Valanginian/ Hauterivian)	Lebanese amber (Jezzine)	Nel et al. 2005
6	*Raptorapax terribilissima* Petrulevicius et al., 2010	Early Cretaceous (Neocomian)	Lebanese amber (Houarij)	Petrulevicius et al. 2010
7	*Spinoberotha mickaelacrai* Nel et al., 2005	Early Cretaceous (Barremian/Aptian)	Lebanese amber (Hammana)	Nel et al. 2005
8	*Oloberotha sinica* Ren et Guo, 1996	Early Cretaceous (Barremian)	Yixian Formation, China	Ren and Guo 1996
9	*Araripeberotha fairchildi* Martins-Neto et Vulcano, 1990	Early Cretaceous (Late Aptian)	Crato Formation, Brazil	Martins-Neto and Vulcano 1990
10	*Carirriberotha martinsi* Martins-Neto & Vulcano, 1990	Early Cretaceous (Late Aptian)	Crato Formation, Brazil	Martins-Neto and Vulcano 1990
11	Berothidae indet.	Early Cretaceous (Early Aptian)	Spanish amber (El Sophao)	Peñalver and Delclòs 2010
12	*Alboberotha petrulevicii* Nel et al., 2005	Early Cretaceous (Late Albian)	Archingeay, France	Nel et al. 2005
13	*Eorhachiberotha burmitica* Engel, 2004	Early Cretaceous (Late Albian)	Burmese amber	Engel 2004
14	*Dasyberotha eucharis* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008
15	*Ethiroberotha elongata* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008
16	*Haploberotha persephone* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008
17	*Iceloberotha kachinensis* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008
18	*Iceloberotha simulatrix* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008
19	*Jersiberotha myanmarensis* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008

	Species	Age	Locality	References
20	*Jersiberotha tauberorum* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008
21	*Scoloberotha necatrix* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008
22	*Systenoberotha magillae* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008
23	*Telistoberotha libitina* Engel et Grimaldi, 2008	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008
24	Berothidae indet. (larva)	Early Cretaceous (Late Albian)	Burmese amber	Engel and Grimaldi 2008: figs 42, 43.
25	*Retinoberotha stuermeri* Schlüter, 1978	Late Cretaceous (Cenomanian)	Bezonnais, France	Schlüter 1978
26	*Plesiorobius sibiricus* Makarkin, 1994	Late Cretaceous (Cenomanian)	Obeshchayushchiy, NE Siberia (Ola Formation)	Makarkin 1994
27	*Jersiberotha luzzii* Grimaldi, 2000	Late Cretaceous (Turonian)	Raritan (New Jersey) amber	Grimaldi 2000
28	*Jersiberotha similis* Grimaldi, 2000	Late Cretaceous (Turonian)	Raritan (New Jersey) amber	Grimaldi 2000
29	*Nascimberotha picta* Grimaldi, 2000	Late Cretaceous (Turonian)	Raritan (New Jersey) amber	Grimaldi 2000
30	*Rhachibermissa phenax* Engel et Grimaldi, 2008	Late Cretaceous (Turonian)	Raritan (New Jersey) amber	Grimaldi 2000
31	*Rhachibermissa splendida* Grimaldi, 2000	Late Cretaceous (Turonian)	Raritan (New Jersey) amber	Grimaldi 2000
32	*Plesiorobius* cf. *canadensis*	Late Cretaceous (Santonian)	Yantardakh, N Siberia	Makarkin 1994
33	*Plesiorobius canadensis* Klimaszewski et Kevan, 1986	Late Cretaceous (Campanian)	Canadian amber	Klimaszewski and Kevan 1986
34	*Albertoberotha leuckorum* McKellar et Engel, 2009	Late Cretaceous (Campanian)	Canadian amber	McKellar and Engel 2009
35	Berothidae indet.	Late Cretaceous (Campanian)	Canadian amber	Engel and Grimaldi 2008: fig. 41
36	*Oisea celinea* (Nel et al., 2005)	Early Eocene	Oise amber, France	Nel et al. 2005
37	*Microberotha macculloughi* Archibald et Makarkin, 2004	Early Eocene	Hat Creek amber, British Columbia	Archibald and Makarkin 2004
38	*Whalfera venatrix* (Whalley, 1983)	Late Eocene	English amber	Whalley 1983
39	*Proberotha prisca* Krüger, 1923	Late Eocene	Baltic amber	Krüger 1923
40	*Whalfera wiszniewskii* Makarkin et Kupryjanowicz, 2010	Late Eocene	Baltic amber	Makarkin and Kupryjanowicz 2010
41	Berothidae indet.	Late Eocene	Baltic amber	Bachofen-Echt 1949: fig. 122

	Species	Age	Locality	References
42	Berothidae indet.	Late Eocene	Baltic amber	Weitschat and Wichard 1998: pl. 55, figs a, b
43	Berothinae indet.	Late Eocene	Baltic amber	MacLeod and Adams 1967
44	Berothinae indet. (larva)	Late Eocene	Baltic amber	Janzen 2002: fig. 58
45	Berothinae indet. (larva)	Late Eocene	Baltic amber	V.Makarkin, S.Wedmann, T.Weiterschan (ongoing research)
46	Berothinae indet. (larva)	Late Eocene	Rovno amber, Ukraine	E.Perkovsky, V.Makarkin (ongoing research)

Abbreviations used in the text and figures are as the follows: 1A–3A, first to third anal veins; CuA, CuP, anterior and posterior branches of the cubital vein (Cu); MA, MP, anterior and posterior branches of the medial vein (M); R1, anterior branch of the radial vein (R); Rs1, most proximal branch of the radial sector (Rs); Rs2, branch of the radial sector located distal to Rs1; Rs3, branch of the radial sector located distal to Rs2; Sc, subcostal vein.

Taxonomy

Family Berothidae Handlirsch, 1906

Genus *Sinosmylites* Hong, 1983, sit. n.

http://species-id.net/wiki/Sinosmylites

Sinosmylites Hong, 1983: 94, 198 [Osmylitidae]; Ren et al. 1995: 101 [?Osmylidae]; Ren and Guo 1996: 466 ['osmylid-like' Neuroptera]; Makarkin and Archibald 2005: 15, 16, 18, 19 [probably Prohemerobiidae]; Yang et al. 2010: 177 [Osmylidae].

Type species. *Sinosmylites pectinatus* Hong, 1983, by original designation.

Diagnosis. Forewing: costal space strongly narrowed basally; humeral veinlet not recurrent and branched; Sc, R1 fused distally; Sc+R1 with 9-11 veinlets, mostly simple; all subcostal veinlets simple; M forked far distal to origin of Rs; CuA pectinate, with seven branches; few crossveins in radial space arranged mainly in 1-2 'inner' gradate series.

Species included. Three species from the Middle Jurassic of China (Jiulongshan Formation): *S. pectinatus* (Liaoning Province), *S. fumosus* sp. n. and *S. rasnitsyni* sp. n. (Inner Mongolia).

Comments. The venation of these two new species is very similar to that of *Sinosmylites pectinatus*. The latter species is represented by a nearly complete forewing (Hong 1983). Unfortunately, however, it is quite poorly figured, and its type is now lost. Nevertheless, all main features of *S. fumosus* sp. n. and *S. rasnitsyni* sp. n. forewings agree well with those confirmed of *S. pectinatus*, i.e., similar size (length 5.5 mm in *S. pectinatus*; about 6.5 mm in *S. fumosus* sp. n.; 6.7 mm in *S. rasnitsyni* sp. n.), coloration (a single, more or less fuscous color), and the venational character states are as provided in the generic diagnosis. The few differences between the type species and the two new species (e.g., the presence of two 'inner' gradate series, and the CuP twice forked in *S. pectinatus*) are at most specific.

***Sinosmylites rasnitsyni* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Sinosmylites_rasnitsyni
Figs 1–3

Diagnosis. Differs from both other species of *Sinosmylites* by more closely spaced subcostal veinlets, and more deeply forked CuP.

Description. Body indistinctly preserved. Antennae moniliform, incomplete; preserved segments transverse (wider than long). Prothorax short. Mesonotum of usual neuropteran morphology. Legs covered with short hairs; fore-, mid-legs relatively short; hind-leg tibia long; fore-, hind-leg basitarsus longest segment of tarsus. Abdomen very poorly preserved.

Forewing with broad-rounded apex, 6.7 mm long, 3.0 mm wide. Costal space moderately broad, strongly dilated at proximal 1/5 of wing length, narrowed basally. Subcostal veinlets simple, regularly arranged, closely spaced. Sc distally fused with R1 far from wing apex; Sc+R1 with 9-11 simple veinlets. Subcostal space broad, with one basal crossveins located immediately after origin of Rs. R1 space narrower than subcostal space; three widely-spaced crossveins before fusion of Sc, R1, one after. Rs with 11 (right wing), 10 (left wing) parallel pectinate regularly-spaced branches; six proximal branches with 2-4 terminal forks, other branches once forked. Rs1 originating near origin of Rs. M appears fused basally for short distance; forked much distal to origin of Rs1. MA, MP almost parallel, distally with one, two quite long forked branches respectively. Cu divided into CuA, CuP proximal to origin of Rs. CuA pectinate, with 7 branches, some once forked. CuP once deeply forked. Anal veins very poorly preserved; 1A, 2A apparently once deeply forked each; 3A simple. Four gradate series of crossveins posterior to stem of Rs partly preserved (series 1-4 of Oswald 1993). First series: crossvein 1r-m (located at origin of Rs). Second series: crossveins 2icu (connecting CuA, anterior branch of CuP), 2icup (between branches

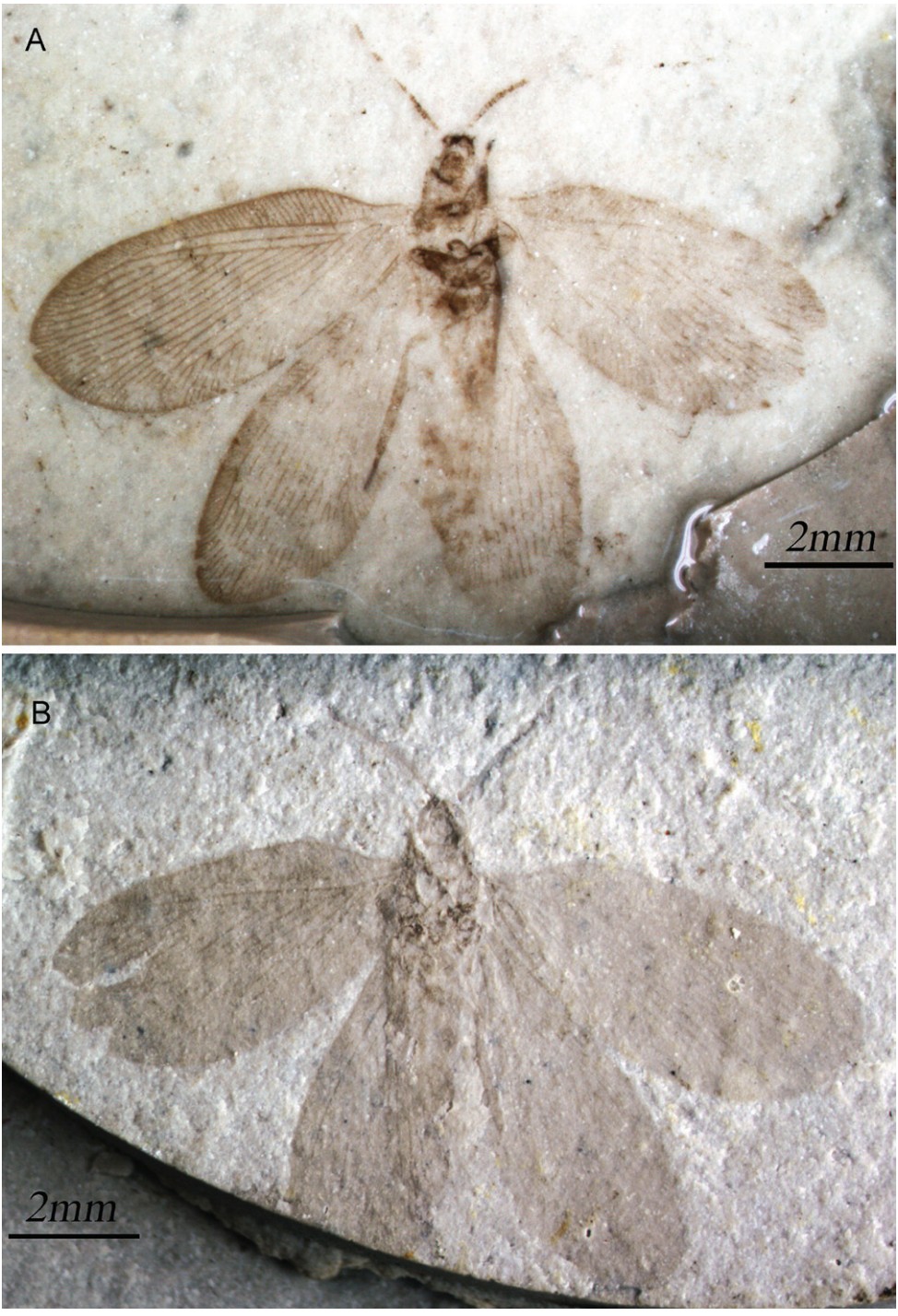

Figure 1. *Sinosmylites rasnitsyni* sp. n. Photograph of the holotype **A** part (CNU-NEU-NN2011002P; in alcohol) **B** counterpart (CNU-NEU-NN2011002C; dry).

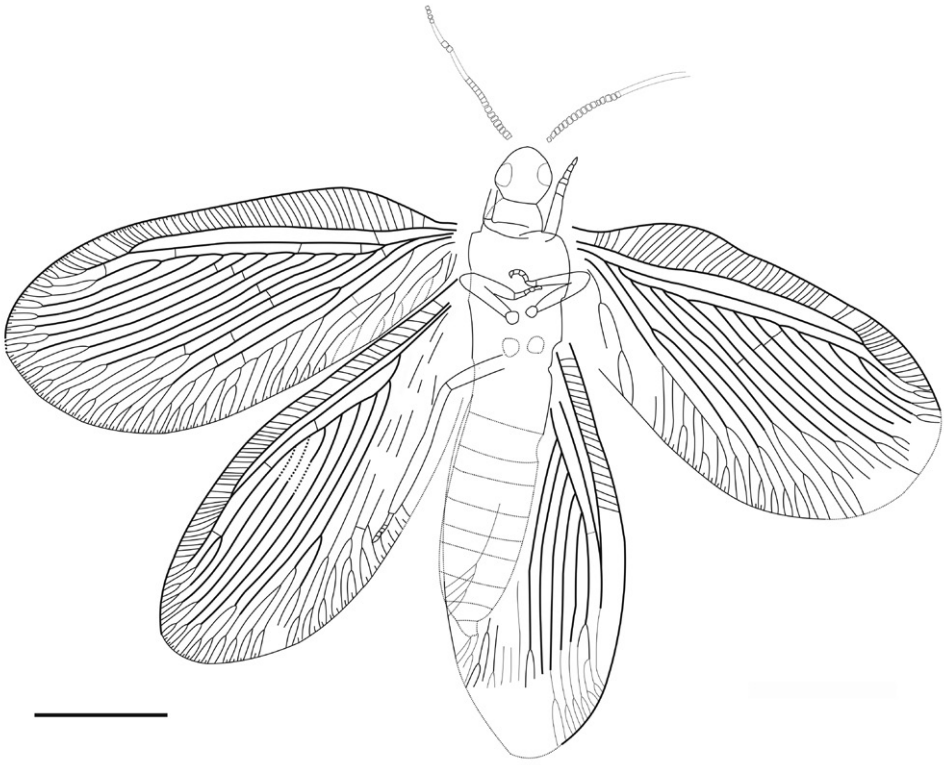

Figure 2. *Sinosmylites rasnitsyni* sp. n. Drawing of the holotype CNU-NEU-NN2011002P. Scale bar is 2 mm.

of CuP). Third ('inner') series: six crossveins preserved (between Rs1, Rs8). Fourth ('outer') series: four irregularly-spaced crossveins preserved (between Rs2, CuA). Wing one color, slightly fuscous. Veins dark brown as preserved.

Hind wing poorly preserved, approximately 6.5 mm long, 2.6 mm wide. Costal space narrow, distally only slightly dilated. Subcostal veinlets simple, rather closely spaced. Sc distally fused with R1 far from wing apex; Sc+R1 with 13 simple veinlets. Subcostal space relatively narrow; no crossveins detected. R1 space broad, dilated basally; two crossveins before fusion of Sc, R1, one after. Rs originating far from wing base, with eight branches, each forked distally 1-3 times except Rs1 which deeply forked four times. Fork of M not detected. MA once forked distally; MP dichotomously branched distally. CuA long, almost parallel to hind margin, its branches poorly preserved. CuA space relatively broad. CuP fragmentary preserved, quite short. Anal veins not preserved. Crossveins posterior to stem of Rs not detected except one distal between MP, CuA (4m-cu).

Material. Holotype CNU-NEU-NN2011002P (part), CNU-NEU-NN2011002C (counterpart), deposited in CNUB. A nearly complete specimen.

Type locality and horizon. Daohugou Village, Shantou township, Ningcheng county, Inner Mongolia, China. Jiulongshan Formation, Middle Jurassic.

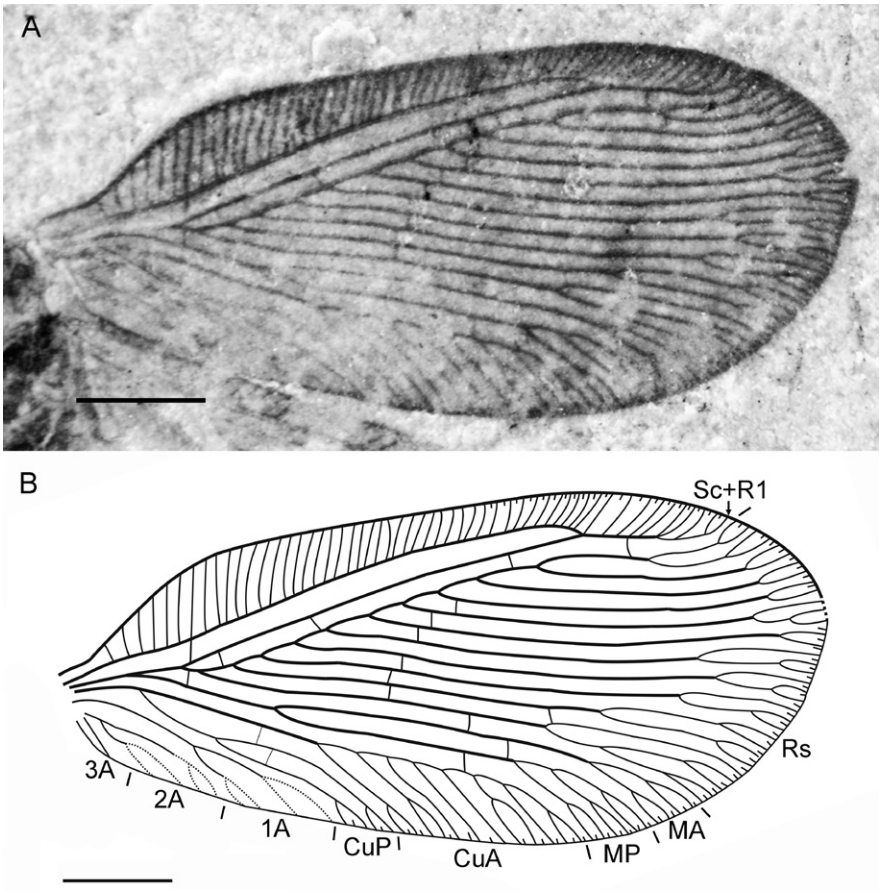

Figure 3. *Sinosmylites rasnitsyni* sp. n. Forewing of the holotype CNU-NEU-NN2011002P (converted to the right). **A** photograph **B** drawing. Scale bar is 1 mm.

Etymology. The species is named in honor of the distinguished Russian paleoentomologist Prof. Alexandr Pavlovich Rasnitsyn.

***Sinosmylites fumosus* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Sinosmylites_fumosus
Figs 4A, B

Diagnosis. Differs from *S. pectinatus* by CuP once forked (twice forked in *S. pectinatus*), by presence of one 'inner' gradate series of crossveins (two in *S. pectinatus*) (see differences from *S. rasnitsyni* sp. n. under that species.).

Description. Forewing with broad-rounded apex, about 6.0 mm long (as preserved, estimated complete length about 6.5 mm), 2.6 mm wide. Costal space mod-

erately broad, most dilated at proximal 1/5 of wing length. Subcostal veinlets simple, regularly arranged, less closely spaced than in previous species. Sc distally fused with R1 far from wing apex; Sc+R1 with nine veinlets (eight simple, one forked). Subcostal space broad, with two basal crossveins. R1 space nearly as wide as subcostal space; six crossveins before fusion of Sc and R1, one after. Rs with nine pectinate, regularly spaced branches; four proximal-most branches with 2-4 terminal forks, other branches once forked. Rs1 originating at some distance from origin of Rs. M not fused basally; forked much distal to origin of Rs1. MA, MP almost parallel, distally with one (simple) , two (one simple) branches respectively. Cu divided into CuA, CuP proximal to origin of Rs. CuA pectinate, with 7 branches; proximal-most branch once forked. CuP once deeply forked. Anal veins incompletely preserved; 1A with single marginal fork; 2A with two marginal short branches; 3A very incomplete, with single fork preserved. Four gradate series of crossveins posterior to stem of Rs, all incomplete. First series consists of three crossveins: 1r-m (located at origin of Rs), 1m-cu, 1a1-a2 (longer than previous); Second series includes two crossveins: 2m-cu (connecting MP, CuA), 2icu (connecting CuA, anterior branch of CuP). Third ('inner') series with six crossveins (3rs-rs7, 3rs5-rs4 to 3rs2-rs1; two between Rs3, Rs2). Fourth ('outer') series with five crossveins (from 4rs2-rs1 to 4m-cu; two between Rs1, MA). Wing one color, fuscous. Veins mainly dark brown as preserved.

Type material. Holotype CNU-NEU-NN2011003, deposited in CNUB. A nearly complete forewing.

Type locality and horizon. Daohugou Village, Shantou township, Ningcheng county, Inner Mongolia, China. Jiulongshan Formation, Middle Jurassic.

Etymology. From the Latin *fumosus*, smoked, in reference to the coloration of wings.

***Sinosmylites* sp.**
http://species-id.net/wiki/Sinosmylites
Figs 5A, B

Description. Hind wing approximately 6.5 mm long, 2.7 mm wide. Humeral lobe not extended; frenulum poorly-developed consisting of few bristles. Costal space narrow, dilated towards apex. Subcostal veinlets simple, more closely-spaced apically. Sc distally fused with R1 far from wing apex; Sc+R1 with seven long veinlets (one forked). Subcostal space relatively broad, with one basal crossveins. R1 space nearly as wide as subcostal space; four crossveins before fusion of Sc, R1. Rs with seven pectinate, regularly spaced branches; one branch deeply forked. Rs1 originating at some distance from origin of Rs. Proximal crossvein m-r long, connecting Rs1 near its origin with M. M forked distal to origin of Rs1. MA, MP almost parallel, distally with few branches. CuA long, slightly incurved, in general parallel to hind margin, with nine forkes branches originated at angle >45 degrees, one simple branch. CuP short, with two branched preserved. 1A–3A not preserved. Crossvein between CuA, 1A (or CuP). One crossvein between Rs, Rs6 in

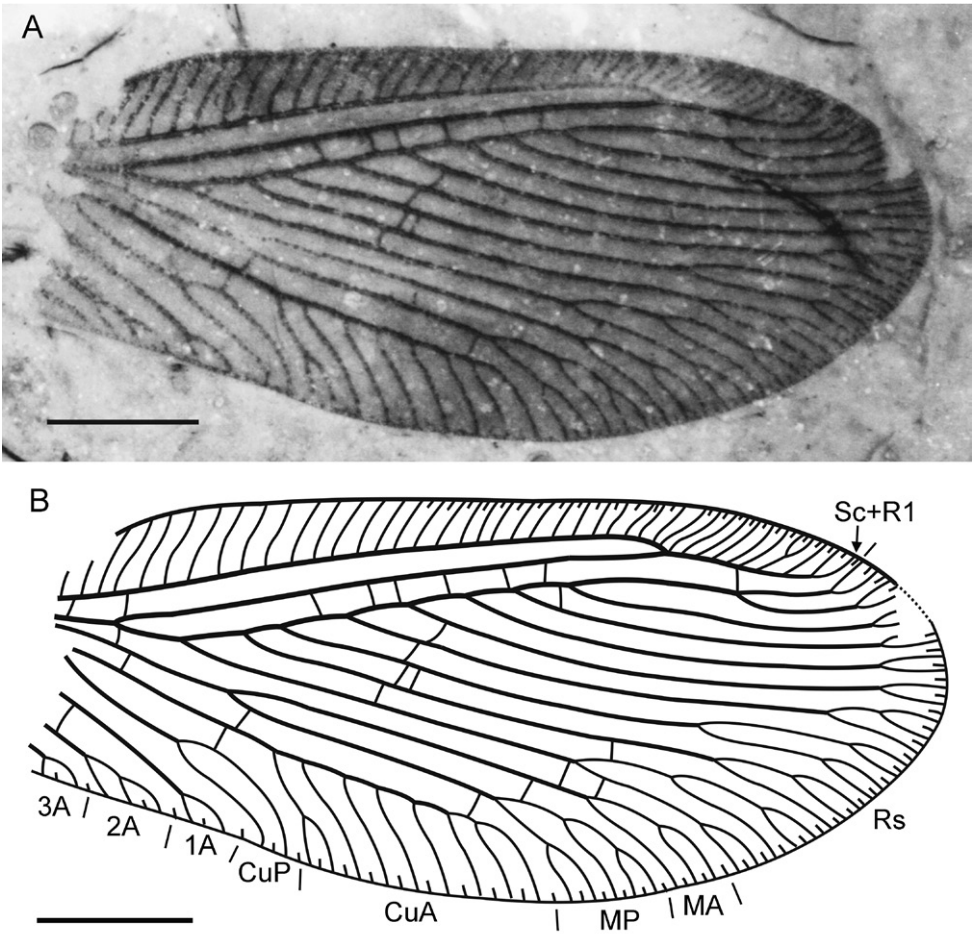

Figure 4. *Sinosmylites fumosus* sp. n. Holotype CNU-NEU-NN2011003, the forewing. **A** photograph **B** drawing. Scale bar is 1 mm.

'inner' gradate series (possibly anomalous). Six crossveins (from Rs4 to CuA) in 'outer' gradate series preserved. Wing one color, fuscous. Veins appear mainly dark brown.

Material examined. Specimen CNU-NEU-NN2011004, deposited in CNUB. A nearly complete hind wing.

Type locality and horizon. Daohugou Village, Shantou township, Ningcheng county, Inner Mongolia, China. Jiulongshan Formation, Middle Jurassic.

Comments. The venation of this hind wing is typical for Berothidae. In particular, the configuration of CuA is characteristic of this family; although this also occurs in the Nevrorthidae, nevrorthid venation is otherwise dissimilar. Also, the basal crossvein between R and M systems is straight, perpendicular to connecting veins; this is characteristic of all Berothidae except Rhachiberothinae. In the vast majority of extant Berothidae, the complete CuP is lost, but the basal or/and distal parts there

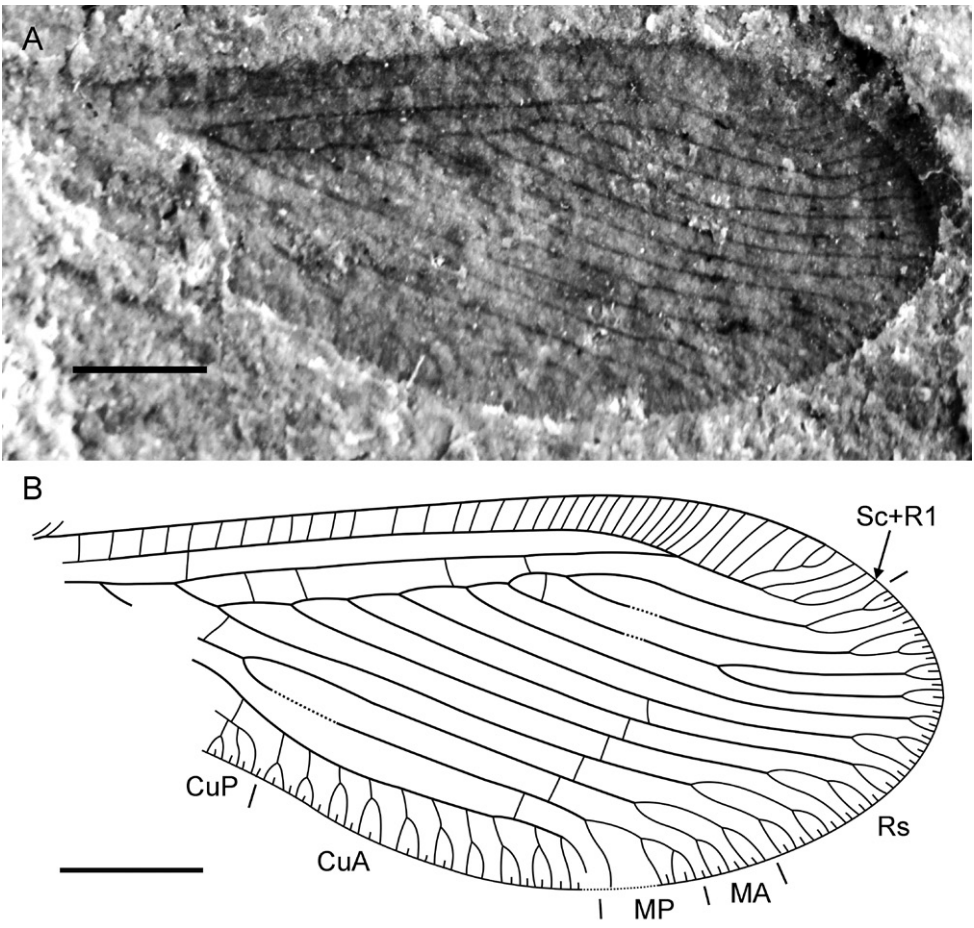

Figure 5. *Sinosmylites* sp. Specimen CNU-NEU-NN2011004, the hind wing. **A** photograph **B** drawing. Scale bar is 1 mm.

are often present. CuP is entirely lost in some genera, both fossil (e.g., *Microberotha macculloughi* Archibald and Makarkin, 2004) and extant (e.g., *Cyrenoberotha* MacLeod and Adams, 1968, *Berlekrumyia* Aspöck and Aspöck, 1988). Therefore, it is hard to determine which vein is preserved in this hind wing, the distal part of CuP or 1A (see Fig. 5B, labeled *CuP*), as the proximal portion of the wing is not preserved. We tentatively consider this vein to be CuP.

This specimen is tentatively assigned to *Sinosmylites*. The hind wings of *Sinosmylites rasnitsyni* sp. n., the only species of the genus in which these are known, are quite poorly preserved and their venation does not enable its generic character states to be determined with confidence. However, this hind wing shares similar size, coloration, and venation (e.g., Sc and R1 are fused; Sc+R1 with many branches; several crossveins between R1 and Rs; the same configuration of the Rs branches) with the forewings of *Sinosmylites* species. Therefore, this generic affinity is most likely.

Discussion

As the type species of the genus *Sinosmylites* is represented by a single forewing, its family affinity cannot be confidently determined. Its venation is more or less similar to that of such families as Berothidae, Sisyridae, Mesoberothidae, Archeosmylidae, and Prohemerobiidae, all except the first two are extinct and poorly understood. Their forewing venations show superficial similarities in the structure of the costal space (narrowed basally), Sc fused with R1 (only convergent distally but not fused in Prohemerobiidae), similar (in general) branching of Rs, M, and Cu, and their sparse cross-venation. One feature occurs rarely (if at all) in these taxa, i.e., the strongly pectinate CuA, complicating family determination. Therefore, based solely on the forewing, it may be theoretically associated with most of these families, at least provisionally. Fortunately, one of two new species described herein bears its hind wing, although poorly preserved. Its structure indicates that the berothid affinity of *Sinosmylites* is most probable, as its general venation does not conflict with that of Berothidae, and the presence of the long CuA running nearly parallel to the hind margin characteristic of the family. Moreover, the berothid affinity of a better preserved hind wing ("*Sinosmylites* sp.") is doubtless, as all of its character states are characteristic only of the Berothidae.

The forewing venation of *Sinosmylites* differs rather greatly from that of the vast majority of extant (advanced) genera of Berothidae. Particularly, M is forked distinctly more distally than in most berothid genera (including Cretaceous genera: see Engel and Grimaldi 2008), and CuP is strongly pectinate as rarely occurs in Berothidae. It appears most closely related to an Early Cretaceous genus from the Purbeck Limestone Group, which is represented by two nearly complete forewings (Jepson et al. submitted). These two genera share common venational character states (including a pectinate CuA and distal forking of M), but the Purbeck genus is much smaller (forewing length 3.7-3.8 mm) and in general has simpler venation. *Sinosmylites* is quite similar also to *Banoberotha enigmatica* Whalley, 1980 from the Early Cretaceous of Lebanese amber by the very similar outline of the costal space, simple veinlets, and M forked much distally to the origin of Rs, but otherwise their venation is different.

The hind wing venation of "*Sinosmylites* sp." appears amazingly modern. Even if our generic attribution turns out to be incorrect, its berothid family affinity is doubtless.

Triassic berothid-like taxa have been treated as belonging to the family Mesoberothidae. This taxon was created by Riek (1955) as the family Proberothidae for two genera from the Late Triassic Mount Crosby Formation in Australia, *Proberotha* Riek, 1955 and *Proberothella* Riek, 1955. The name Proberothidae was later replaced with Mesoberothidae by Carpenter (1991) as its type genus turned out to be a junior homonym of *Proberotha* Krüger, 1923. The family has never been revised, with Riek's two genera its only members (Jell 2004). It has remained, as Carpenter (1992: p. 349) noted, a "little-known family".

Mesoberotha is represented by a single forewing specimen of *M. superba* Riek, 1955, whose venation is similar to that of *Sinosmylites* (especially *S. fumatus* sp. n.,

known from a better preserved forewing), i.e., the costal space is similarly constructed, narrowed basally; Sc and R1 are fused; the subcostal space is relatively broad; few crossveins are present, most of which are arranged in a gradate series of crossveins; M, Cu, CuA and CuP are branched in a similar manner; 1A with only marginal (shallow) branches. As mentioned above, this genus cannot be assigned to a particular family with confidence based only on characters of the forewing. However, the similarity of the venation between *Sinosmylites* and *Mesoberotha* is so distinct as to strongly suggest that *Mesoberotha* may belong to Berothidae, and that Mesoberothidae is, therefore, a synonym of Berothidae. However, it is necessary to find and examine the *Mesoberotha* hind wing in order to test this hypothesis.

Riek (1955) believed that the family Mesoberothidae "seems to be directly ancestral to the Berothidae." (p. 674). Similarly, Mesoberothidae was referred by Engel and Grimaldi (2008) to the epifamily Mantispoidae (or 'dilarid clade') of the superfamily Hemerobioidea, which also contains Berothidae, Rhachiberothidae, Mantispidae, and Dilaridae. Haring and Aspöck (2004) stated that "the Berothidae are the sister group of the ithonid clade + (Mantispidae + (Chrysopidae + Hemerobiidae))" (p. 427). The oldest known taxon of the latter group is the mantispid genus *Liassochrysa* Ansorge and Schlüter, 1990 from the Early Toarcian of Dobbertin (Germany) (Wedmann and Makarkin 2007), and, therefore, the Berothidae must be at least of the same Early Jurassic age. Estimates of divergences times based on molecular analysis indicate that the clade consisting of Berothidae and Mantispidae arose during the Early Triassic (Winterton et al. 2010). Consequently, the Late Triassic Mesoberothidae may well represent an early group of Berothidae.

'Archeosmylus' ?costalis Riek, 1955 from the same Australian locality as *Mesoberotha* probably also belongs to the Mesoberothidae. Its venation differs not sufficiently from that of *Mesoberotha superba*, and it may possibly belong to this genus. The family affinity of '*Archeosmylus' stigmatus* Riek, 1955 is not yet clear.

Acknowledgements

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RESEARCH ARTICLE

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A new fossil silky lacewing genus (Neuroptera, Psychopsidae) from the Early Cretaceous Yixian Formation of China

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Abstract

A new genus and species, *Undulopsychopsis alexi* **gen. et sp. n.,** is described from the Early Cretaceous Yixian Formation of western Liaoning Province, China. This genus is probably most closely related to the Asian Cretaceous genus *Kagapsychops* Fujiyama, 1978. The family affinity of *Undulopsychopsis* **gen. n.** is discussed. The genus is preliminarily assigned to Psychopsidae, although it shares some character states with Osmylopsychopidae (e.g., crossveins are very scarce; Rs1 and 1A are multi-branched).

Keywords

Psychopsidae, Osmylopsychopidae, fossil, Mesozoic, Huangbanjigou, China

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Introduction

The extant Psychopsidae is a small family (five genera and 27 described species), currently restricted to disjunct regions in southern Africa, southeastern Asia and Australia (New 1988; Oswald 1993a; Wang and Bao 2006). Adult psychopsids are recognized by their broad wing shape, dense venation, the presence of *vena triplica*, spectacularly patterned and hairy wings, which gives psychopsids the common name of silky lacewings (New 1989; Oswald 1993a, 1995).

Fossil psychopsids were much more widely distributed than the extant taxa. Since the early 20th century, fossil psychopsids have increasingly been found from all over the world, with species ranging in age from the Triassic to the Tertiary. The earliest fossil record of the Psychopsidae is *Triassopsychops* Tillyard, 1922 from the Late Triassic of Australia (Tillyard 1922), which possesses a true *vena triplica*, characteristic of this family. While many fossil psychopsids were recorded from the Mesozoic, few representatives have been described from the Tertiary. Hitherto, 35 fossil species (24 genera) have been referred to Psychopsidae (Table 1). The psychopsid affinity of many Jurassic and Cretaceous genera is debatable. For example, Jepson et al. (2009) believe that some genera (e.g., *Grammapsychops* Martynova, 1954, *Embaneura* G. Zalessky, 1953, *Pulchroptilonia* Martins-Neto, 1997, and *Kagapsychops* Fujiyama, 1978) may belong to another psychopsoid family, Osmylopsychopidae. The position of these and some other fossil genera from the Mesozoic is questionable, due to certain differences in details of the wing venation between fossil and extant psychopsids (e.g., the pattern of Rs branches, the configuration of M and Cu in the forewing, the structure of *vena triplica*), although their general venational pattern is similar to that of extant representatives. Furthermore, the combination of a small number of known extant species and the often poor preservation of fossil representatives has greatly hindered the understanding of fossil psychopsids. The ambiguous diagnoses of many fossil psychopsids have resulted in potential confusion with other Mesozoic neuropterans (Andersen 2001; Makarkin and Archibald 2003). More evidence is needed to further the knowledge of fossil psychopsids. In recent years, many Mesozoic psychopsids described from Asia (particularly from Russia and China) have drawn increased attention to fossil psychopsids. In this paper, we describe a new genus and species of Psychopsidae from the Early Cretaceous Yixian Formation of Huangbanjigou Village, Liaoning Province, China.

Material and methods

The specimen described herein is from the Yixian Formation of Huangbanjigou Village, Shangyuan County, Beipiao City, western Liaoning Province, northeastern China. The principal fossil-bearing layers in Huangbanjigou locality are silty mudstone, yellowish to grayish, rich in insects, fish and plants (Chen et al. 2005). The age of these fossil-bearing strata in Sihetun area (including Huangbanjigou) is considered to be well supported by radiometric dating as Early Cretaceous (Middle/Late Barremian), from

Table 1. Fossil species currently ascribed to the family Psychopsidae.

	Species	Age	Locality
1	*Triassopsychops superbus* Tillyard, 1922	Late Triassic (Carnian)	Denmark Hill, Queensland, Australia
2	*Archepsychops triassicus* Tillyard 1919	Late Triassic (Carnian)	Denmark Hill, Queensland, Australia
3	*Apeirophlebia grandis* Handlirsch, 1906	Early Jurassic (Early Toarcian)	Dobbertin, Germany
4	*Cretapsychops decipiens* Peng et al., 2010	Middle Jurassic (Aalenian/Bajocian)	Daohugou, Inner Mongolia, China
5	*Beipiaopsychops triangulatus* Hong, 1983	Middle Jurassic (Aalenian/Bajocian)	Haifanggou, Liaoning, China
6	*Sinopsychops chengdeensis* Hong, 1982	Middle Jurassic (Aalenian/Bajocian)	Chengde, Hebei, China
7	*Calopsychops extinctus* Panfilov, 1980	Late Jurassic (Oxfordian/ Kimmeridgian)	Karatau, Kazakhstan
8	*Propsychops karatavicus* Panfilov, 1980	Late Jurassic (Oxfordian/ Kimmeridgian)	Karatau, Kazakhstan
9	*Angaropsychops sinicus* Hong in Wang, 1980	?Early Cretaceous	Heishangou, Liaoning, China
10	*Kagapsychops aranea* Fujiyama, 1978	Early Cretaceous (Valanginian/Barremian)	Kuwajima, Japan
11	*Angaropsychops turgensis* Martynova, 1949	Early Cretaceous (Hauterivian)	Turga, Transbaikalia, Russia
12	*Psychopsites rolandi* Jepson et al., 2009	Early Cretaceous (Hauterivian)	Lower Weald Clay, Wealden, England
13	*Valdipsychops minimus* Jepson et al., 2009	Early Cretaceous (Hauterivian)	Lower Weald Clay, Wealden, England
14	*Baisopsychops lambkini* Makarkin, 1997	Early Cretaceous (pre-Barremian)	Baissa, Transbaikalia, Russia
15	*Epipsychopsis fusca* Makarkin, 2010	Early Cretaceous (pre-Barremian)	Baissa, Transbaikalia, Russia
16	*Epipsychopsis variegata* Makarkin, 2010	Early Cretaceous (pre-Barremian)	Baissa, Transbaikalia, Russia
17	*Undulopsychopsis alexi* gen. et sp. n.	Early Cretaceous (Barremian)	Huangbanjigou, Liaoning, China
18	*Cretapsychops corami* Jepson et al., 2009	Early Cretaceous (Barremian)	Upper Weald Clay, Wealden, England
19	*Micropsychops parallelus* Jepson et al., 2009	Early Cretaceous (Barremian)	Upper Weald Clay, Wealden, England
20	*Valdipsychops brigidae* Jepson et al., 2009	Early Cretaceous (Barremian)	Upper Weald Clay, Wealden, England
21	*Valdipsychops logunovi* Jepson et al., 2009	Early Cretaceous (Barremian)	Upper Weald Clay, Wealden, England
22	*Valdipsychops proudlovei* Jepson et al., 2009	Early Cretaceous (Barremian)	Upper Weald Clay, Wealden, England
23	*Valdipsychops maculosus* Jepson et al., 2009	Early Cretaceous (Barremian)	Upper Weald Clay, Wealden, England

	Species	Age	Locality
24	*Pulchroptilonia espatifata* Martins-Neto, 1997	Early Cretaceous (Aptian)	Araripe Basin, Brazil
25	*Putzneura parcimoniosa* Martins-Neto & Rodrigues, 2010	Early Cretaceous (Aptian)	Araripe Basin, Brazil
26	*Litopsychopsis burmitica* Engel & Grimaldi, 2008	Early Cretaceous (Albian)	Burmese amber
27	*Embaneura vachrameevi* G. Zalessky, 1953	Late Cretaceous (Cenomanian)	Emba, Kazakhstan
28	*Grammapsychops lebedevi* Martynova, 1954	Late Cretaceous (Cenomanian)	Kem' River, Siberia, Russia
29	*Kagapsychops continentalis* Makarkin, 1994	Late Cretaceous (Turonian)	Kzyl-Zhar, Kazakhstan
30	*Arctopsychops zherikhini* Makarkin, 1994	Late Cretaceous (Turonian)	Arkagala, NE Siberia, Russia
31	*Propsychopsis helmi* Krüger, 1923	Eocene (Lutetian/ Bartonian)	Baltic amber
32	*Propsychopsis hageni* MacLeod, 1971	Eocene (Lutetian/ Bartonian)	Baltic amber
33	*Propsychopsis lapicidae* MacLeod, 1971	Eocene (Lutetian/ Bartonian)	Baltic amber
34	*Miopsychopsis relicta* Makarkin, 1991	Late Eocene/Early Oligocene	Amgu, Sikhote-Alin, Russia
35	*Miopsychopsis sikhotensis* Makarkin, 1991	Late Eocene/Early Oligocene	Amgu, Sikhote-Alin, Russia

126.1 ± 1.7 to 124.6 ± 0.1 Ma (e.g., Swisher et al. 1999; Wang et al. 2001b; Chen et al. 2004; Yang et al. 2007), although the upper-most beds of Huangbanjigou locality have an Early Aptian age, 123.3 ± 0.5 – 122.8 ± 1.6 Ma (Wang et al. 2001a; Yang et al. 2007). The specimen is deposited in the Chaoyang Bird Fossil National Geopark, Chaoyang City, Liaoning Province, China.

The material was examined using a Leica MZ12.5 dissecting microscope. The photographs were taken using a Nikon D100 digital camera coupled to a Nikkor 105mm macro lens, and final photographs were adjusted by using Adobe Photoshop 4.0 image-editing software. All line drawings were drawn made directly using CorelDraw 12 graphic software.

We follow the traditional (*sensu* Wootton 2003) venational terminology of Comstock (1918) with the recent interpretation of Oswald (1993b) and Archibald and Makarkin (2006). The abbreviations used in the text are: C, costa; Sc, subcosta; hv, humeral veinlet; R, radius; R1, first branch of R; Rs, radial sector; Rs1, basal-most branch of Rs; M, media; MA, media anterior; MP, media posterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; 1A–2A, first to second anal veins.

Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Family Psychopsidae Handlirsch, 1906

Genus *Undulopsychopsis* gen. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Undulopsychopsis

Type species. *Undulopsychopsis alexi* sp. n.

Diagnosis. Forewings: costal gradate series absent; branches of Rs dichotomously branched; Rs1 multi-branched, pectinate with branches directed anteriorly; M forked far distal to origin of Rs; CuP dichotomously branched. Hind and outer margins of both wings undulate.

Etymology. The generic name is derived from the Late Latin *undula* (meaning a small wave, refers to its undulate wing margins) and *Psychopsis* (the type genus of the family). The gender is feminine.

Remarks. This new genus differs from all other psychopsids by possessing undulate outer and hind margins of both wings. The combination of the following forewing character states is also characteristic: no costal gradate series; branches of Rs dichotomously branched; the basal-most branch of Rs multi-branched, and M forked far distal to the origin of Rs. The new genus has scarce costal crossveins, which are not arranged in gradate series, in contrast to the genera *Grammapsychops*, *Miopsychopsis* Makarkin, 1991, *Baisopsychops* Makarkin, 1997, *Cretapsychops* Jepson et al., 2009 and *Epipsychopsis* Makarkin, 2010. *Undulopsychopsis* gen. n. possesses the dichotomously branched branches of Rs; this condition is also present in the following psychopsid genera: *Triassopsychops*, *Angaropsychops* Martynova, 1949, *Psychopsites* Jepson et al., 2009, *Valdipsychops* Jepson et al., 2009, *Epipsychopsis*, *Pulchroptilonia*, *Putzneura* Martins-Neto et Rodrigues, 2010, *Kagapsychops*, *Grammapsychops*, and *Embaneura*. Among these the new genus is most similar to those genera which have the multi-branched Rs1 and M forked far distal to the origin of Rs. This combination is present only in the genus *Kagapsychops*. The type species of this genus (*K. aranea* Fujiyama, 1978) is fragmentary and poorly preserved, but *K. continentalis* Makarkin, 1994 is well-preserved (although incomplete). *Undulopsychopsis* gen. n. clearly differs from *Kagapsychops* by being a much smaller size (the forewing of the former is approximately twice shorter than that of the latter), and the absence of the gradate series of crossveins in the radial space. Other fossil psychopsids, for example *Propsychopsis* Krüger, 1923, *Litopsychopsis* Engel et Grimaldi, 2008 and *Micropsychops* Jepson et al., 2009 differ strongly from the new genus by having mostly unbranched veins of Rs before end-twigging and several long gradate series of crossveins in the radial space.

***Undulopsychopsis alexi* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Undulopsychopsis_alexi
Figs 1–3

Material. Holotype CYNB044, a well-preserved specimen, with body partially preserved and four wings overlapping pairwise.

Diagnosis. As for the genus.

Description. Body: only partial thorax preserved. Pronotum sub-rectangular, 1.2 mm long, 2.8 mm wide, suffused with many long hairs. Mesonotum 3 mm long, 3.5 mm wide, with some long hairs laterally.

Forewing (Fig. 3) subtriangular, 21.5 mm long, 12.3 mm wide. Costal space broad throughout; subcostal veinlets forked; humeral veinlet slightly recurrent, branched. Subcostal space much broader than R1 space. R1 space narrow. Sc and R1 close distally but not fused. Rs with 10 primary branches, branches of Rs dichotomously branched; Rs1 pectinately branched with branches directed anteriorly. M appears originating from R, forked far from origins of Rs1. MA and MP probably simple (their terminal parts not preserved). Cu forked near wing base. CuA pectinately branched distal to fork of M. CuP multi-branched, dichotomous. Anal area well-developed. 1A long, dichotomously branched. 2A multi-branched (incompletely preserved). Only few crossveins detected: costal space basally with scarce crossveins, not forming gradate series; subcostal space with 4 crossveins preserved; R1 space with 5 crossveins preserved; medial space with 2 crossveins preserved. Veins covered with dense hairs, particularly long basally. Trichosors distinct. Wing membrane in general brownish; colour pattern consists mainly of two pale transverse zigzagged bands which are proximally darker than other portions of wing; indistinctly mottled basally and apically. Wing margin haired; hind and outer margins undulate.

Hind wings almost entirely hidden under forewing, about 16.5 mm long as preserved, 10 mm wide. Venation very poorly preserved; no details visible. Outer margin undulate.

Etymology. The specific name is named in honor of the distinguished Russian paleoentomologist Prof. Alexandr ('Alex') Rasnitsyn.

Type locality and horizon. Yixian Formation, Huangbanjigou Village, Shangyuan County, Beipiao City, Liaoning Province, China.

Discussion

Based on the configuration of the venation in the radial space of the forewing, fossil psychopsids can be divided into two groups. One group includes the taxa with simple branches of Rs, the majority of which are not branched before end-twigging. This group is represented by the genera *Propsychopsis*, *Baisopsychops*, *Cretapsychops*, *Micropsychops* and *Litopsychopsis*. The crossveins in these genera are usually arranged in one to two

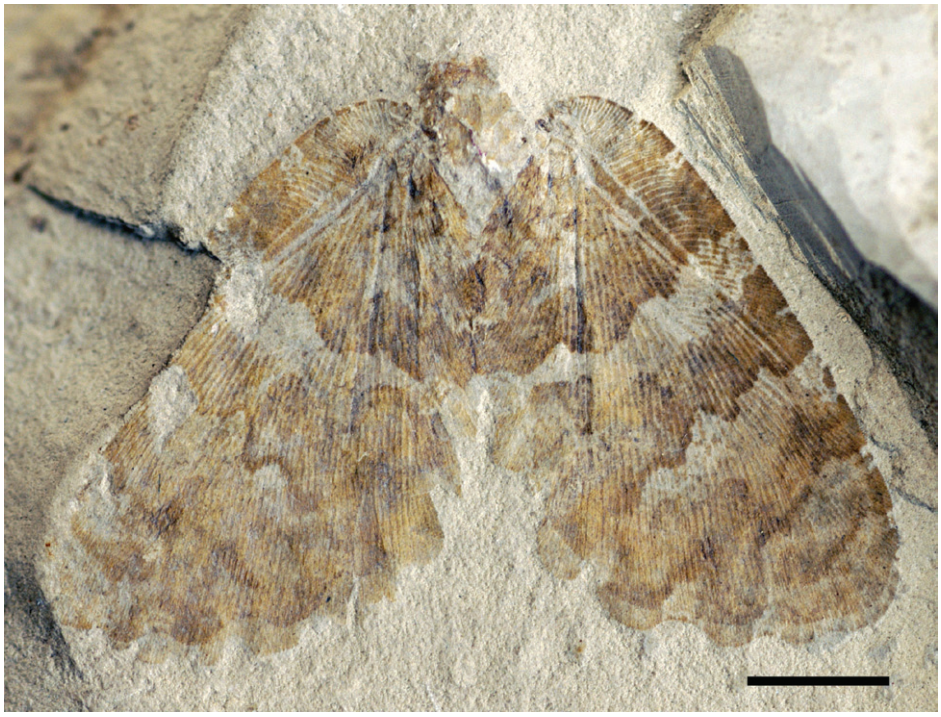

Figure 1. *Undulopsychopsis alexi* gen. et sp. n. The holotype CYNB044. Photograph. Scale bar = 5 mm.

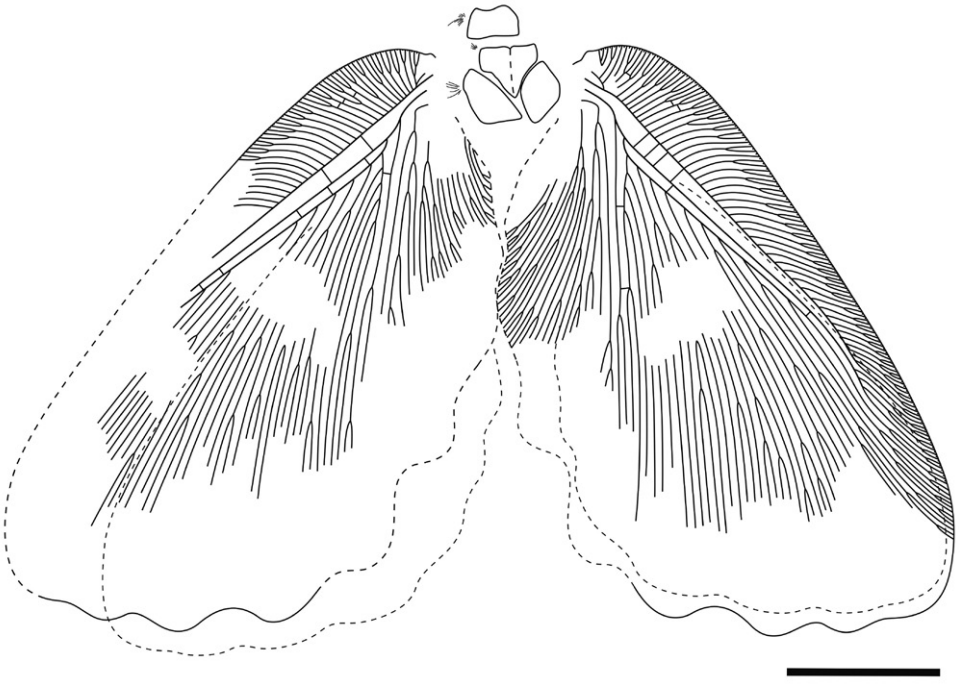

Figure 2. *Undulopsychopsis alexi* gen. et sp. n. The holotype CYNB044. Drawing. Scale bar = 5 mm.

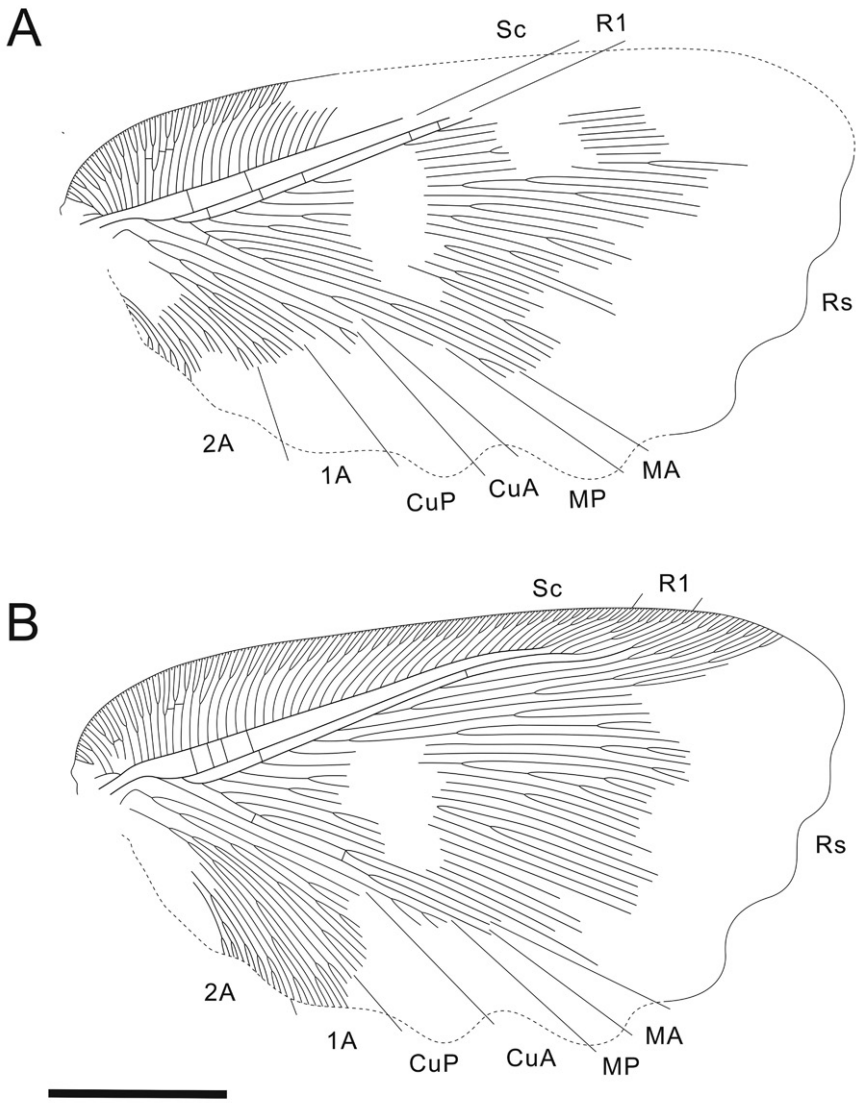

Figure 3. *Undulopsychopsis alexi* gen. et sp. n. The forewing venation of the holotype CYNB044. **A** left forewing (converted to the right) **B** right forewing. Scale bar = 5 mm.

gradate series in the costal space, and two to four long gradate series in the radial space. They occur in the Cretaceous and Eocene; all extant genera belong to this group as well.

The other group includes the taxa which have the branches of Rs dichotomously branched, and often the basal-most branch of Rs multi-branched. Representative genera of this group are the earliest psychopsid *Triassopsychops*, and other Mesozoic psychopsids, e.g., *Angaropsychops*, *Grammapsychops* and *Kagapsychops* (see complete list above). They possess numerous radial crossveins, arranged in many short gradate series (often irregular), and usually no costal gradate series. *Undulopsychopsis* gen. n. belongs to the latter group. It is preliminarily assigned to Psychopsidae, as its Sc and R1 are not fused apically, and the costal space is broad, although it almost lacks crossveins. The latter feature, and the multi-branched Rs1 and 1A are shared by this genus with another Mesozoic psychopsoid family Osmylopsychopidae (especially with its type genus) known from the Triassic of Australia and Central Asia (Lambkin 1992; Shcherbakov 2008). However, in the family Osmylopsychopidae Sc and R1 are clearly fused apically. Some genera currently ascribed to Psychopsidae also have venation similar to that of Osmylopsychopidae (e.g., Sinopsychops Hong, 1982; *Grammapsychops*). Unfortunately, the majority of these are either fragmentary or incompletely described and are in need of re-examination. Therefore, until the revision of psychopsoids has been completed, we consider all species enumerated in Table 1 as tentatively belonging to Psychopsidae.

Previously, only four species have been recorded from the Mesozoic of China, i.e., *Angaropsychops sinicus* Hong in Wang, 1980 (probably from the Early Cretaceous Yixian Formation), *Sinopsychops chengdeensis* Hong, 1982, *Beipiaopsychops triangulatus* Hong, 1983, and *Cretapsychops decipiens* Peng et al., 2010 (all from the Middle Jurassic Jiulongshan Formation). *Undulopsychopsis* gen. n. is the fifth representative of the Chinese psychopsids found from the different locality (Huangbanjigou). It is characterized by the undulate wing margin, a unique character state among known Psychopsidae, and the forewing venation that is not typical for this family compared with most other genera of Psychopsidae.

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RESEARCH ARTICLE

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A new ground beetle (Carabidae, Protorabinae) from the Lower Cretaceous of Inner Mongolia, China

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Abstract

Cretorabus rasnitsyni **sp. n.**, belonging to the extinct subfamily Protorabinae of Carabidae, was described based on a well-preserved specimen from the Lower Cretaceous Yixian Formation of Yangshuwanzi, Inner Mongolia. The diagnostic characters for *Cretorabus* are revised, and the key to species of the genus was presented. The fossil record of Protorabinae was summarized. *Sinocarabus* Hong, 1982 and *Obesofemoria* Hong, 1982 cannot be attributed to Protorabinae.

Keywords

Protorabinae, Coleoptera, Lower Cretaceous, Inner Mongolia, China

Introduction

Protorabinae is an extinct subfamily of Carabidae, and differs remarkably from all other carabid beetles in that the metepisterna are extending to the mesocoxal cavities (Ponomarenko 1977). The earliest Protorabinae, *Lithorabus incertus* Ponomarenko,

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1977, was described from the Lower Jurassic of Issyk-Kul, Kirghizia (Ponomarenko 1977). Up to date, nearly 30 species within 8 genera are known from the Jurassic of Central Asia and the Lower Cretaceous of Mongolia, Russia, China and UK (Gromov et al. 1993; Ponomarenko 1977, 1980, 1986, 1989; Ponomarenko et al. 2005; Ren 1995). However, some Chinese Protorabinae require more detailed descriptions and revisions. The famous Early Cretaceous Jehol Biota yields abundant, well-preserved insects, including beetles. However, no record of Carabidae was reported from this lagerstätte until now. Herein, a new species of Protorabinae is described based on a well-preserved beetle from the Yixian Formation of Inner Mongolia, and the current fossil record of Protorabinae is summarized herein.

Material and methods

The specimen (NIGP152464) was from the Lower Cretaceous Yixian Formation of Yangshuwanzi Village, Bisiyingzi Township, Ningcheng County, Chifeng City, Inner Mongolia. The fossils from Yangshuwanzi are commonly preserved in yellow silty mudstone. The horizon in this locality is equivalent to either the Jianshangou or Dawangzhangzi bed (about 124–122 Ma) of the Yixian Formation (Chang et al. 2009). The coleopteran assemblages from this locality were dominated by a variety of scarabs.

The specimen was examined dry and under alcohol, using a Nikon SMZ1000 stereomicroscope and drawings were made with the aid of a camera lucida. The photographs were prepared using a digital camera (DXM1200) connected to the above stereomicroscope, and the line drawings were readjusted on photographs using image-editing software (CorelDRAW X4 and Adobe Photoshop CS). In drawings, the broken lines denote the hidden and presumably missing body parts. Body length was measured along the midline from the anterior margin of frons to apex of elytra, and width was measured across the broadest part of elytra. The length of pronotum was measured along the midline; the width was measured across the broadest part of pronotum.

Systematic Paleontology

Family Carabidae Latreille, 1802
Subfamily Protorabinae Ponomarenko, 1977

Genus *Cretorabus* Ponomarenko, 1977
http://species-id.net/wiki/Cretorabus

Type species. *Cretorabus capitatus* Ponomarenko, 1977; by original designation.

Type horizon and locality. Zaza Formation, Lower Cretaceous; Baissa, Buryatiya, Russia.

Diagnosis. Body wide, small or medium-sized. Head large, strongly transverse. Pronotum transverse, widest in anterior or middle portion, constricted behind middle. Mesoventrite longer than mesocoxae. Metepisterna posteriorly tapering. Metacoxal plates tapering strongly in lateral half, extending as a narrow tongue up to lateral margins of metacoxae. Abdomen short, with rounded apex; last ventrite long, its anterior margin two-thirds narrower than base of abdomen. Legs short, femora slightly extending beyond body sides. Elytra smooth or with numerous rows of large punctures.

Remarks. The genus is different from other genera in the metacoxal plates tapering strongly in lateral half, extending as a narrow tongue up to the lateral margins of metacoxae. Furthermore, it differs from *Cordorabus* Ponomarenko, 1977 in having the mesoventrite longer than mesocoxae, and abdomen short, with apex rounded; from *Ovrabites* Ponomarenko, 1977 in possessing the pronotum constricted behind middle, abdomen short, with apex rounded; from *Protorabus* Ponomarenko, 1977 by the last ventrite much narrower than base of abdomen, and elytra with grooves; from *Lithorabus* Ponomarenko, 1977 in having the metepisterna posteriorly tapering; from *Nebrorabus* Ponomarenko, 1989 in possessing the wider body and shorter legs.

Species included. Six species: *C. capitatus* Ponomarenko, 1977 and *C. latus* Ponomarenko, 1977 from the Lower Cretaceous of Baissa; *C. orientalis* Ponomarenko, 1989 from the Lower Cretaceous of Khutel Khara of Mongolia; *C. ovalis* Ponomarenko, 1989 from the Lower Cretaceous of Bon-Tsagan of Mongolia; *C. sulcatus* Ponomarenko, Coram & Jarzembowski, 2005 from the Lower Cretaceous Purbeck Limestone Group of England; and *C. rasnitsyni* sp. n. from the Lower Cretaceous Yixian Formation of Inner Mongolia of China.

Key to species of *Cretorabus*

1	Body small or medium-sized (length < 10 mm)	**3**
–	Body large (> 13 mm)	**2**
2	Metacoxae 1.8 times as wide as long	***C. latus* Ponomarenko, 1977**
–	Metacoxae 2.5 times as wide as long	***C. ovalis* Ponomarenko, 1989**
3	Body small (length 3.7 mm); elytra with punctate furrows	***C. sulcatus* Ponomarenko, Coram & Jarzembowski, 2005**
–	Body medium-sized; elytra smooth	**4**
4	Prosternal process narrow, 0.4 times as wide as procoxae, slightly longer than procoxae; metacoxae 1.5 times as wide as long	***C. capitatus* Ponomarenko, 1977**
–	Prosternal process almost as wide as procoxae, much longer than procoxae; metacoxae 2.5 times as wide as long	**5**
5	Metaventrite twice as wide as long; metacoxal plates with emargination in lateral part of posterior margin	***C. orientalis* Ponomarenko, 1989**
–	Metaventrite 3 times as wide as long; metacoxal plates with lateral part of posterior margin not emarginate	***C. rasnitsyni* sp. n.**

***Cretorabus rasnitsyni* Wang & Zhang, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Cretorabus_rasnitsyni
Figs 1–5

Holotype. NIGP152464, male, a well-preserved beetle in ventral aspect. Yixian Formation, Lower Cretaceous; a fossil locality (41°25'N, 118°57'E) near Yangshuwanzi Village, Bisiyingzi Township, Ningcheng County, Chifeng City, Inner Mongolia, China. Deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

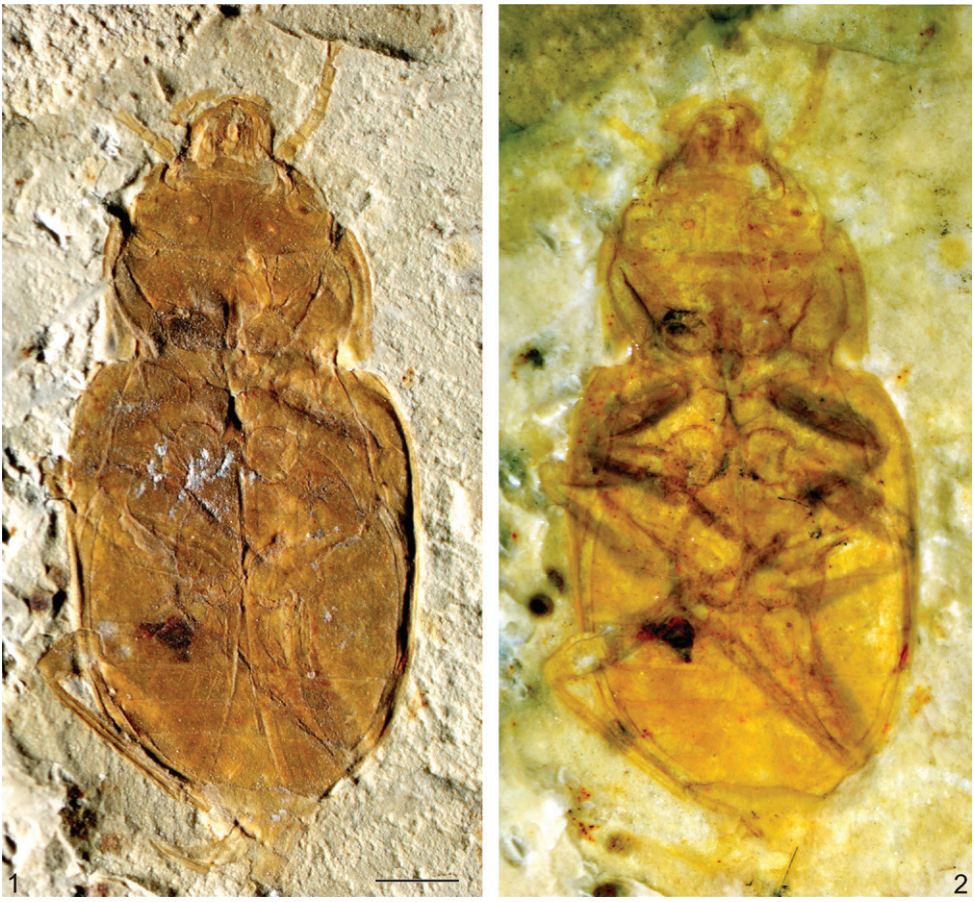
Diagnosis. Body medium-sized. Pronotum 1.8 times as wide as long. Prosternal process almost as wide as procoxae, much longer than procoxae. Metaventrite 3 times as wide as long. Metacoxae 1.8 times as wide as long. Metacoxal plates with lateral part of posterior margin not emarginate.

Description. Head and pronotum strongly transverse. Length of head (including mandibles) slightly shorter than occiput width. Head capsule narrowing anteriorly from base. Eyes shorter than temples. Gular plate 1.5 times as long as wide, widened anteriorly. Antennae inserted at anterior margin of eyes; scape dilated; pedicellum slightly shorter than scape; first flagellomere slightly longer than scape. Mandibles large, slightly incurved, asymmetrical, with retinaculum small. Maxillary palps 4-segmented, conspicuously longer than mandibles; palpomere 4 with apical margin subtruncate.

Pronotum 1.8 times as wide as long, widest nearly in the middle; pronotal angles pointed, concealing the base of head dorsally. Propleura narrow. Prosternum before procoxae 1.4 times longer than procoxae. Prosternal process wide, 1.4 times as long as procoxae. Mesoventrite transverse, with subtriangular depression for reception of prosternal process. Mesepisternum almost rectangular, transverse. Mesepimeron short, extending to mesocoxal cavities, slightly widened laterally. Metaventrite short, 3 times as wide as long; its anterior margin half as long as the posterior. Metepisterna subtriangular, gradually widened anteriorly, its length 1.5 times width at anterior margin. Metacoxae oblique, slightly projecting over abdomen, 3 times as wide as long. Metacoxal plates slightly longer than coxae. Abdomen a little longer than meso- and metathorax combined, widened from base to apex of second visible sternite, then narrowing. Parameres rather long, with penis slightly projecting.

Profemur and protibia widened apically, almost equal in length. Tarsal segments widened apically; tarsomeres 1 almost as long as tarsomeres 2; tarsomeres 2 slightly longer than tarsomeres 3. Mesofemur and mesotibia almost equal in length. Mesotibia widened apically, 1.2 times as long as protibia. Metatrochanters one-third as long as metafemora. Metatibiae 1.1 times as long as metafemora, slightly widened apically; its outer side possibly with pits.

Measurements. Body length 7.8 mm, width 4.0 mm. Head length (including mandibles) 1.9 mm, occiput width 2.6 mm; mandible length 0.8 mm. Pronotum:

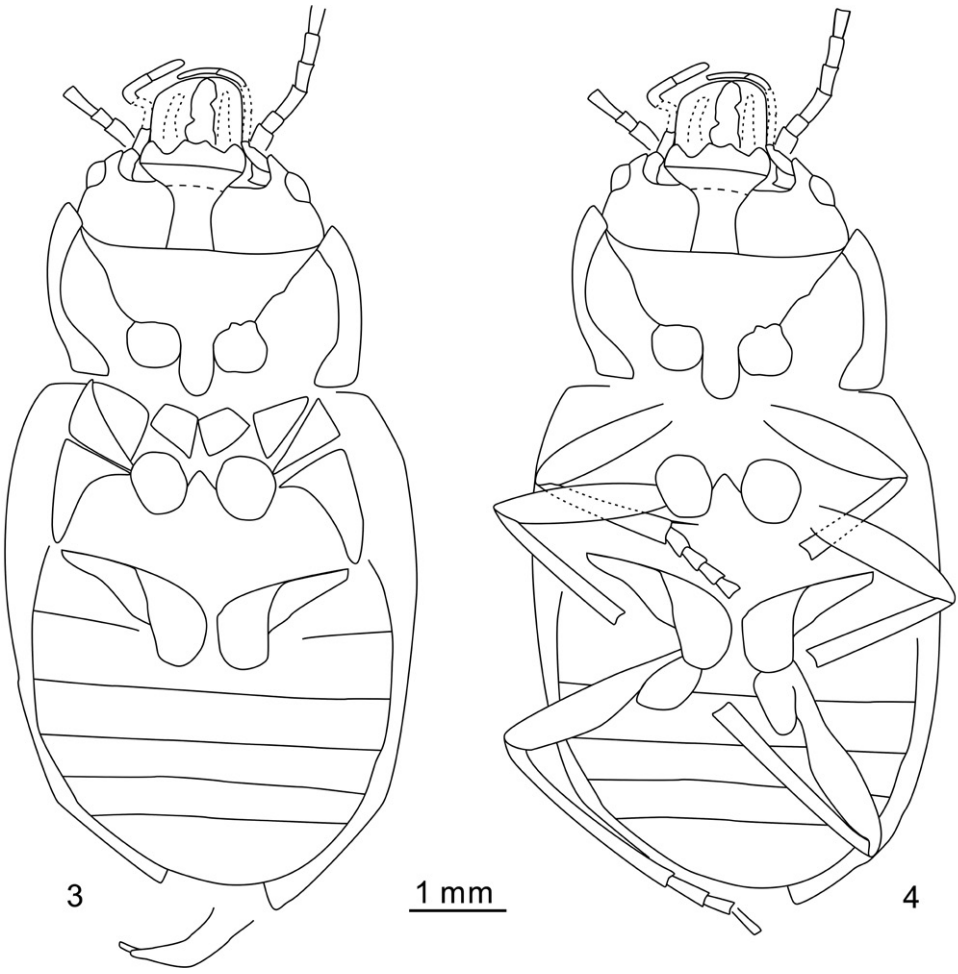


Figures 1–2. *Cretorabus rasnitsyni* sp. n., photomicrograph of holotype NIGP152464 **1** dry **2** under alcohol. Scale bar represents 1 mm.

length 1.8 mm, maximal width 3.2 mm. Abdomen: length 3.3 mm. Fore legs: femur length 1.5 mm; tibia length 1.5 mm. Middle legs: femur length 1.7 mm; tibia length 1.7 mm. Hind legs: femur length 2.0 mm; tibia length 2.3 mm.

Etymology. Specific epithet is devoted to Alexander P. Rasnitsyn, an outstanding Russian palaeoentomologist.

Remarks. This specimens can be undoubtedly attributed to *Cretorabus* by the following characters: the pronotum constricted behind middle; mesoventrite longer than mesocoxae; metacoxal plates tapering strongly in lateral half, extending as a narrow tongue up to the lateral margins of metacoxae; and abdomen short, with rounded apex. The species mostly resembles *C. orientalis* in having the prosternal process much longer than procoxae, and metacoxae 2.5 times as wide as long, but differs from the latter in possessing the metacoxal plates with the lateral part of the margin not emar-



Figures 3–4. *Cretorabus rasnitsyni* sp. n., drawings of holotype NIGP152464 **3** without legs **4** with legs.

ginate. Furthermore, it is different from *C. capitatus* in having the comparatively wider prosternal process and metacoxae.

Discussion

Ponomarenko and Kirejtshuk (2011) have revised and summarized the fossil record of Protorabinae, but the Chinese data require further revisions. Two monotypic genera, *Sinocarabus* Hong, 1982 and *Obesofemoria* Hong, 1982 were described from the Lower Cretaceous of Yumen of Gansu by Hong (1982), and also recorded

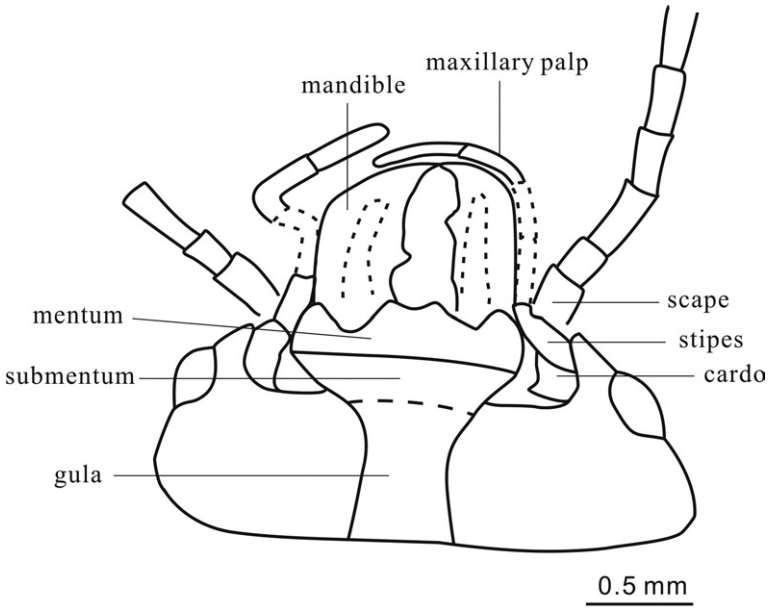


Figure 5. *Cretorabus rasnitsyni* sp. n., drawing of mouthparts of holotype NIGP152464.

in the list of fossil beetles by Ponomarenko and Kirejtshuk (2011). *Sinocarabus leptoceroides* Hong, 1982 was erected based on a specimen with the part and counterpart (Hong 1982). Judging from the original photograph (Hong 1982, plate 26, Figs 3, 4), this specimen seems to belong to Carabidae because of its body shape and strong mandibles. In the Hong's original description, he stated that the "metacoxae round" and "metacoxae distant from each other". Therefore, this specimen is not a carabid beetle. Moreover, Tan et al. (2004) also pointed out that the original drawing of this species showed some clear characters of Polyphaga. Thus, the systematic position of this specimen remains unclear. *Obesofemoria* Hong, 1982 was described based on a poorly-preserved specimen in dorsal aspect. This specimen does not show any diagnostic characters of Adephaga; thus more clear evidence is needed to resolve its taxonomic issue. Three specimens from the Lower Cretaceous Lushangfen Formation of Lushangfen of Beijing were transferred to Protorabinae by Ponomarenko and Kirejtshuk (2011): *Penecupes rapax* Ren, 1995, *Aethocarabus levigata* Ren, 1995, and *Nebrorabus tumoculus* (Ren, 1995). As a result, only four species, including the species described herein, within Protorabinae have been reported from the Mesozoic strata of China (Table 1). The diversity of Chinese Protorabinae based on the present data probably has been underestimated. More investigations on this topic should be done to understand better the true diversity of Protorabinae.

Table 1. Fossil record of Protorabinae.

Taxon	Occurrence
Lithorabus incertus Ponomarenko, 1977	Lower Jurassic of Issyk-Kul, Kirghizia
Protorabus planus Ponomarenko, 1977	Upper Jurassic of Karatau, Kazakhstan
P. magnus Ponomarenko, 1977	Upper Jurassic of Karatau, Kazakhstan
P. nigrimonticola Ponomarenko, 1977	Upper Jurassic of Karatau, Kazakhstan
P. kobdoensis Ponomarenko, 1986	Lower Cretaceous of Myangad, Mongolia
P. crassus Ponomarenko, 1989	Lower Cretaceous of Shiviya, Transbaikalia
P. tsaganensis Ponomarenko, 1989	Lower Cretaceous of Bon-Tsagan, Mongolia
Ovrabites ovalis Ponomarenko, 1977	Upper Jurassic of Karatau, Kazakhstan
O. jurassicus Ponomarenko, 1977	Upper Jurassic of Karatau, Kazakhstan
O. incertus Ponomarenko, 1993	Lower Cretaceous of Khetana, Russian Far East
Cordorabus notatus Ponomarenko, 1977	Upper Jurassic of Karatau, Kazakhstan
C. antennatus Ponomarenko, 1977	Upper Jurassic of Karatau, Kazakhstan
C. minimus Ponomarenko, 1977	Upper Jurassic of Karatau, Kazakhstan
C. vittatus Ponomarenko, 1980	Lower Cretaceous of Manlay, Mongolia
C. striatus Ponomarenko, 1986	Lower Cretaceous of Gurban-Ereney, Mongolia
Cretorabus capitatus Ponomarenko, 1977	Lower Cretaceous of Baissa, Transbaikalia
C. latus Ponomarenko, 1977	Lower Cretaceous of Baissa, Transbaikalia
C. orientalis Ponomarenko, 1989	Lower Cretaceous of Khutel Khara, Mongolia
C. ovalis Ponomarenko, 1989	Lower Cretaceous of Bon-Tsagan, Mongolia
C. sulcatus Ponomarenko, Coram & Jarzembowski, 2005	Lower Cretaceous of Dorset, England
C. rasnitsyni sp. n.	Lower Cretaceous of Inner Mongolia, China
Nebrorabus baculum Ponomarenko, 1989	Lower Cretaceous of Chernyshevsk, Transbaikalia
N. capitatus Ponomarenko, 1989	Lower Cretaceous of Baley, Transbaikalia
N. nebrioides Ponomarenko, 1989	Lower Cretaceous of Bon-Tsagan, Mongolia
N. ?*elongatus* (Ponomarenko, 1986)	Lower Cretaceous of Myangad, Mongolia
N. tumoculus (Ren, 1995)	Lower Cretaceous of Lushangfen, China
Aethocarabus levigata Ren, 1995	Lower Cretaceous of Lushangfen, China
Penecupes rapax Ren, 1995	Lower Cretaceous of Lushangfen, China

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A long-living species of the hydrophiloid beetles: *Helophorus sibiricus* from the early Miocene deposits of Kartashevo (Siberia, Russia)

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Abstract

The recent hydrophiloid species *Helophorus* (*Gephelophorus*) *sibiricus* (Motschulsky, 1860) is recorded from the early Miocene deposits of Kartashevo assigned to the Ombinsk Formation. A detailed comparison with recent specimens allowed a confident identification of the fossil specimen, which is therefore the oldest record of a recent species for the Hydrophiloidea. The paleodistribution as well as recent distribution of the species is summarized, and the relevance of the fossil is discussed. In addition, the complex geological settings of the Kartashevo area are briefly summarized.

Keywords

Coleoptera, Hydrophiloidea, *Helophorus*, Miocene, Kartashevo, long-living species, environmental stability

Introduction

The understanding of the evolution of beetles in the late Cenozoic has changed drastically within recent decades. This concerns especially the Pleistocene beetles preserved as unmineralized subfossil specimens. Originally, the remains from the Pleistocene peatbog or asphalt deposits were assigned to extinct species by historical authors

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(e.g. Łomnicki 1894, Grinell 1908, Orchymont 1927, Pierce 1946, 1948, 1949, 1964, Scudder 1900), supporting the idea of a high evolutionary rate induced by the climate changes during the Pleistocene. Later, more detailed studies of subfossil specimens sometimes based even on the study of their well-preserved genitalia revealed that the majority of Pleistocene subfossil beetles belong to recent species (Elias 2010; for examples of taxonomic revisions see e.g., Darlington 1938, Angus 1973, 1997a, Miller and Peck 1979, Doyen and Miller 1980, Miller et al. 1981) and resulted in the Pleistocene evolutionary stasis paradigm (Coope 1970, 2004). Recent studies of many beetle groups based on molecular data contradict the results based on the fossil record for many beetle groups and indicate a high evolutionary rate during the Pleistocene (e.g., Ribera and Vogler 2004, Cardoso and Vogler 2005, Goméz-Zurita et al. 2007, Borer et al. 2010, Ribera and Faille 2010). This disagreement of molecular and fossil results is interpreted as resulting from fossil data being only available for high latitude areas (Ribera and Vogler 2004, Abellán et al. 2011).

The presence of recent species in Pleistocene deposits invites the question as to whether the same might not be the case even in older, Pliocene or Miocene deposits. Pre-Pleistocene beetle fossils were mostly assigned to extinct species of recent genera (Scudder 1891, 1900, Handlirsch 1908). However, this traditional view has been contradicted recently by many molecular studies showing the pre-Pleistocene origin of various beetle species (e.g., Gómez-Zurita et al 2007, Sota et al. 2008, Papadopoulou et al. 2009, Ribera et al. 2010a,b, Stüben and Astrin 2010). The fossil record reliably supporting the hypothesis of long-living species is, however, rather scarce so far (Matthews 1977, Grebennikov 2010, Hörnschemeyer et al. 2010) as most published data are based on approximate identification of fragmentary remains only (e.g., Matthews 1977, Bennike and Böcher 1990, Matthews et al. 2003).

Representatives of the hydrophiloid genus *Helophorus* Fabricius, 1775 are frequently used in the studies of Quaternary beetle communities. The taxonomy as well as recent distribution of most species is well known due to the studies by the third author (largely summarized by Angus (1997b)) and Smetana (1985), and reliable species identification is often possible even without the examination of male genitalia, using the external characters as e.g. sculpture and shape of the pronotum, width of pronotal flanks and morphology of the elytron. These characters often allow recognition of very similar sibling species which makes *Helophorus* one of the best model beetle taxa for evaluating the changes of beetle faunas during the Pleistocene (e.g. Angus 1973, 1997a, Morgan 1989, Elias 2010). Ca. 45 species of *Helophorus* were recorded from the latest Pliocene, Pleistocene and Holocene subfossil deposits so far (Scudder 1890, Morgan and Morgan 1980, Buckland and Buckland 2006), all of them belonging to recent species (the only exception is *H. rigescens* Scudder, 1890 whose revision is impossible as its type specimen is lost; Fikáček, unpubl. data). Four extinct species were described from the late Miocene deposits in Alaska (2 spp.) and southern Germany (2 spp.) by Matthews (1976) and Heer (1862). No other fossils of the genus are known from older Tertiary deposits.

Detailed examination of a well-preserved Miocene *Helophorus* fossil from the collection of the Paleontological Institute in Moscow revealed that it may be reliably

assigned to the living species *H. sibiricus* and represents therefore the oldest record of recent species for hydrophiloid beetles. The results of the studies of this fossil are summarized within this paper and the relevance of the record is discussed.

We would like to dedicate this contribution to Alexandr P. Rasnitzyn on the occasion of his 75th birthday as our thanks for his outstanding contribution to the paleontology and entomology and his massive support of younger generations of entomologists and paleontologists all over the world. We wish him many more scientifically productive years full of good health and cheerfulness!

Geological setting

The geology of the area around Kartashevo village on the right bank of the Irtysh river (56° 06'54" N 74° 41'27" E) is rather complex especially in the eroded parts where two formations of different age are in contact: the older Abrosimovka Formation and the overlying Beshcheul Formation.

The Abrosimovka Formation was dated recently by the comparison of its palynological spectra with the Upper Baygubek Subhorizon of Aral and the North Ustyurt by Zykin (2009), and its age was considered as upper Oligocene. This was in agreement with the opinion of Dorofeev (1963) who dated the fossil flora of the Abrosimovka Formation to the upper Oligocene as it retains the basic structure of the Lagernosad-Rezhenka floras with many archaic elements. Alternative dating was proposed by Volkova et al. (2001) who dated the Abrosimovka Horizon to the lower Miocene (Aquitanian–Burdigalian).

The overlying Beshcheul Formation was dated as middle Miocene by Dorofeev (1963) due to the similarities of its fossil flora with the Sarmatian floras of the Russian plain. Middle Miocene was adopted as the age of the formation even in more recent publications (e.g., Volkova 1982, LePage 2007, Durnikin 2010).

When describing the fossil flora of the Kartashevo region, Dorofeev (1963) recognized five layers in the coastal section of the Irtysh river (listed from deeper parts towards the current surface): (1) the outputs of lignite, (2) the horizon of the blue-gray, very dense clay with layers of plant detritus 0–5 m from the water edge (the Kartashevo clay stratum), (3) the characteristically stratified suglino-loam of the Beshcheul Formation with layers of plant detritus ca, between 14–16 m from the water edge, (4) sand without plant residues, possibly related to the Ishim Formation, and (5) soil and a thick layer of compost. The fossil specimen refered in this paper was collected from the exposed Kartashevo clay stratum (i.e., layer 2 sensu Dorofeev (1963)) on the right bank of the Irtysh River under and just above the water edge (E. K. Sychevskaya, pers. comm.). The clay stratum was originally assigned to the Abrosimovka Formation and therefore refered as upper Oligocene in age e.g. by Sukacheva (1982). Recently, it was found to represent a separate Ombinsk Formation overlying the Abrosimovka Formation and underlying the Beshcheul Formation in the Kartashevo area. The Ombinsk Formation is currently dated to the lower Miocene (V.S. Zykin, pers. comm.). The

samples of spores, pollen and dinocysts from the stratum were analyzed by M. A. Akhmet'ev and N. I. Zaporozhets and confirmed the lower Miocene origin of the stratum (E. K. Sychevskaya, pers. comm.). The Oligocene-Miocene boundary is currently placed between the Abrosimovka and Ombinsk Formations in western Siberia (Zykin 2009), which also corresponds well with the lower Miocene age of the Kartashevo clay stratum. Hence, the fossil presented in this paper may be realiably assigned to the Burdigalian or Aquitalian stages, and approximately dated as 16–23 million years old. Zykin (2009) mentioned that the climate was relatively stable, moderately warm and rather humid in the area on the Oligocene-Miocene boundary.

Only one insect species was previously known from the Kartashevo clay stratum – the caddisfly case described as *Terrindusia* (s.str.) *eugeniae* Sukatcheva, 1982 (originally assigned to the Abrosimovka Formation by Sukatcheva (1982) as the Ombinsk Formation was not recognized at that time). Besides the *Helophorus* fossil described in detail within this paper, there is also another fragmentary fossil from this stratum (PIN 3285/6) which may belong to the hydrophilid genera *Hydrochara* Berthold, 1827, *Hydrobiomorpha* Blackburn, 1888 or *Brownephilus* Mouchamps, 1959 based on preserved morphological characters. More detailed identification is not possible and the fossil is therefore not treated further in this paper.

Material and methods

The fossil specimen presented in this paper was examined in dry condition. Habitus photographs of both fossil and recent specimens were taken using the Canon D-550 digital camera with attached Canon MP-E65mm f/2.8 1–5X macrolens, drawings were traced from the photographs along with a simultaneous check of the fossil specimen. Scaning electron micrographs of fossil as well as recent specimens were prepared using the Hitachi S-3700N environmental electron microscope in the Department of Entomology, National Museum in Prague. Data on the morphology of recent *Helophorus sibiricus* are based on the specimens deposited at the Department of Entomology, National Museum in Prague, and the Natural History Museum in London.

The Pleistocene records of *Helophorus sibiricus* from Europe were taken from the BugsCEP database available on-line (Buckland and Buckland 2006; data file updated on 18th January 2011), data on records in Siberia and North America were taken from the published papers (Morgan and Morgan 1980, Garry et al. 1990, Andreev et al. 2004, Sher et al. 2005, Elias et al. 2006). Published Holocene subfossil records are not considered in this paper and are also omitted in Fig. 10 as they are too recent and therefore not relevant to the topic of this paper; moreover, they mostly fall into the recent distribution range of the species. Data on the recent distribution were adopted from the papers by Angus (1973, 1992), Smetana (1985) and Hansen (2004) and the species range was slightly adapted according to the unpublished faunistic data known to the authors.

Results

Superfamily Hydrophiloidea
Family Helophoridae

***Helophorus* (*Gephelophorus*) *sibiricus* (Motschulsky, 1860)**
http://species-id.net/wiki/Helophorus_(Gephelophorus)_sibiricus

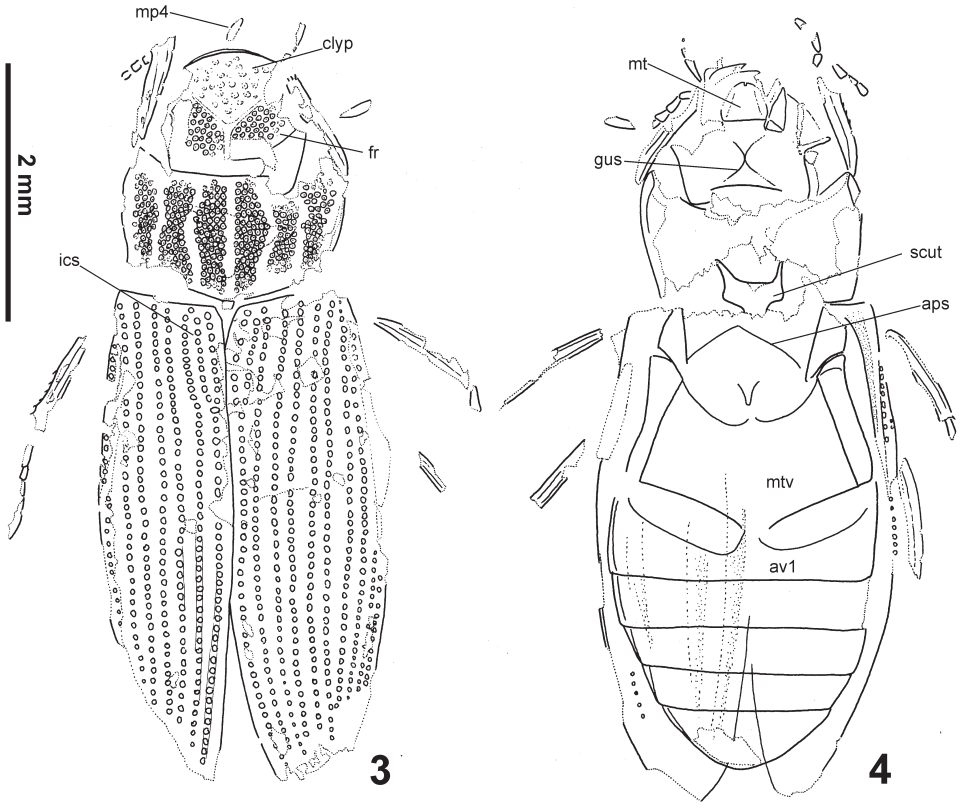
Empleurus sibiricus Motschulsky, 1860: 104 – Type locality: recent: Russia, East Siberia, "Tourkinsk" [=Turka] at Lake Baikal.
Helophorus sibiricus (Motschulsky): transferred to *Helophorus* by Gemminger & Harold (1868).
For complete synonymy see Hansen (1999).

Material examined. PIN 3285/5 (piece and counterpiece): Russia, Omsk region, Western Siberia, right bank of Irtysh river at Kartashevo village [56°6'54.11"N 74°41'27.20"E], leg. E. K. Sychevskaya 1966. Ombinsk Formation, early Miocene, ca. 23–16 million years ago. Deposited in the collection of the A.A. Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Description of the fossil (Figs 1–4, 6, 9)**.** Body length 5.76 mm. Head black, with a deeply impressed Y-shaped frontoclypeal suture, basal portion of the groove wide, slightly widened anteriorly. Clypeus with weak remnants of granules only, frons bearing very distinct large setiferous granules isolated by ca. a half of their diameters. Gula strongly constricted behing tentorial pits, gular sutures meeting at one point. Mentum 1.3× wider than long, bearing a deep median emargination on anterior margin (Fig. 6, see the arrow). Apical segment of maxillary palpi asymmetrical. Pronotum 1.85× as wide as long, widest at anterior third bearing five wide longitudinal furrows. Bottom of the grooves without granulation. All intervals bearing a uniform, rather dense granulation, granules rather weakly delimited, nearly contacting each other; granulation becoming sparser sublaterally, consisting of several isolated granules along pronotal margins (Fig. 9). Lateral margin regularly convex, not excised subbasally, lacking any apparent tooth-like projections. Pronotal flanks moderately wide anteriorly, slightly narrowing posteriad. Elytra with 8 preserved series of large rounded to subquadratic punctures (lateral series not preserved due to deformation of elytra during fossilization). Intervals bearing fine and small irregular series of punctures. Scutellar stria present, very long, consisting of 9 punctures on both elytra. Alternate elytral intervals elevate into low ridges (preserved as elongate ridges and furrows on the ventral imprint of the counter-piece). Epipleuron with rather narrow inner pubescent portion, ca. as wide or slightly narrower than elytral flanks. Mesoventrite subtriangular, anapleural sutures nearly straight. Metaventrite wider than long, metanepisternum ca. 5.2× as long as wide, with a transverse ridge anteriorly. Abdomen with five ventrites, ventrite 5 without median emargination, finelly denticulate on whole posterior margin. Legs rather long and slender, protarsi with five tarsomeres.

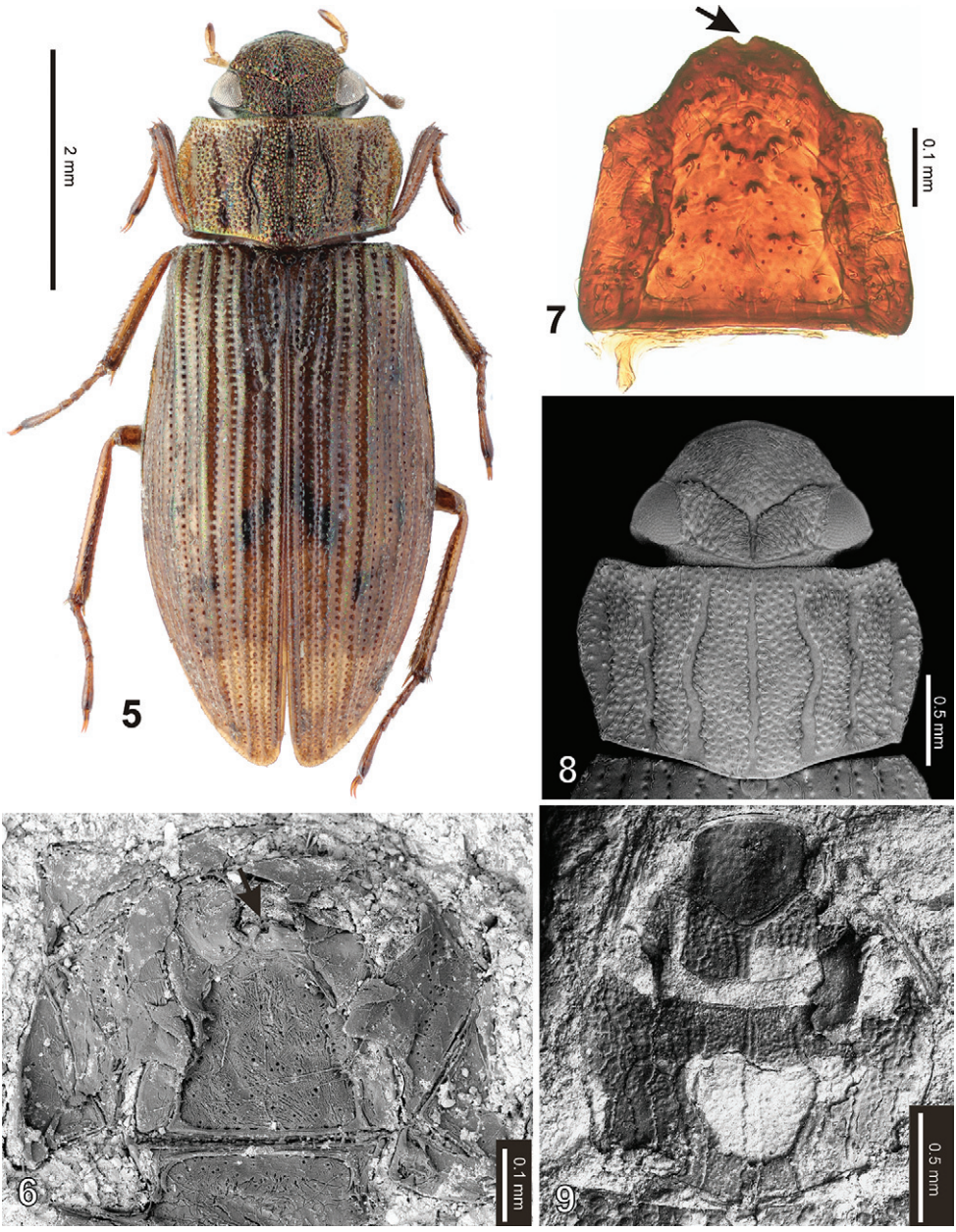
Figures 1–2. *Helophorus sibiricus* (Motschulsky, 1860), photo of the early Miocene fossil No. PIN 3285/5 from Kartashevo **1** piece **2** counterpiece.

Species attribution. The subgenus *Gephelophorus* Sharp, 1915 to which we assign the fossil is easily recognizable from other *Helophorus* subgenera by the combination of large body size (4.6–7.0 mm), asymmetrical apical segment of maxillary palpi, elevated alternate elytral intervals, pronotal flanks moderately wide anteriorly and narrowing posteriorly, elytral flanks slightly wider than epipleura. *Helophorus sibiricus* to which we assign the fossil may be recognized from the only other species of *Gephelophorus*, *H.* (*G.*) *auriculatus* Sharp, 1884, by the continuously curved sides of pronotum not excised behind the anterolateral corners (deeply excised anteriorly and projecting into lateral lobes in *H. auriculatus*), alternate elytral intervals evenly elevated throughout (bearing only isolated elevate tubercles in *H. auriculatus*), and completely and densely granulate pronotal intervals (internal and median interval nearly lacking granules in *H. auriculatus*). Besides, the fossil corresponds with the recent *H. sibiricus* also in other preserved characters: (1) scutellar stria present and very long [absent in several subgenera, extremelly long especially in *H. sibiricus*]; (2) mentum 1.3× wider than long [more than 1.5× as wide as long in *Rhopalohelophorus* Kuwert, 1886, *Helophorus* s.str., and *Lihelophorus* Zaitzev, 1908]. The shape of gular sutures is sexually dimorphic in *H. sibiricus*: the gular sutures are separated throughout in males but meeting in one point in females. Based on this character, we can conclude that the fossil specimen is a female.



Figures 3–4. *Helophorus sibiricus* (Motschulsky, 1860), drawings of the early Miocene fossil No. PIN 3285/5 from Kartashevo **3** piece **4** counterpiece. Abbreviations: **mp4** maxillary palpomere 4, **clyp** clypeus, **fr** frons, **ics** intercalary stria, **mt** mentum, **scut** mesoscutellum, **aps** anapleural sutures of mesothorax, **mtv** metaventrite, **av1** abdominal ventrite 1.

Recent and fossil distribution (Fig. 10). *Helophorus sibiricus* is at present widely distributed throughout the Holarctic region, from the northern parts of Scandinavia and European Russia through the whole of Siberia and the Russian Far East to Alaska (Angus 1973, 1992, Hansen 2004, Smetana 1985). Its distribution generally corresponds with the range of taiga biome in Eurasia, but slightly exceeds to the temperate and montane forests and grasslands in northern China, Mongolia and Honshu Island, and to the tundra on the north. The species is also reported from Chinese province of Yunnan on the basis of a single historical specimen without precise locality (Angus 1995) – this record may represent a relict mountain population or could be based on mislabeled specimen, and needs to be confirmed by additional material. The northern limit of the distribution of *H. sibiricus* on the Taymyr peninsula is unknown, the northernmost record known to us comes from the environs of Norilsk (S. K. Ryndevich, pers. comm. 2011). In North America, *H. sibiricus* only occurs west of the delta of Mackenzie river and does not reach further east even though both taiga and tundra biomes



Figures 5–9. *Helophorus sibiricus* (Motschulsky, 1860) **5** habitus of a recent specimen (Mongolia, Baga-Tenger, coll. National Museum, Prague) **6–7** detail of mentum, the arrow indicates a characteristic emargination on the anterior margin of mentum (**6** fossil specimen, SEM micrograph **7** recent specimen, view from inside) **8–9** detail granulation of head and pronotum, SEM micrographs (**8** recent specimen **9** fossil specimen).

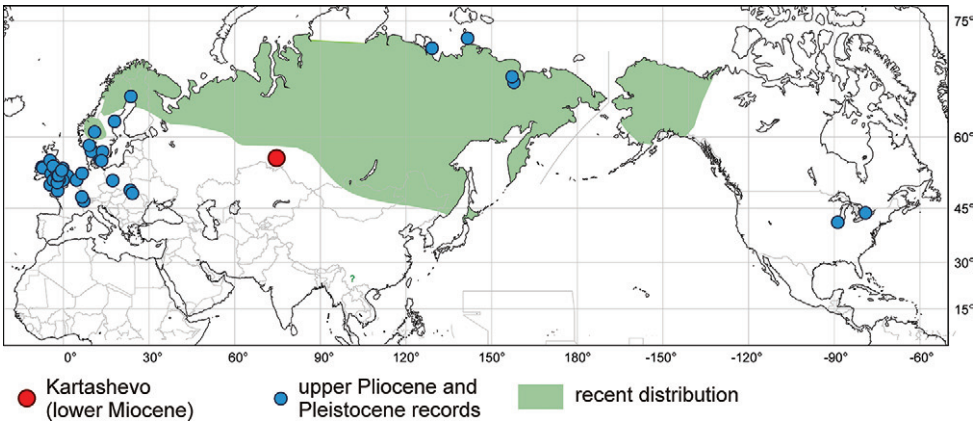


Figure 10. Fossil and recent distribution of *Helophorus sibiricus* (Motschulsky, 1860). Subfossil Holocene records omitted.

are present throughout the higher latitudes in Canada. In fossil record, *H. sibiricus* is frequently found in the glacial deposits dated back to late (Devensian/Weichselian) or middle Pleistocene (Saalian) in northern and central Europe (Buckland and Buckland 2006). In North America two known fossil records comes from the late Pleistocene glacial (Wisconsinian) deposits in the Great Lakes area (Morgan and Morgan 1980: Canada, Scarborough; Garry et al. 1990: USA, Illinois). Four records are known from northern Siberian deposits dated back to last glacial (Weichselian; Mamntovy Khayata, Sher et al. 2005), Eemian interglacial (an island in Laptev Sea, Andreev et al. 2004) and late Pliocene to early Pleistocene (Olyorian suite of Krestovka and Chukochya river, Elias et al. 2006). The lower two findings were the oldest records of *H. sibiricus* known so far. The lower Miocene record presented in this paper is situated slightly south of the recent limit of the range of *H. sibiricus*.

Biology. Aquatic species; it is recorded from various kinds of water bodies predominantly with sandy bottom in southern Yamal Penninsula (northeastern Siberia) (Prokin et al., 2008); Angus (1973) considers it as characteristic for river edges in Scandinavia and mentions that it is frequently found in grassy temporary pools particularly those resulting from melting snow in Siberia. Adults of all *Helophorus* species are detritivorous. Larvae of *H. sibiricus* are unknown but they may be expected to be terrestrial and predaceous as in most other species of the genus *Helophorus* (Angus 1997).

Discussion

The genus *Helophorus* is currently divided into 11 subgenera whose monophyly and phylogenetic relationships have not been tested so far. Regardless, its subgroups differ sharply by their morphological and taxonomic diversity. Most *Helophorus* subgenera consist of few species only, each rather distinct morphologically from the others, and are traditionally considered as the remnants of ancient divergences (Fikáček and

Angus 2006). On the other hand, a few subgroups (especially the subgenus *Rhopalohelophorus* and parts of the subgenera *Helophorus* s.str. and *Empleurus* Hope, 1838) contain numerous morphologically very uniform species which are sometimes reliably recognizable by few details of morphology and/or karyotypes only (e.g., Angus 1982, 1984, Angus and Aouad 2009, Angus and Toledo 2010). These groups are intuitively considered as results of rather recent diversifications (Fikáček and Angus 2006). *Helophorus sibiricus* represents the first type, as the subgenus *Gephelophorus* only contains two easily distinguishable species at present.

The presented early Miocene fossil of *Helophorus sibiricus* is still too young to be taken as a proof of the relic character expected for *Gephelophorus* due to its high morphological difference but low species diversity. In spite of that, it is the first fossil definitely indicating that at least some small subgenera of *Helophorus* contain species of rather ancient origin rather than recently diverged ones. This seems to contradict the evolutionary scenario proposed for another small and morphologically distinct subgroup within *Helophorus*, subgenus *Kyphohelophorus* Kuwert, 1886, by Matthews (1976). He studied two extinct species of the subgenus (*H. coopei* Matthews, 1976 from late Miocene Lava Camp, and *H. meighenensis* Matthews, 1976 from Meighen Island, both in Alaska) and considered them to be ancestors of the only recent species of the subgenus, *H. tuberculatus* Gyllenhal, 1808. This would indicate either a quick anagenetic change or high divergence and extinction rates of the subgenus during the late Miocene. Recently, Kiselev and Nazarov (2009) recorded *H. tuberculatus* from the late Miocene deposits of Ary-Mas (Taymyr Peninsula, western Siberia) and Letyatkin Cape (north-eastern Siberia). If the identification of these fossils is correct, they would show that all three *Kyphohelophorus* species lived at the same time, proposing a scenario different from Matthews' (1976) one: all three *Kyphohelophorus* species may originate during the Miocene (or earlier) but only *H. tuberculatus* survived until present. *Helophorus sibiricus* might fit a similar scenario based on the fossil presented within this paper.

The Miocene record of *Helophorus sibiricus* presented in this paper is not the only pre-Pleistocene record of recent hydrophiloid beetles. Hayashi (2001) and Hayashi et al. (2003) recorded modern Japanese species *Coelostoma stultum* Walker, 1858, *C. orbiculare* (Fabricius, 1775), *Hydrochara libera* (Sharp, 1884), *Sternolophus rufipes* (Fabricius, 1792) and *Regimbartia attenuata* (Fabricius, 1801) from the Japanese early Pliocene (Tsubusagawa Formation) and late Pliocene deposits (Uonuma, Ookui and Oizumi Formations). Unfortunately, all these taxa were only found as isolated elytra and pronota lacking any species-specific diagnostic characters, and it is therefore impossible to imply if the fossils really represent recent taxa. Similar uncertainty concerns the late Miocene records listed by Kiselev and Nazarov (2009), identified as *Helophorus tuberculatus* (mentioned above) and *Coelostoma orbiculare*, as no details on the morphology of the fossils are provided. On the other hand, the morphology of the early Miocene fossil of *Hydrophilus* cf. *pistaceus* Castelnau, 1840 was studied in detail by Fikáček et al. (2008), but the preserved morphological characters only allowed for its approximate identification. Although all these records indicate that the Miocene age may not be

exceptional for a hydrophiloid species, the early Miocene fossil of *Helophorus sibiricus* presented here represent the first hydrophiloid fossil of this age in which the preserved characters allow a reliable identification. Early Miocene (i.e., ca. 16–23 mya) may be thus considered as the maximum age of a recent hydrophiloid species known at present. In contrast, all well-preserved late Oligocene and older fossils studied by us so far were found to belong to extinct species (Wedmann 2000, Fikáček et al. 2010a,b,c).

The habitat as well as climatic requirements of the beetle species are usually considered stable over the time (Coope 2004, Elias 2007, Hörnschemeyer et al. 2010), which provides three possible ways to explain the survival of these species since the Tertiary: (1) life-style of the species is associated with a habitat which is stable over the time, (2) the species was able to track suitable environmental conditions though the climate changed over the time; (3) the species is surviving in a single area with stable environmental conditions over several millions of years. Although the generalized aquatic life-style makes the habitat-based explanation seemingly improbable for *Helophorus sibiricus*, the occurrence of the notostracan "living fossils" in temporary pools (Mantovani et al. 2004) indicates that this kind of waters may provide stable conditions over a geological time for taxa adapted for their seasonality. *Helophorus sibiricus* is also able to track suitable environmental conditions when climate is changing: its distribution was largely affected by the Pleistocene climate changes even though it presently inhabits an area with wide range of climatic conditions (mean January temperature below –2°C, mean July temperature varying between 3–14°C; S. Elias, pers. comm.). The survival of *H. sibiricus* in the long-lasting stable environment in south-western Siberia cannot be excluded either as the environment in many parts of Central Asia was shown to remain extremely stable at least since the Pleistocene (e.g., Chytrý et al. 2010). The early Miocene is characterized by the formation of the first stable grasslands alternating with coniferous-small leaved forests in south-western Siberia (Velichko and Spasskaya 2002), which may correspond with the recent environment inhabited by *H. sibiricus* in the southern part of its range. Hence, we cannot exclude that some locally limited ecosystems of south-western Siberia might have been stable enough since the late Tertiary, allowing the survival of *H. sibiricus* and other Tertiary species.

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Third contribution on Rovno amber silken fungus beetles: a new Eocene Species of *Cryptophagus* (Coleoptera, Clavicornia, Cryptophagidae)

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Abstract

Cryptophagus alexagrestis Lyubarsky & Perkovsky **sp. n.** is described based on a fossil inclusion in Late Eocene Rovno amber (Ukraine). The new species is similar to the extant *Cryptophagus skalitzkyi* Reitter and *C. dilutus* Reitter, differing from the latter by having a very transverse, short and dilated 10th antennal segment, and from the former by the very elongate segments of the flagellum.

Keywords

Cryptophagidae, *Cryptophagus,* Late Eocene, Rovno amber, Ukraine

Introduction

The family Cryptophagidae is a group of small beetles with about 800 described species placed in approximately 50 genera and represented in all biogeographic realms. Most members of the family are free-living and mycophagous.

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Silken fungus beetles are very common in the litter of forests in temperate climatic regions, where only Staphylinidae, Curculionidae and Carabidae are more abundant (Hyvärinen et al. 2006, Foottit and Adler 2009, Nitu et al. 2009, Šustek and Kristofik 2009). Most cryptophagids are nidicolous beetles; they are one of the most abundant beetles in the nests and burrows of rodents, birds and social insects (Lyubarsky 1996). On the other hand, in tropical Africa silken fungus beetles are rarely collected in litter (Kouadio et al. 2009). Cryptophagidae (together with Latridiidae) are fire-favoured insects (Muona and Rutanen 1994, Wikars and Schimmel 2001). Both adults and larvae of silken fungus beetles are commonly found on mold, fungi, under bark, as well as in decaying vegetation. Some genera are characterized by inquilinism with termites and social hymenopterans (Apidae, Vespidae and Formicidae) (Leschen 1999). Unlike many other groups of beetle symbionts, cryptophagid inquiline lineages do not have marked increases in speciation rates, despite the fact that the first records of some inquiline genera are from Late Eocene Baltic amber (Leschen 1999).

Discoveries of cryptophagids in fossil resins (see Lyubarsky and Perkovsky 2010) are of particular interest; over time, the generalization of such data can help to understand paleoclimates. Late Eocene Rovno amber represents a southern coeval analogue of the famous Baltic amber (Perkovsky et al. 2007, Perkovsky et al. 2010), collected in the northwest of Ukraine. The amber collection of the Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, Kiev (SIZK) contains more than 950 inclusions of beetles from unselected Rovno amber (Perkovsky et al. 2010; Kazantsev 2010), among them only three specimens are of silken fungus beetles (Lyubarsky and Perkovsky 2010; Lyubarsky and Perkovsky in press, this paper): one specimen of *Micrambe* Thomson, 1863 and two specimens of *Cryptophagus* Herbst, 1863. The amber piece containing the holotype of the new species described herein was mined in Pugach quarry (Klesov, north of Rovno region). Besides findings from fossil resins, Paleogene representatives of *Cryptophagus* are known as compression fossils from Argentina (*Cryptophagus suncholensis* Cockerell) and United States (*Cryptophagus bassleri* Wickham, *C. petricola* Wickham) (Ponomarenko and Kirejtshuk 2011).

The tarsal formula 5–5–5, 3-segmented antennal club, and closed procoxal cavities of the new species are quite characteristic of the family Cryptophagidae. The new species has antennal insertions exposed in dorsal view; pronotum with a well-developed marginal callosity; mesocoxal cavity closed laterally by the sternum; ventrite 1 longer than the remaining ventrites; and confused elytral punctation. These characters are indicative of the genus *Cryptophagus* (Cryptophaginae). Representatives of *Cryptophagus* are found in all biogeographic realms; the genus includes 137 species from the Palaearctic Region (Johnson et al. 2007).

Photographs were taken at the Paleontological Institute, Russian Academy of Sciences (Moscow) by V.A. Kolyada and the second author using a Leica M 165 microscope. To create diffused illumination, a cup of white styrofoam was placed between an object and a light source. The captured images were assembled with Helicon Focus 5.01 software.

Taxonomy

Family Cryptophagidae Kirby, 1837
Subfamily Cryptophaginae Kirby, 1837
***Cryptophagus* Herbst, 1863**

***Cryptophagus alexagrestis* Lyubarsky & Perkovsky, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Cryptophagus_alexagrestis
Figs 1–2

Material. Holotype, SIZK K-24572, Klesov, Rovno amber, Late Eocene. Syninclusion: Chironomidae. Sex of the holotype unknown.

Etymology. From Alex, in honour of Prof. Alexandr Rasnitsyn, and "agrestis" from Latin *ager* for field, farm.

Description. Body broadly elongate, slightly convex; head, pronotum, and elytra brown. Elytra slightly convex, covered with elevated pubescence.

Head transverse, of normal size, with hemispherical, somewhat coarsely facetted eyes, strongly and sparsely punctured. Antennae long, slender, with club reaching beyond base of pronotum, joints of flagellum elongate, 4th, 6th segment more than 1.5 times as long as broad, 5th 2 times as long as broad, 9th and 10th transverse, 11th obliquely oval, joints 9–11 equal in width.

Pronotum flat, not very strongly narrowed basally, distinctly transverse, barely 1.6 times broader than long, moderately not strongly and sparsely punctured (distance between punctures more than their diameter), an individual puncture less than the diameter of a facet. Pronotum without sublateral line, somewhat convex, sides narrowed basally and apically, with a single lateral tooth. Sides finely margined, anterior edge weakly sinuate. Callosity occupies at most one-seventh of side margin, with a small, elongate-oval patch of bare surface invisible from above; caudolateral corner obtuse angular, callosity without point. Lateral tooth far before middle of lateral margin. Posterior corners obtuse, base round, slightly sinuate, basal groove narrow.

Scutellum small, transverse. Elytra oval, humeral corners rounded, shoulders a little broader than maximum breadth of pronotum, 1.7 times as long as wide and 3.0 times as long as thorax, moderately convex, slightly flattened behind scutellum, with slightly rounded sides and a narrowly rounded apex, punctuation less strong and more sparse than that on pronotum.

Length of body 1.8 mm.

Remarks. *Cryptophagus alexagrestis* sp. n. is most similar to the modern *C. laterangulus* Reitter (Caucasus, Iraq, Iran, Turkmenistan, Kazakhstan), *C. pseudoschmidti* Woodroffe (Eastern Europe, Siberia, Mongolia), *C. dilutus* Reitter (Holarctic: North Africa, Europe, Caucasus, Middle Asia, Iran, Iraq, India, China, Siberia, North America), *C. skalitzkyi* Reitter (Europe, Caucasus, Turkey, Iran, Turkmenistan, Uzbekistan,

Figure 1. *Cryptophagus alexagrestis* sp. n., holotype (SIZK K-24572, Schmalhausen Institute of Zoology, Kiev) **a** body, dorsal **b** body, lateral **c** front part, dorsal.

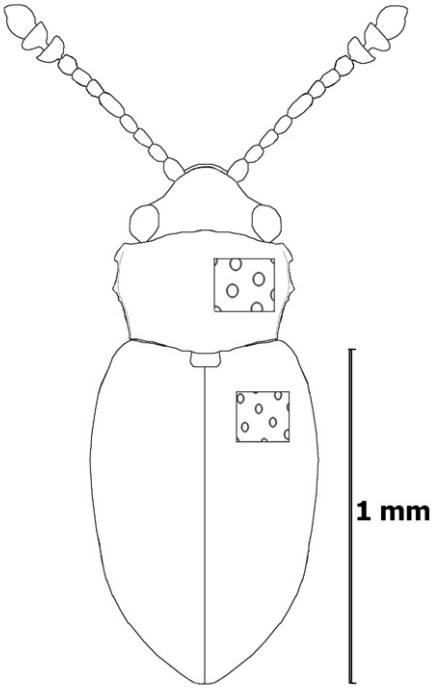

Figure 2. Dorsal view, *Cryptophagus alexagrestis* sp. n.

Tajikistan, Afghanistan, Pakistan, India, Kyrgyzstan, Kazakhstan, Eastern Siberia) with elevated elytral pubescence, bare surface of callosity not visible from above, 4th segment of antenna elongate, nearly 1.5 times as long as broad, lateral tooth far before middle of pronotum, small length of callosity (see Lyubarsky 2002). All mentioned modern species are widely distributed in steppe and desert zones, less common in the forest zone. *Cryptophagus dilutus* is common in the steppe and desert zones of Eurasia – in materials from Iraq, Iran, China, and Central Asia it is quite common. All mentioned species can be included in the key for identification of *Cryptophagus* (see Lyubarsky 2002, pp. 324–325, synthesis 17 and the following) with some changes, as shown below:

1 Punctation of prothorax distinctly dense. Eyes often strongly prominent, hemispherical, with large facets. Lateral tooth extremely strongly prominent, but very small. Length 2.3–2.5 mm ..... ***C. laterangulus***

– Punctation of prothorax sparse. Lateral tooth not extremely prominent **2**

2 Eyes large, length greater than half the length of the head, asymmetrical conical, prominent, with large facets, diameter of facet more than 11 μm. 5th segment of antenna weakly elongated, 1.5 times as long as broad. Callosity occupies from 1/5 to 1/4 of length of lateral margin. Lateral tooth of prothorax normal or small, nearly reduced. Length 2.6–3.4 mm ..... ***C. pseudoschmidti***

– Eyes normal in size, length less than half the length of the head, slightly prominent, with small facets, diameter of facet less than 11 μm. Lateral tooth of prothorax normal. Callosity occupies from 1/8 to 1/5 of length of lateral margin **3**

3 10th segment of antenna rounded, about 1.5 times as broad as long. Callosity with point. Callosity occupies 1/6–1/5 length of lateral margin of pronotum. Length 2.1–2.7 mm ..... ***C. dilutus***

– 10th segment of antenna short and dilated, very transverse, as least twice as broad as long. Callosity short, its length occupying 1/8–1/6 length of lateral margin of pronotum **4**

4 Facets of eyes small, diameter of facet less than 8 μm. Segments of flagellum weakly elongate, 4th, 5th, 6th segment 1.5 times as long as broad. Prothorax convex, very strongly narrowed basally. Punctuation of prothorax moderately dense, distance between neighbouring punctures equal to diameter of puncture or slightly less. Length 1.9–2.3 mm ..... ***C. skalitzkyi***

– Facets of eyes large, diameter of facet more than 11 μm. Segments of flagellum strongly elongate, 4th, 6th segment more than 1.5 times as long as broad, 5th 2 times as long as broad. Prothorax flat, not very strongly narrowed basally. Length 1.8 mm ..... ***C. alexagrestis* sp. n.**

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The earliest Mesopsychidae and revision of the family Mesopanorpodidae (Mecoptera)

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Abstract

The family Mesopanorpodidae is revised. Most taxa referred to this family are not related to the type genus *Mesopanorpodes* Tillyard, 1918. The type species of the latter, *Mesopanorpodes wianamattensis*, is closely related to *Mesopsyche* Tillyard, 1917. Therefore *Mesopanorpodes* is transferred to Mesopsychidae Tillyard, 1917 (= Mesopanorpodidae Tillyard, 1918, **syn. n.**). The earliest Mesopsychidae are described from the Upper Permian of European Russia (Severodvinian; Isady locality, Vologda Province): *Permopsyche issadensis* **gen. et sp. n.** (type species) and *P. rasnitsyni* **sp. n.** Two species described under *Mesopanorpodes* from the Upper Permian of Australia are also included into *Permopsyche*: *P. belmontensis* (Riek, 1953) **comb. n.**, *P. robustus* (Riek, 1953) **comb. n.** The first pre-Triassic *Mesopsyche*, *M. incompleta* **sp. n.** is described from the uppermost Permian (the town of Vyazniki, Vladimir Province). *Bittacopanorpa javorskii* Zalessky, 1935 from the uppermost Permian or basal Triassic of Kuznetsk Basin is identified as a hindwing of *Mesopsyche*: *M. javorskii* (Zalessky, 1935) **comb. n.** The origin, evolutionary history, and stratigraphic occurrence of Mesopsychidae are discussed.

Keywords

Mesopsychidae, Mesopanorpodes, *Mesopsyche*, *Permopsyche*, *Bittacopanorpa*, Permian, Triassic, new taxa, revision

Introduction

Tillyard (1917b) described *Mesopanorpa wianamattensis* from the Middle Triassic Ashfield Formation of the Wianamatta Group in New South Wales as an aberrant Mecop-

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tera and erected the family Mesopanorpidae. Later (Tillyard 1918) he changed the genus name to *Mesopanorpodes* to avoid homonymy with *Mesopanorpa* Handlirsch, 1906. Subsequently (Tillyard 1919b: 611–612) he decided that *Mesopanorpodes* was closely related to *Mesopsyche* and the allied genera *Aristopsyche*, *Triassopsyche,* and *Neuropsyche* (the three latter have eventually been synonymized under *Mesopsyche* by Riek 1956), all described from the Upper Triassic Blackstone Formation, Queensland (Tillyard 1917a; Fig. 1E), and transferred *Mesopanorpodes* into the order Paratrichoptera.

Confusingly, this remark passed completely unnoticed by all the subsequent authors who discussed the composition and taxonomy of the Mesopanorpodidae. Riek (1953) placed into Mesopanorpodidae two new species of *Mesopanorpodes*, *M. belmontensis* and *M. robustus* (Fig. 1C–D), and the genus *Prochoristella* Riek, 1953 with six species from the Upper Permian of New South Wales (Belmont fossil beds). Since then, *Mesopanorpodes* and *Prochoristella* have been considered together either as forming a separate family Mesopanorpodidae (Riek 1955, 1974, Jell and Duncan 1986, Willmann 1978, 1989, Carpenter 1992, Van Dijk and Geertsema 1999, Hong et al. 2002, Hong and Guo 2003, Hong 2007, Sun et al. 2007a, b), or as two closely related genera within Permochoristidae (Martynova 1962, Novokshonov 1997b, Novokshonov et al. 2004).

In fact, species of *Prochoristella* (with the possible exception of *P. belli* Riek, 1953, known only from a hindwing) display characters typical of Permochoristidae, that is, first of all, a deep fork on MA vein and an oblique base of CuA, either fused with MP for a distance, or forming cubito-median Y-vein. *Prochoristella* and *Mesopanorpodes* are similar only in the number of RS+MA and MP endings being reduced to four. However, this is characteristic of many independent lineages, e.g. Permotanyderidae + Liassophilidae, Nannochoristidae, or Bittacidae, and cannot be accepted as a reliable apomorphy. I consider *Prochoristella*, including its possible junior synonyms (or at least closely related genera) *Afristella* Riek, 1974, *Mesotanyderus* Riek, 1955, and *Austrochoristella* Willmann, 1989, as belonging to Permochoristinae (Permochoristidae) and not related to *Mesopanorpodes*.

Equally unacceptable is the assignment to Mesopanorpodidae of a number of species from the mid-Triassic Tongchuan Fm of Shaanxi Province, China, described by Hong You-Chong and co-authors (Hong et al. 2002, Hong and Guo 2003, Hong 2007). *Erdosia pectinata* Hong, Guo & Wang, 2002 can be placed with certainty into Parachoristidae, as indicated by the typical pectinate RS and 5- or 6-branched MP. *"Mesopanorpodes" shaanxiensis* Hong, Guo & Wang, 2002 is based on a highly incomplete hindwing and may belong to either Parachoristidae, Permochoristidae, or Mesopsychidae. The systematic position of *Ladinochorista lata* Hong, 2007 is uncertain because of the poor preservation of the holotype. Several other taxa described in Mesopanorpodidae do not even belong to Mecoptera. *Triassochoristites jinsuoguanensis* Hong & Guo 2003 has already been recognized as a member of the dipteran family Vladipteridae (Blagoderov et al. 2007). *Forcinerva tongchuanensis* Hong and Guo 2003 belongs to the order Miomoptera (as determined by A.P. Rasnitsyn). *Allochorista erdosensis* Hong, 2007 and *Longifurcula hejiafangensis* Hong, 2007 cannot be attributed to any particular order based on the published photos and drawings. It should be noted that many descriptions of fossil insects from the Tongchuan Formation, and particularly Mecoptera, are based on inad-

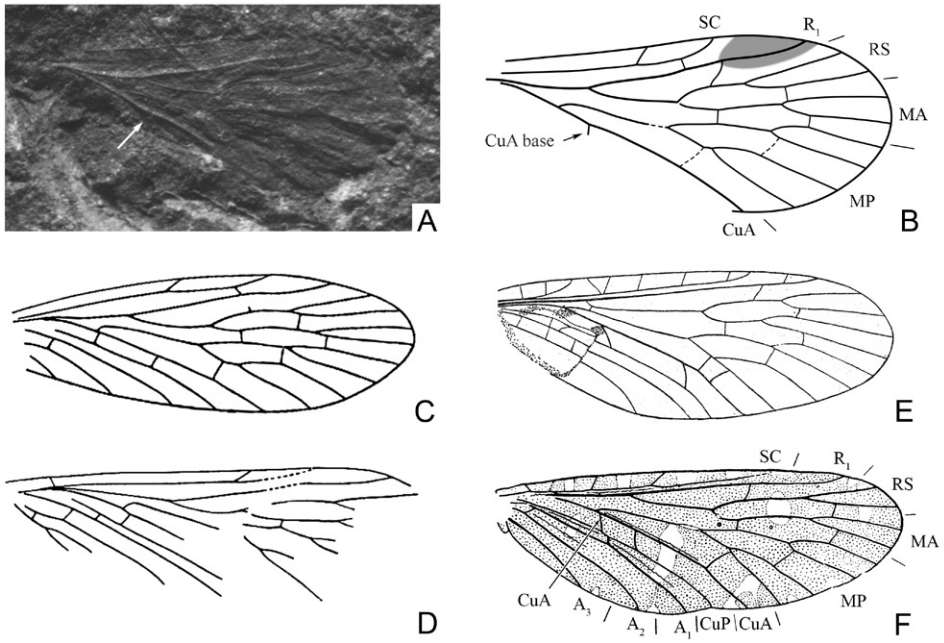

Figure 1. Wings of *Mesopanorpodes* and *Mesopsyche*, for comparison **A** photograph of *Mesopanorpodes wianamattensis* Tillyard (position of CuA base marked with arrow) **B** *Mesopanorpodes wianamattensis*, line drawing (orig.) **C** *Mesopanorpodes belmontensis*: from Riek (1953) **D** *Mesopanorpodes robustus*: from Riek (1953) **E** *Mesopsyche triareolata* Tillyard (= *Aristopsyche superba* Tillyard): from Tillyard, 1919a **F** *Mesopsyche dobrokhotovae* Novokshonov, modified after Novokshonov (1997c). Not to scale.

equately preserved specimens and contain inaccurate drawings and fantastic venational interpretations, in which obvious artifacts are interpreted as characters of specific or even generic rank and hindwings are often misinterpreted as forewings. Thus, these taxa should be considered as of unknown systematic position until revised in detail.

The Jurassic genera *Itaphlebia* Sukatcheva, 1985 and *Chrysopanorpa* Ren, 1995 were originally placed in Mesopanorpodidae as well. Novokshonov (1997a, b) synonymized these two genera and transferred them to Nannochoristidae. *Itaphlebia* appears to be the most common and widespread nannochoristid during the Jurassic. Its diagnosis, composition, and distribution, as well as the overall composition of the Mesozoic Nannochoristidae have been discussed recently by Liu et al. (2010).

Hong (2007) referred *Itaphlebia* again to Mesopanorpodidae and described *I. tongchuanensis* from the Tongchuan Formation of Shaanxi. However, this species is not related to *Itaphlebia,* being instead rather similar to *Mesopsyche*, where it apparently belongs.

Stylopanorpodes eurypterus, *Netropanorpodes decorosus*, and *N. sentosus* Sun, Ren & Shih, 2007 (Sun et al. 2007b) from the mid-Jurassic Jiulongshan Formation of Inner Mongolia, China, originally placed in Mesopanorpodidae, are venationally similar to the species of *Itaphlebia* occurring in the same deposits (Sun et al. 2007c, Liu et al. 2010) and belong to Nannochoristidae as well.

Mesopanorpodes mostovskii Novokshonov et al., 2004 from the basal Triassic of Northern Russia has been transferred to the related family Nedubroviidae (Bashkuev 2011).

Therefore, with the above-mentioned taxa discarded, Mesopanorpodidae remain composed of only three species of *Mesopanorpodes* from the Upper Permian and Middle Triassic of Australia. But are they actually congeneric?

Re-examination of available photographs of *M. wianamattensis* reveals that its CuA is distinctly bent distal to the origin of MP, and the base of CuA is shifted distad and inclined backwards, like in *Mesopsyche* (Fig. 1A–B). Thus, *Mesopanorpodes* appears venationally indistinguishable from *Mesopsyche*. Here I provisionally retain *Mesopanorpodes* as a separate genus until the complete revision of *Mesopsyche*. Unlike *M. wianamattensis* and *Mesopsyche*, both species described by Riek have the base of CuA short and transverse, with the intercubital space not expanded, which is presumed to be a plesiomorphic condition. These species are included here in the new genus *Permopsyche* gen. n.

In this paper, two new species of *Permopsyche*, *P. issadensis* sp. n. (type species) and *P. rasnitsyni* sp. n., are described from the Upper Permian of European Russia. These are the oldest currently known records of Mesopsychidae. The new material includes a number of well-preserved fore- and hindwings, which allow establishing yet another difference between *Permopsyche* and *Mesopsyche*, the position of the hindwing CuA vein with respect to the membrane. In *P. issadensis* CuA is concave (while the R_1 is convex), as is typical of Permochoristidae, while in *Mesopsyche* spp., including the Permian species, as well as the other Mesozoic mesopsychid genera, both CuA and R_1 are convex, like in most post-Paleozoic Mecoptera.

The earliest record of *Mesopsyche*, and the only one known so far to be definitely pre-Triassic, *Mesopsyche incompleta* sp. n., is described from the uppermost Permian of the European Russia.

Bittacopanorpa javorskii Zalessky, 1936 from the transitional Permian–Triassic sequence of the Kuznetsk Basin (Babiy Kamen' locality, Maltsevo Formation), known only from a wing base (Fig. 8G–H), originally placed in Neorthophlebiidae and tentatively transferred to Permotipulidae (Bechly and Schweigert 2000), can be identified as a hindwing with venation almost identical to that of the above-mentioned *Mesopsyche incompleta* sp. n. (Fig. 8B).

Material and methods

The study is based on examination of ca. 60 fossil specimens from the collection of Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). The holotype of *Bittacopanorpa javorskii* Zalessky is preserved in the collection of the Central Research Geological Prospecting Museum, Saint Petersburg (CRGPM).

Fifty-three isolated wings of *Permopsyche* were collected from a lens of fluvio-lacustrine deposits within the Sukhona River section, in Vologda Province, north-central Russia (Isady locality). It corresponds to the Kalikino Member of the Poldarsa Formation, and is dated the latest Severodvinian (correlated with the Lower Wuchiapingian: Golubev in press).

Five specimens of *Mesopsyche* were collected from the Balymotikha locality, an outcrop of lacustrine deposits of Vyazniki Permian–Triassic sequence, at the town of Vyazniki, Vladimir Province, central Russia. It is dated the latest Vyatkian (Late Changhsingian), somewhat below the Permian–Triassic boundary (Newell et al. 2010).

The fossils were examined with a Leica M165C stereomicroscope and photographed using an attached Leica DFC 425 digital camera. Images were digitally processed with Helicon Focus v. 5.1 and Adobe Photoshop CS3 graphic software. Line drawings were made using Inkscape v. 0.48 vector graphics editor.

On the line drawings the wings are oriented with their apices to the right, while some photographs are reversed left-right for better comparison.

The wing venation terminology follows Novokshonov (2002).

Systematic paleontology

Family Mesopsychidae Tillyard, 1917
http://species-id.net/wiki/Mesopsychidae

= Mesopanorpodidae Tillyard, 1918, syn. n.

Included genera. *Mesopsyche* Tillyard, 1917, *Mesopanorpodes* Tillyard, 1918, *Vitimopsyche* Novokshonov & Sukatsheva, 2001, *Baissopsyche* Novokshonov & Sukatsheva, 2001, *Lychnomesopsyche* Ren et al., 2009, *Permopsyche* Bashkuev, gen. n.

Remarks. The genus *Mesopanorpodes* is restricted here to its type species, *M. wianamattensis*. Though *Mesopanorpodes* appears venationally indistinguishable from *Mesopsyche*, it doesn't seem appropriate to synonymize these genera prior to the complete revision of the latter. The genus *Mesopsyche* (*sensu* Novokshonov 1997c, Novokshonov and Sukacheva 2001) includes apparently quite diverse insects and is quite loosely defined and likely heterogeneous, so its further dividing into several genera cannot be excluded.

Genus *Permopsyche* gen. n.
http://species-id.net/wiki/Permopsyche

Mesopanorpodes: Riek, 1953, p. 70 (partim, quoad *M. belmontensis* and *M. robustus*).

Type species. *Permopsyche issadensis* sp. n.; Upper Permian, European Russia.

Etymology. From the Permian and Greek *psyche*, "soul" or "mind," the word often used for devising names of delicately winged insects. Gender feminine.

Diagnosis. In forewing, SC long, bearing only inclined fore branch, connecting distally with R_1 by crossvein. Costal space narrow. Both RS and MA forks not longer than their stems. MP 4-branched. CuA base oblique to transverse, not distinctly in-

clined backwards; M_5 present or lost. Anal area not expanded. Crossveins not numerous. In hindwing, CuP concave with respect to membrane (in contrast to convex R_1).

Comparison. Differs from the closest genus *Mesopsyche* by the base of CuA being oblique to transverse (not inclined backwards), costal space narrower, and hindwing CuP concave with respect to membrane.

Composition. In addition to the type species, from the same locality, *P. rasnitsyni* sp. n.; and from the Upper Permian of Australia, *P. belmontensis* (Riek, 1953) comb. n. and *P. robustus* (Riek, 1953) comb. n.

Remarks. The assumption that one of the key characters, the position of hindwing CuP with respect to the membrane, known in the type species only, is shared by the other species is tentative and requires further verification.

Permopsyche issadensis sp. n.

http://species-id.net/wiki/Permopsyche_issadensis

Figs 2–4, 6

Etymology. From the Isady locality.

Holotype. PIN, no. 3840/336, well-preserved forewing (part and counterpart).

Paratypes. 21 forewings (see Table 1) and 6 hindwings: PIN, no. 3840/725, 1381–1383, 1385, 1389a. Additionally, 8 forewings and 10 hindwings incomplete or poorly preserved, excluded from the type series.

Locality and horizon. Isady locality, Vologda Province, North European Russia; Poldarsa Formation, uppermost Severodvinian (Lower Wuchiapingian), Upper Permian.

Diagnosis. Differs from *P. belmontensis* by wing shape, with anterior margin straight and posterior apical margin tending to oblique, different crossveins arrangement, and strongly unsclerotized MP stem. Differs from *P. robustus* by branch of SC located more basally and A_3 simple. Additionally differs from both species by considerably smaller size.

Description. Forewing. Moderately broad (length/width ratio 2.3–2.9:1); anterior margin nearly straight, slightly convex basally; apex obtuse to rounded. SC long, reaching or almost reaching basal margin of pterostigma; SC branch approximately at middle of RS+MA stem (somewhat variable in paratypes). Pterostigma distinct, widened, with oblique basal margin. R_1 simple, gently bending posteriad at pterostigma. RS and MA forks equally short, approximately as long as their stems. Nodal line distinct, arched, running from tip of SC to hind margin at apex of CuA. Thyridium present as unsclerotized section on MP stem spanning from approximately 1/3–1/2 of its length down to fork, accompanied by desclerotized spot at point of branching of RS and MA ("thyridulum", the term introduced by A.P. Rasnitsyn in Ren et al. 2009). Connection between CuA and MP variable (Fig. 4; see also Remarks), from joined at one point (X-junction), with CuA base oblique and M_5 lost, to forming well-developed cubitomedian Y-vein with almost equal arms at obtuse angle, with CuA base transverse and M_5 quite long. cua-cup crossvein transverse. Three simple anal veins. Crossveins not nu-

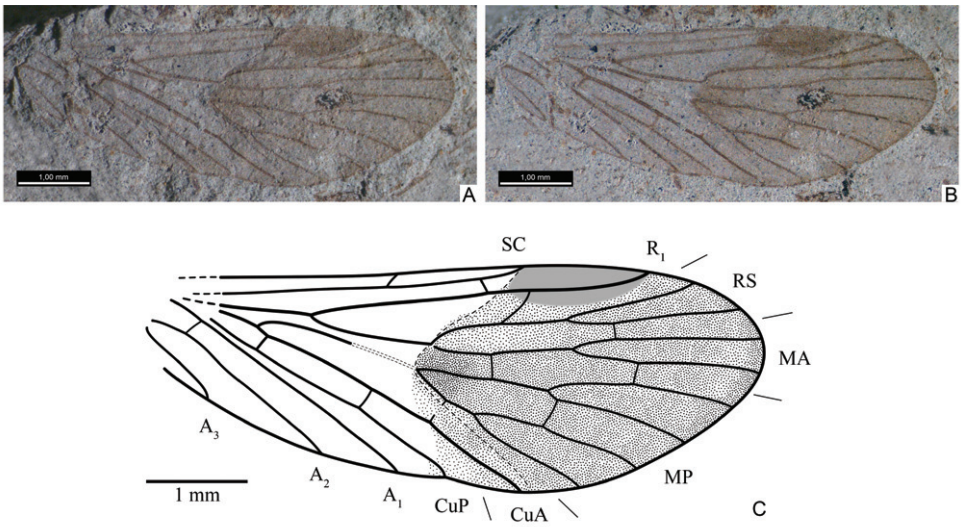

Figure 2. *Permopsyche issadensis* gen. et sp. n. **A–B** photographs of the holotype, under different illumination **C** line drawing of holotype.

merous, mainly distinct or slightly weakened, forming rather stable pattern: one long, oblique, sigmoidally curved r_1-rs crossvein; four crossveins between RS, MA, and MP branches; mp-cua and cua-cup crossveins of standard position; cup-a_1 and a_1-a_2 located stepwise along with the base of CuA; occasionally, a_2-a_3 present. Wing membrane darkened in distal wing half, restricted by nodal line, with saturated patch at center of wing.

Hindwing. Both venation scheme and coloration similar to those in forewing, adjusted for general difference between fore- and hindwings typical of Mecoptera. SC short, reaching wing midlength, variably forking apically (Fig. 6). Pterostigma distinct. R_1 with inclined branch in pterostigmal area. A_1 separating from CuP relatively closely to base.

Measurements (mm). Forewing length, 4.25–6.35, width, ca. 1.5–2.5; hindwing length, 3.9–5.5, width, 1.5–2.25.

Remarks and discussion. In *P. issadensis* the wing size varies conspicuously. As shown in the size distribution diagram for forewings (Fig. 5; Table 1), the presence of Y-vein and the transverse (rather than oblique) shape of CuA base (hollow squares *vs* filled squares) both correlate with the increased wing size (irrespectively of the length/width ratio). However, the size distributions of the two morphotypes overlap broadly. The two wing morphotypes may represent sexual dimorphism. Alternatively, they can be attributed to slight differences in flight mechanics depending on the body size. The distinctive and uniform wing color pattern makes it unlikely that the morphotypes represent two closely related species.

The nodal line (the line of wing flexion) in the forewing of the new species is essentially similar to that of both *Mesopsyche* (Novokshonov 1997c) and the recent *Panorpa* (Ennos and Wooton 1989), suggesting a similarity between flight mechanics of Mesopsychidae and Panorpidae.

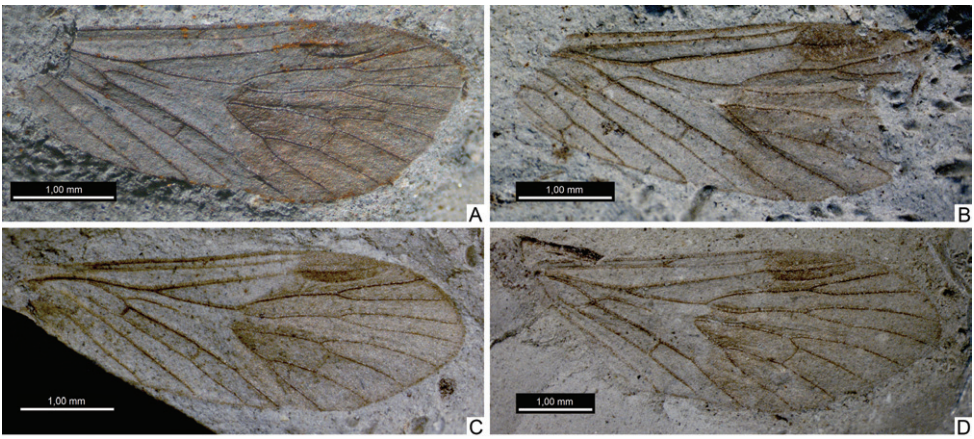

Figure 3. Photographs of forewings of *Permopsyche issadensis* gen. et sp. n. **A** paratype PIN, no. 3840/717; **B** paratype PIN, no. 3840/1354 **C** paratype PIN, no. 3840/1355 **D** paratype PIN, no. 3840/1357. All except **D** reversed left-right.

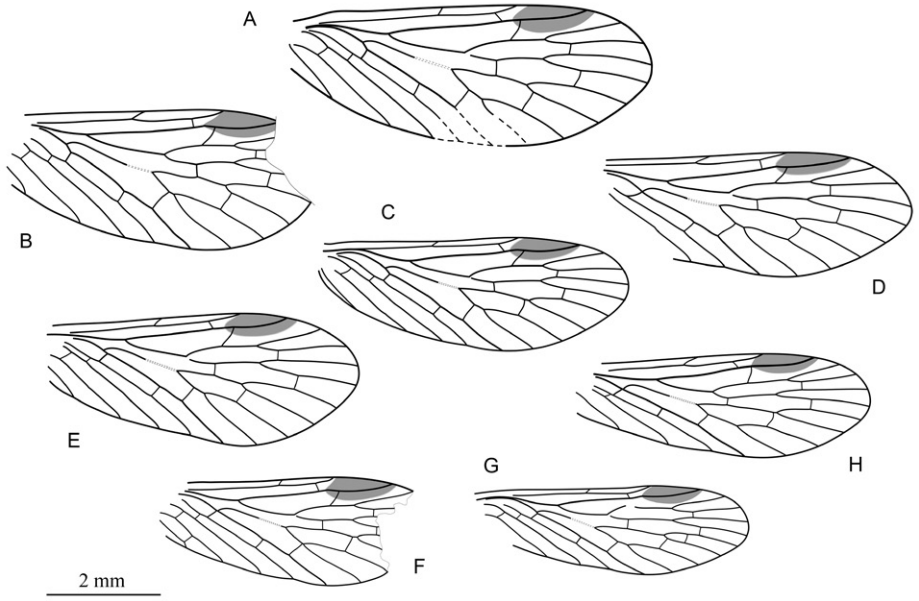

Figure 4. Line drawings of paratypes of *Permopsyche issadensis* gen. et sp. n. showing the variability of venation and wing size **A** PIN, no. 3840/718 **B** PIN, no. 3840/719 **C** PIN, no. 3840/105 **D** PIN, no. 3840/1357 **E** PIN, no. 3840/1352 **F** PIN, no. 3840/1354 **G** PIN, no. 3840/728 **H** PIN, no. 3840/729. All to the same scale.

Hindwings of *Permopsyche* are almost as abundant at Isady as the forewings. All the hindwings examined, as far as their preservation allows to tell, have the set of characters (including coloration) diagnostic of the forewings of *P. issadensis* and can be confidently referred to the same species.

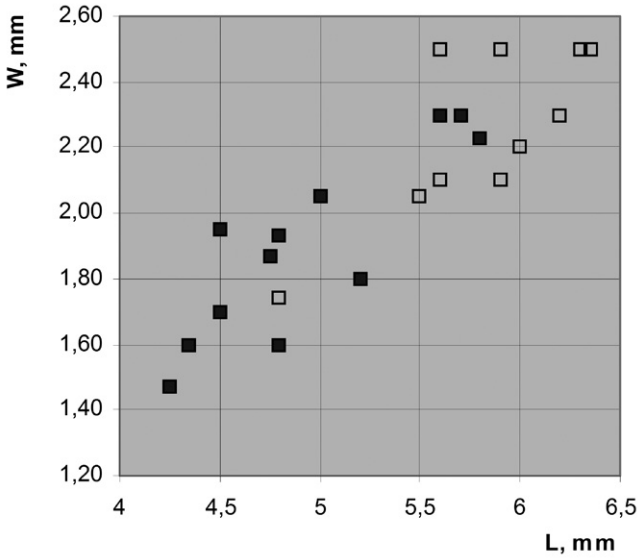

Figure 5. Correlation between wing size and structure of connection between CuA and MP in *Permopsyche issadensis*, based on Table 1; see text for explanation.

Table 1. Forewing sizes of *Permopsyche issadensis* gen. et sp. n. Some measurements are acceptably approximate due to restoration of wing base and/or apex.

PIN, no. 3840/…	Length	Width	L:W	CuA/MP fusion
730	4.25	1.47	2.89	■
1362	4.35	1.6	2.72	■
1360	4.5	1.7	2.65	■
723	4.5	1.95	2.31	■
1367	4.75	1.87	2.54	■
728	4.8	1.6	3.00	■
1355	4.8	1.74	2.76	□
1354	4.8	1.93	2.49	■
1359	5.0	2.05	2.44	■
729	5.2	1.8	2.89	■
105	5.5	2.05	2.68	□
1349	5.6	2.1	2.67	□
1352	5.6	2.3	2.43	■
719	5.6	2.5	2.24	□
1358	5.7	2.3	2.48	■
1357	5.8	2.23	2.60	■
1353	5.9	2.1	2.81	□
1350	5.9	2.5	2.36	□
1366	6.0	2.2	2.73	□
336	**6.2**	**2.3**	**2.70**	□
717	6.3	2.5	2.52	□
718	6.35	2.5	2.54	□

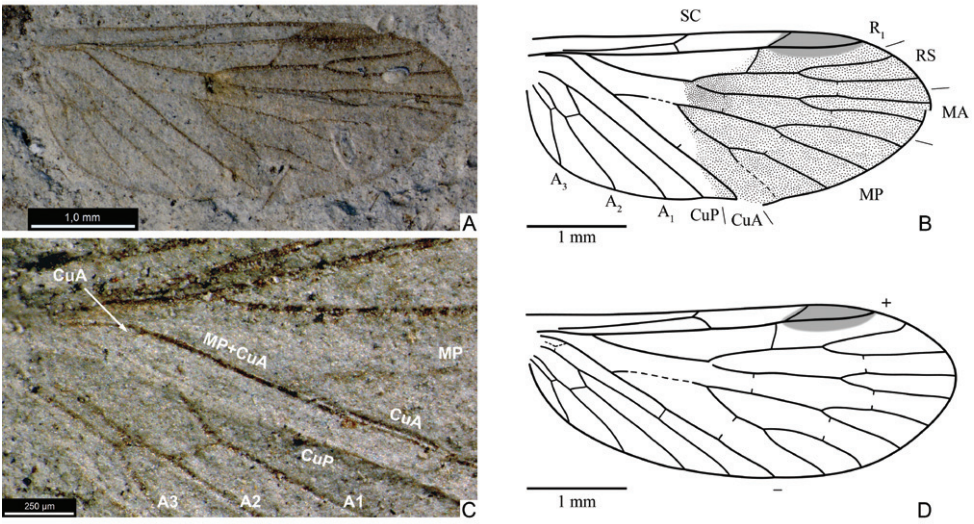

Figure 6. Hindwings of *Permopsyche issadensis* **gen. et sp. n. A–B** paratype PIN, no. 3840/1381, photograph and line drawing **C–D** paratype PIN, no. 3840/1382 **C** details of cubito-anal structure **D** line drawing of hindwing **A, C** reversed left-right.

***Permopsyche rasnitsyni* sp. n.**
http://species-id.net/wiki/Permopsyche_rasnitsyni
Fig. 7A–D

Etymology. In honor of an outstanding paleoentomologist, Prof. Dr. Alexandr Rasnitsyn.

Holotype. PIN, no. 3840/1351, well-preserved forewing (part and counterpart), with apex missing.

Paratypes. PIN, no. 3840/733, 1363, 1371, incomplete forewings.

Locality and horizon. Isady locality, Vologda Province, North European Russia; Poldarsa Formation, uppermost Severodvinian (Lower Wuchiapingian), Upper Permian.

Diagnosis. Similar to *P. issadensis* in general venation scheme, but of larger size, with MA fork shortened, intercubital space widened, and wing membrane almost uncolored.

Description. Forewing length/width ratio about 2.8–3:1; anterior margin nearly straight; apex obtuse to rounded. Costal space very narrow along its entire length. MA fork distinctly shorter than RS fork. MP unsclerotized for more than 1/2 of its length. CuA base long, nearly transverse, M_5 present or lost. Intercubital space rather expanded. Wing membrane mostly uncolored, with small diffuse dark patch at center of wing.

Measurements (mm). Holotype length, as preserved, 6.7, width, 2.5; paratypes lengths, ca. 7.0–8.5, width unmeasurable due to widthwise deformation.

***Permopsyche* sp.**
Fig. 7E–F

Material. PIN, no. 3840/1556, well-preserved forewing (part and counterpart).

The wing is 6 mm long, 2.1 mm wide, subtriangular, with anal area narrowed and posterior apical margin slightly oblique; MA forking before RS. The wing is entirely uncolored (neither part, nor counterpart showing any trace of coloration). The specimen may either be an aberrant specimen of *Permopsyche issadensis*, or represent a different species, but describing a separate species based on a single wing does not seem well justified.

Genus *Mesopsyche* Tillyard, 1917
http://species-id.net/wiki/Mesopsyche

Triassopsyche Tillyard, 1917: Riek 1956, p. 100.
Aristopsyche Tillyard, 1919: Riek 1956, p. 100.
Neuropsyche Tillyard, 1919: Riek 1956, p. 100.
Mesoses Riek, 1976: Novokshonov and Sukatcheva 2001, p. 71.
Bittacopanorpa Zalessky, 1935, syn. n.
Itaphlebia Hong, 2007, syn. n. (partim, quoad *I. tongchuanensis*)

Type species. *Mesopsyche triareolata* Tillyard, 1917; Upper Triassic, Australia.

Diagnosis. Forewing relatively broad. SC rather long, with single or multiple fore branches. Costal space typically expanded. Both RS and MA forks not longer than their stems. MP 4-branched. CuA base from transverse to distinctly inclined backwards, usually situated much more distally than MP origin. Crossvein cua-cup of same inclination as CuA base. Intercubital space rather expanded. Crossveins not numerous, their arrangement rather stable. In hindwing, CuP convex with respect to membrane; fused with A_1 very close to base.

Comparison. Differs from *Permopsyche* by the base of CuA being inclined backwards, costal space widened, and hindwing CuP convex.

Composition. In addition to the type species, from the beds near the Permian–Triassic boundary of Kuznetsk Basin, *M. javorskii* (Zalessky, 1935) comb. n.; from the Middle Triassic of China, *M. tongchuanensis* (Hong, 2007) comb. n.; from the Middle–Upper Triassic Madygen Formation of Kyrgyzstan, *M. shcherbakovi*, *M. justa*, *M. ordinata*, *M. tortiva*, and *M. gentica* (Novokshonov 1997c, Novokshonov and Sukatcheva 2001); from the Upper Triassic of South Africa, *M. optata* (Riek, 1976), *M. magna* (Riek, 1976); from the Upper Triassic of Ukraine, *M. dobrokhotovae* (Novokshonov 1997c).

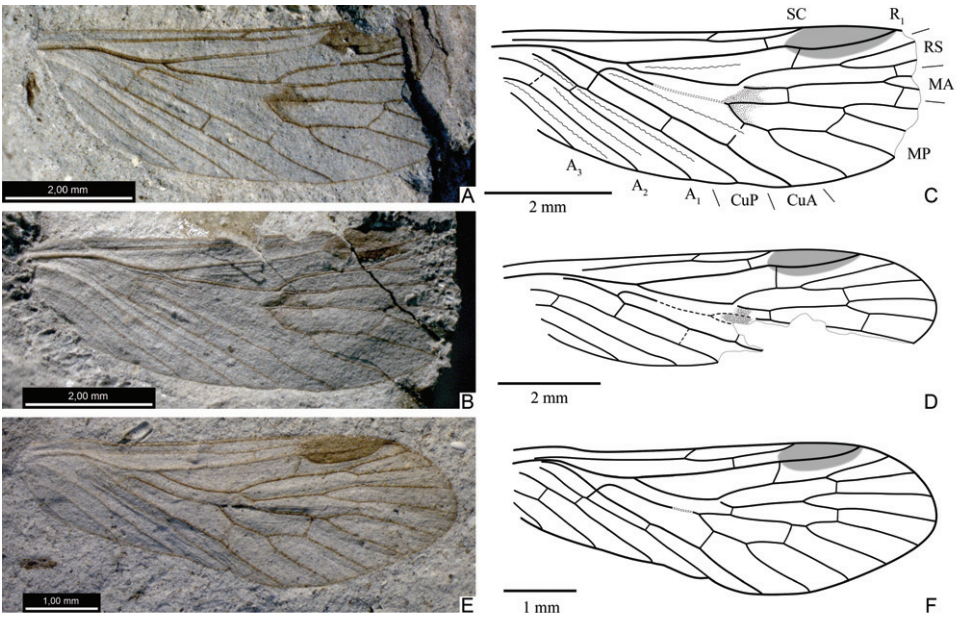

Figure 7. A–D forewings of *Permopsyche rasnitsyn*i gen. et sp. n. **A–B** photograph of holotype, PIN, no. 3840/1351, part and counterpart **C** line drawing of holotype, PIN, no. 3840/1351 **D** line drawing of paratype, PIN, no. 3840/1363 **E–F** *Permopsyche* sp., photograph and line drawing of specimen PIN, no. 3840/1556.

***Mesopsyche incompleta* sp. n.**
http://species-id.net/wiki/Mesopsyche_incompleta
Fig. 8

Etymology. Latin *incompletus*, "incomplete".

Holotype. PIN, no. 5103/286, hindwing (part and counterpart), with cubito-anal area missing.

Paratypes. PIN, no. 5103/122, incomplete forewing (basal half only), part and counterpart; PIN, no. 5103/123, incomplete forewing (anterior half only, with apex, basal and posterior parts missing), part and counterpart. In addition, two forewing fragments apparently belonging to the same species.

Locality and horizon. Balymotikha locality, Vyazniki town, Vladimir Province, Central European Russia; uppermost Vyatkian (Upper Changhsingian), Upper Permian.

Description. Forewing. Anterior margin slightly convex. Costal space somewhat wider than subcostal one. Pterostigma distinct, lanceolate. SC not reaching the pterostigma, bearing one oblique distal branch; connected distally with R_1 by short transverse crossvein. R_1 sharply curved posteriad at origin of weak distal branch in pterostigmal area. RS forking somewhat before than MA. Thyridium at MP stem before fork.

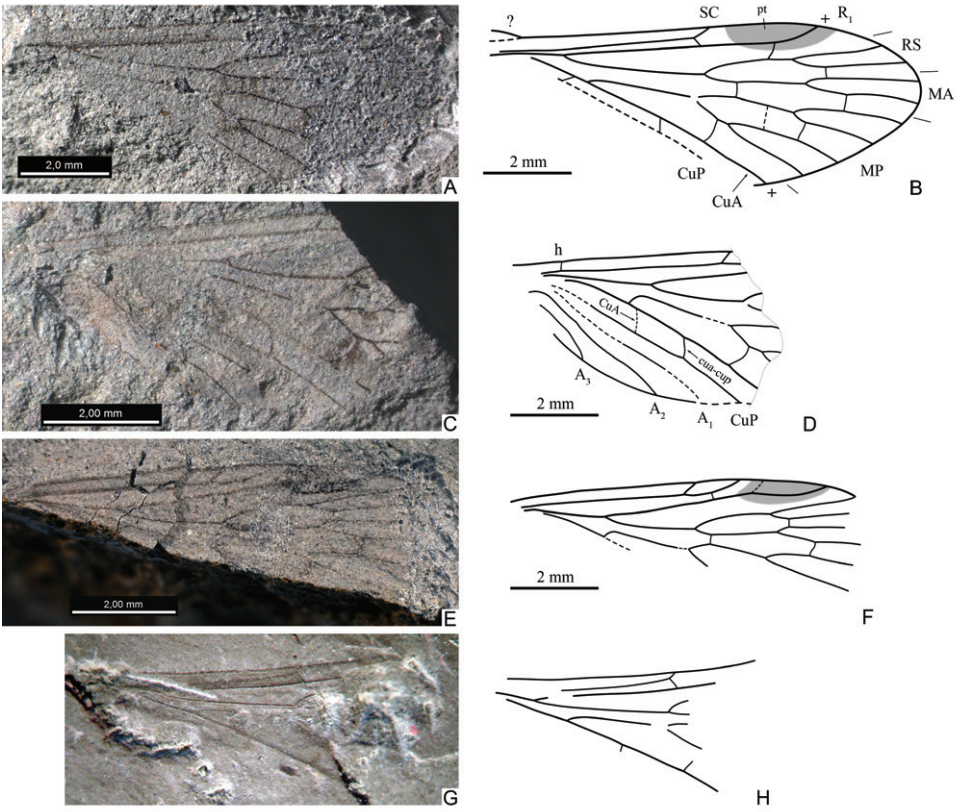

Figure 8. A–F, wings of *Mesopsyche incompleta* sp. n. **A–B** holotype PIN, no. 5103/286, hindwing, photograph and line drawing **C–D** paratype PIN, no. 5103/122, forewing, photograph and line drawing **E–F** paratype PIN, no. 5103/123, forewing, photograph and line drawing **G–H** *Mesopsyche javorskii* (Zalessky) comb. n., holotype hindwing, photograph (by D. Shcherbakov) and line drawing (orig.), not to scale **A, C, G** reversed left-right.

CuA base obscure, presumably curved backwards and located somewhat distal to M_5. Crossvein cua-cup slightly sigmoid, distinctly curved backwards. Crossvein pattern typical of genus. Color pattern in form of sparse dark spots, mostly around crossveins.

Hindwing venation and coloration similar to those in forewing. SC slightly shortened, reaching level of RS+MA bifurcation, somewhat beyond wing midlength, forking apically. Pterostigma distinct. R1 nearly straight, turning apically towards anterior margin. R_1 branch obscure. CuA distinctly convex along the whole length.

Measurements (mm). hindwing length of holotype, 9.8; forewing length of paratype PIN, no. 5103/122, 6.1, as preserved; paratype PIN, no. 5103/123, 7.9, as preserved.

Comparison. The new species substantially differs from others by SC with a single, distally located fore branch.

Discussion

The systematic position of Mesopsychidae and the entire "suborder" Paratrichoptera was discussed by Novokshonov and Sukatcheva (2001). Recent studies of complete mesopsychid fossils from the Middle Jurassic and Lower Cretaceous of China revealed the long siphonate mouthparts indicating fluid feeding on reproductive organs of gymnosperm plants (Ren et al. 2009, 2010). Mesopsychidae, together with mid-Mesozoic Aneuretopsychidae, Pseudopolycentropodidae, and now the Late Permian to Early Triassic Nedubroviidae (Bashkuev 2011), form a distinct long-proboscid clade within Mecoptera, the Aneuretopsychina.

The finds described herein reveal main trends in the evolution of Mesopsychidae after their separation from the permochoristid-like ancestor. These are:

– Change in the forewing CuA base inclination and position: from proximal and inclined forwards (typical of Permochoristidae) to inclined backwards, and probably also shifted distad.
– Change in position of the hindwing CuA: from concave (*Permopsyche*) to convex (most Mesopsychidae).
– Loss of fusion of CuP and A_1 veins in the hindwing: from quite basally fused in *Permopsyche*, through a rudimentary basal fusion in *Mesopsyche* (as indicated by Novokshonov (1997c) in *M. shcherbakovi*), to becoming secondary free along their whole length in the mid-Jurassic and early Cretaceous genera.
– Increase in the average wing size, from 5–6 mm in the Late Permian to 20–30 mm since the Late Triassic.

The Permian Mesopsychidae occurred together with Nedubroviidae (in Isady, Balymotikha, and probably Belmont; Bashkuev 2011), which already have typical long siphonate mouthparts, and the possession of those in early mesopsychids (and even in the ancestral permochoristid lineage) can be assumed as well.

New finds also cast light on the stratigraphic distribution of the Aneuretopsychina scorpionflies, which appear to be the most common group of Mecoptera during the latest Permian – early Middle Triassic time interval (viz. Mesopsychidae, Nedubroviidae, and later also Pseudopolycentropodidae). They initially replaced Permochoristidae in the end of Permian, and were in turn progressively supplanted during the Triassic – Early Jurassic by Parachoristidae and Orthophlebiidae, which gave rise to the modern mecopteran lineages. In the mid-Jurassic – Lower Cretaceous insect assemblages, Aneuretopsychina scorpionflies are rather rarely found, constituting only a minor component of the mecopteran faunas.

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RESEARCH ARTICLE

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A new long-proboscid genus of Pseudopolycentropodidae (Mecoptera) from the middle Jurassic of China and its plant-host specializations

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Abstract

We describe a new genus and species of Mecoptera with siphonate mouthparts, *Sinopolycentropus rasnitsyni* **gen. et sp. n.**, assigned to the family Pseudopolycentropodidae Handlirsch, 1925. The specimen was collected from late middle Jurassic nonmarine strata of the Jiulongshan Formation in Inner Mongolia, northeastern China. The new material provides additional evidence for an early diversification of pseudopolycentropodids that was ongoing during the middle Jurassic. This diversity also adds to the variety of known pseudopolycentropodids with tubular proboscides that apparently fed on ovulate fluids produced by Mesozoic gymnosperms.

Keywords

Pseudopolycentropodidae, fossil scorpionfly, new taxon, Jiulongshan Formation, proboscis, insect-plant associations, gymnosperms

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Introduction

The Pseudopolycentropodidae is an extinct and relatively nonspeciose family considered as phylogenetically basal to recent Mecoptera (Handlirsch 1925, Bode 1953, Willmann 1989, Carpenter 1992, Novokshonov 2002). Novokshonov (1997a) provided a general description of *Pseudopolycentropus latipennis* Martynov, 1927, then the best known species, and stated that all structural details of *P. latipennis* appear typical of the entire family except forewing shape. Grimaldi and colleagues (2005) comprehensively reviewed pseudopolycentropodid scorpionflies; they included additional details of seven previously described species of *Pseudopolycentropus* and their spatiotemporal distributions, and described the new taxa of *Pseudopolycentropus daohugouensis* Zhang, 2005, *Pseudopolycentropodes virginicus* Grimaldi & Fraser, 2005, *Parapolycentropus burmiticus* Grimaldi & Rasnitsyn, 2005, *and P. paraburmiticus* Grimaldi & Rasnitsyn, 2005. This contribution considerably expanded knowledge of the Pseudopolycentropodidae, and provided inferences on the possible diets of these bizarre, mid-Mesozoic insects.

Currently, the Pseudopolycentropodidae consists of thirteen described species assigned to three genera from the mid-Triassic to the mid-Cretaceous (Whalley 1985, Papier et al. 1996, Ansorge 1996, 2003, Novokshonov 1997a, 1997b, Grimaldi et al. 2005, Ren et al. 2009, Ren et al. 2010a). Five of these described species were based on fossils of forewings only, and one was based on fore- and hindwings. Of the remaining, seven species were described from wings and bodies; only five of which have preserved mouthparts, summarized in Table 1. They are *Pseudopolycentropus latipennis* (mid Late Jurassic of Karatau, Kazakhstan); *P. daohugouensis*, *P. janeannae* Ren, Shih & Labandeira, 2010, *P. novokshonovi* Ren, Shih & Labandeira, 2010 (all from the late middle Jurassic of Daohugou, Inner Mongolia, China), and *Parapolycentropus burmiticus* (late Early Cretaceous of Kachin Province, northern Myanmar).

These five scorpionfly taxa are highly significant because *Pseudopolycentropus* possessed distinctive, elongate tubular, or siphonate, proboscides for surface fluid feeding on exposed plant fluids, such as the pollination drops of seed plants (Ren et al. 2009, Labandeira 2010). By contrast, one known species of *Parapolycentropus* bore a proboscis housing styliform structures. Although this genus, like other Pseudopolycentropodidae, probably imbibed ovulate fluids of seed plants (Grimaldi et al. 2005; Labandeira et al. 2007; Ren et al. 2009), the presence of one or perhaps two unserrated, styliform structures ensheathed within a proboscis is anomalous. One explanation is that this species of *Parapolycentropus* may have fed in a manner similar to a technical ink drawing pen with a central elongate wire for assisting laminar flow when food tube diameters are very narrow. Several genera of long-proboscid clades of Diptera have similar food tube arrangements, in which a thin, centrally positioned, rod-like but flexible hypopharynx extends to almost the proboscis terminus (Nagatomi and Soroida 1985, e.g. Figs 409, 425, 437). Such styliform processes lack serrations or apical piercing structures, and would be inconsistent with a blood feeding diet mentioned by Grimaldi et al. (2005).

Table 1. Mouthpart, wing and antennal features of Mid-Mesozoic long-proboscid scorpionflies

Taxon	Localities and age	Body Length (mm)	Forewing		Proboscis Features					Clypeal area (mm^2)	Antenna type	Sex
			Length (mm)	Width (mm)	Length (mm)	Width (mm)	Food tube dia. (mm)	Surface	Terminus			
Pseudopolycentropodidae												
Sinopolycentropus rasnitsyni gen. et sp. n.[1]	Daohugou, Inner Mongolia, China; Middle Jurassic (Bathonian–Callovian boundary)	5.5	6.1	2.4	1.9	0.1	0.027	Fine setae	Absent	??	Moniliform – compact with annulate hairs	♀
Parapolycentropus burmiticus Grimaldi & Rasnitsyn 2005[1]	Tanai, Kachin, Myanmar; Early Cretaceous (Albian)	3.0	4.0	–	1.3	0.121	0.014	Setate, annulated	Lobate (Type 4)	—	Moniliform–aristate	♀
Pseudopolycentropus latipennis Martynov 1927	Aulie, Chimkent, Kazakhstan; Late Jurassic (Kimme-ridgian)	6.5	~9.8	~4.3	1.85	0.085	??	Fine setae	Tip broken	—	Filiform– compact	♀
Pseudopolycentropus daohugouensis Zhang 2005	Daohugou, Inner Mongolia, China; Middle Jurassic (Bathonian–Callovian boundary)	7.5	~7.0	~3.7	1.82	0.146	0.048	?	Tip broken	—	Moniliform	?
Pseudopolycentropus janeannae Ren, Shih & Labandeira 2010	Daohugou, Inner Mongolia, China; Middle Jurassic (Bathonian–Callovian boundary)	7.0 7.0	7.5 7.0	3.8 3.0	1.7 1.75	0.130 0.125	0.038 0.038	Fine setae	Absent	—	Filiform–compact	♀,♂
Pseudopolycentropus novokshonovi Ren, Shih & Labandeira 2010	Daohugou, Inner Mongolia, China; Middle Jurassic (Bathonian–Callo vian boundary)	7.0	8.0	3.9	1.5	0.13	0.038	Transversely ridged?	Tip broken	0.468	Filiform– compact	?

Taxon	Localities and age	Body Length (mm)	Forewing		Proboscis Features					Clypeal area (mm^2)	Antenna type	Sex
			Length (mm)	Width (mm)	Length (mm)	Width (mm)	Food tube dia. (mm)	Surface	Terminus			
Mesopsychidae												
Lichnomesopsyche gloriae Ren, Labandeira & Shih 2010	Daohougou, Inner Mongolia, China; Middle Jurassic (Bathonian–Callo vian boundary)	28.0 23.0 23.0 –	25.0 24.0 27.0 24.0	7.0 8.0 8.0 8.0	9.9 8.9 8.9 10.1 >8.0 9.0	0.24 0.28 0.18 0.25 0.24 0.30	0.111 0.130 0.060 0.138 0.137 0.132	Coarse setae	Pseudo-labellum (Type 1)	0.387 (n = 7)	Filiform –broad	♀,♂
Lichnomesopsyche daohugouensis Ren, Labandeira & Shih 2010	Daohougou, Inner Mongolia, China; Middle Jurassic (Bathonian–Callo vian boundary)	>14	22.0	6.5	8.8	0.34	0.094	Coarse setae	Pseudo-labellum (Type 1)	0.361	Filiform broad	–
Vitimopsyche kozlovi Ren, Labandeira & Shih 2010	Pingquam, Hebei China, Early Cretaceous (Barremian)	–	24.0	8.0	9.0	0.58	0.14	Smooth	Absent	0.436	–	–
Aneuretopsychidae												
Jeholopsyche liaoningensis Ren, Shih & Labandeira 2011	Huangbanjigou, Liaoning, China, Early Cretaceous (Barremian)	23.0	21.5	6.0	6.8	0.34	0.10	Smooth, annulated	V-shaped pseudo-labellum (Type 2)	0.493	Filiform–compact	♂
Aneuretopsyche minima Rasnitsyn & Kozlov 1990	Aulie, Chimkent, Kazakhstan; Late Jurassic (Kimme-ridgian)	—	~10.5	—	4.7	0.18	0.060?	Fine setae, transversely ridged	Absent	—	Filiform–compact	?

Taxon	Localities and age	Body Length (mm)	Forewing		Proboscis Features					Clypeal area (mm²)	Antenna type	Sex
			Length (mm)	Width (mm)	Length (mm)	Width (mm)	Food tube dia. (mm)	Surface	Terminus			
Aneuretopsyche rostrata Rasnitsyn & Kozlov 1990	Aulie, Chimkent, Kazakhstan; Late Jurassic (Kimme-ridgian)	21.0	25.0	~7.1	7.3	0.21	0.075?	Fine setae, transversely ridged	Faint pseudo-labellum (Type 3)	–	Filiform–compact	♀
Nedubroviidae												
Nedubrovia shcherbakovi Bashkuev 2011	Isady, Vologda, Russia (Late Permian (Wuchiapingian)	~3.0	3.4	~1.3	>.035	NR[2]	NR[2]?	Fine setae,	??	–	??–	?

[1] *Parapolycentropus* and *Sinopolycentropus* are the only two genera of Pseudopolycentropodidae known to have labial palps, albeit they are diminutive (Figs 2B, 2E, Grimaldi et al. 2005).

[2] NR: not reported.

Ren and colleagues (2009, 2010a, 2010b, 2011) reported that three families of mid Mesozoic, Eurasian Mecoptera had particularly elongate siphonate proboscides. They were the Mesopsychidae (*Lichnomesopsyche gloriae* Ren, Labandeira & Shih 2010, *L. daohugouensis* Ren, Labandeira & Shih 2010, and *Vitimopsyche kozlovi* Ren, Labandeira & Shih 2010), Aneuretopsychidae (*Jeholopsyche liaoningensis* Ren, Shih & Labandeira 2011), and the afore-mentioned Pseudopolycentropodidae (*Pseudopolycentropus janeannae* and *P. novokshonovi*). Structural details of these and other long-proboscid scorpionfly taxa are listed in Table 1, indicating together with other insect and botanical evidence, that these taxa fed on gymnospermous ovulate fluids such as pollination drops and likely engaged in pollination mutualisms with their host plants (Ren et al. 2009, Labandeira 2010).

The long proboscides of Mecoptera, in addition to other clades such as nemestrinid flies, seem to have originated during a 15 million-year interval during the mid Jurassic from a 170 to 155 Ma (Ren et al. 2009), indicated in part by earlier, Late Triassic pseudopolycentropodids lacking proboscides. However, this burst of long-proboscid origination is preceded by two considerably antecedent lineages that bear small but long proboscides, both from Late Permian of Russia: the relatively miniscule neuropteran Permithonidae, *Tschekardithonopsis*, from Chekarda of Perm Province (Labandeira 2010), and the somewhat larger, mecopteran Nedubroviidae from Isady of Vologda Province (Bashkuev 2011). Although much poorly known than the aneuretopsychine Mecoptera of the later mid Mesozoic, both the Late Permian and mid Mesozoic long-proboscid assemblages considerably antedate the similar and independent associations of nectar-feeding by flies, moths, and beetles on angiosperms several tens of millions of years later (Grimaldi 1999, Labandeira et al. 2007, Labandeira 2010). All three scorpionfly families became extinct during the later Early Cretaceous to mid-Cretaceous, coincident with global gymnosperm-to-angiosperm turnover (Ren et al. 2009, Labandeira 2010).

Adding to this inventory of long-proboscid scorpionflies, we recently collected a well-preserved fossil pseudopolycentropodid from the middle Jurassic Jiulongshan Formation in Daohugou Village, Ningcheng County, Inner Mongolia, China. Based on its unique combination of antennae, mouthparts, and wing venation, a new genus and species is erected herein.

Geological and paleobiological context

The Jiulongshan Formation is a lacustrine sequence that crops out near Daohugou Village, Shantou Township, Ningcheng County, in Inner Mongolia of northeastern China (41°19.532' N, 119°14.589' E) (Ren et al. 1995, Ren et al. 2002). The section at Daohugou is composed of grey tuffaceous sandstone and sandy mudstone. The paleoenvironment reconstructed for this locality was a volcanic region with montane streams and lakes (Ren et al. 2002). Daohugou has yielded an abundant and

diverse insect fauna in addition to the Mecoptera, (Ren et al. 2010c) consisting of complete specimens of Ephemeroptera, Odonata, Plecoptera, Blattodea, Grylloblattida, Dermaptera, Orthoptera, Phasmatodea, Heteroptera, Sternorrhyncha, Neuroptera, Raphidioptera, Coleoptera, Hymenoptera, Diptera, Trichoptera and Lepidoptera. Apart from insects, Daohugou also has produced spiders, freshwater conchostracans, salamanders, feathered dinosaurs, pterosaurs, and mammals.

There is considerable evidence for a diverse local flora at Daohugou, which was important for plant interacting insects, such as pseudopolycentropodid scorpionflies. The Jiulongshan Formation has provided evidence for the floral composition of the surrounding forests. These forests were dominated by arborescent seed plants, principally Coniferopsida (*Pityophyllum*, *Rhipidiocladus*, *Elatocladus*, *Schizolepis*, *Podozamites*), Ginkgopsida (*Ginkgoites*, *Ginkgo, Baiera*, *Czekanowskia*, *Phoenicopsis*), Cycadopsida (*Pseudoctenis*, *Zamites*), and Bennettitopsida (*Anomozamites*) (Mi et al. 1996). Lower statured plants, including herbaceous ground cover, consisted of Lycopsida (*Lycopodites*, *Selaginellites*), Sphenopsida (*Equisetum*), and Filicopsida (*Todites*, *Coniopteris*) (Mi et al. 1996). These paleobotanical data were interpreted as indicating humid and warm-temperate climate (Tan and Ren 2002), although ecological amplitudes of specific habitats have yet to be determined. Verifiable $^{40}Ar/^{39}Ar$ and SHRIMP $^{238}U/^{206}Pb$ dating shows that the age of the volcanic rocks overlying the Daohugou fossil-bearing beds is ca. 164-165 Mya, and consequently the age of this fossil-bearing beds is slightly older than or equal to 165 Mya (Chen et al. 2004). Combined with the above-mentioned composition of insect fauna and conchostracans, the age of Daohugou biota is considered as middle Jurassic (Zhang et al. 1987, Ren et al. 1995, 2002, Wang et al. 2000, Shen et al. 2003), equivalent to the Bathonian–Callovian boundary interval (Ogg et al. 2008).

Materials and methods

This study is based on a fossil specimen (CNU-MEC-NN-2010044 p/c), with part and counterpart, housed in the fossil insect collection of the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator). The specimen was examined dry or under alcohol using a Leica M165 C dissecting microscope, and illustrated with the aid of a drawing tube attachment. Photographs of specimens were taken by Leica dfc500 and line drawings in Figure 1 were made by CorelDraw 12. The drawing in Figure 2 was done as a camera lucida tracing that subsequently was inked on polyester film and then reduced in size. Illumination for the drawing of this specimen consisted of three types of light and variation in light angle and origin for accentuation of morphological features, such as wing venation, that normally were difficult to observe and typically unavailable at lower magnification microscopes. The morphological terminology used herein is that of Grimaldi et al. (2005).

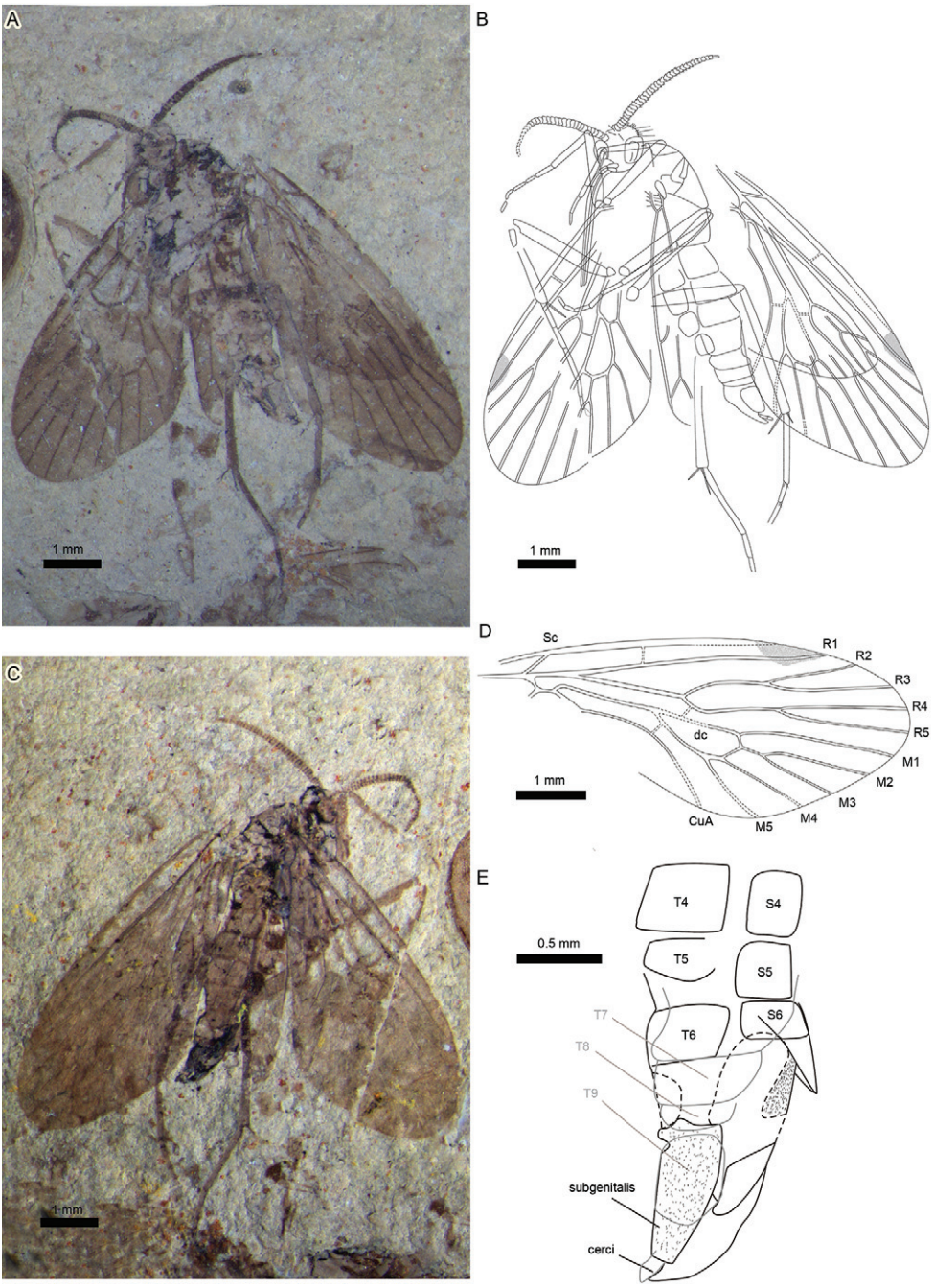

Figure 1. Photographs and line drawings of holotype *Sinopolycentropus rasnitsyni* gen. et sp. n. (specimen no. CNU-MEC- NN2010044 p/c) **A** Digital image of part, no.CNU-MEC-NN2010044p **B** Line drawing of part, no.CNU-MEC-NN2010044p **C** Digital image of counterpart, no.CNU-MEC-NN2010044c **D** Line drawing of forewing venation, no.CNU-MEC-NN2010044p **E** Line drawing of abdomen and terminalia, no.CNU-MEC-NN2010044c. Scale bars: 1.0 mm or 0.5 mm as shown in figures..

Systematic paleontology

Family Pseudopolycentropodidae Handlirsch, 1925

Genus *Sinopolycentropus* Shih, Yang, Labandeira & Ren, gen. n.

urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Sinopolycentropus

Type species. *Sinopolycentropus rasnitsyni* Shih, Yang, Labandeira & Ren, sp. n.

Etymology. The generic name is a combination of the prefix "*Sino*" for China, and a shortened version, with the infix removed, of the type genus of its referred family, "*Pseudopolycentropus*". The gender is masculine.

Diagnosis. Forewing broad and rounded, triangular in overall shape, with base of Sc merging with R; R_2+R_3 forking earlier than R_4+R_5 forking. Antennae moniliform, compact, robust and thick, multiarticulate with annulate hairs. Distinct, multiarticulate labial palps and long occipital bristles also distinguish this taxon from all previously described Pseudopolycentropodidae except for *Parapolycentropus* Grimaldi & Rasnitsyn 2005.

Remarks. This genus can be assigned to the Pseudopolycentropodidae by a short Sc, simple R_1, Rs with four branches, M with five branches, a dc cell present, and a simple CuA. It can be differentiated readily from all other genera of Pseudopolycentropodidae by the base of Sc merging with R, R_2+R_3 forking earlier than R_4+R_5, and moniliform antennae consisting of compact, robust, relatively short, articles with annulate hairs. Distinctive labial palps and long occipital bristles also distinguish this taxon from all previously described Pseudopolycentropodidae except for *Parapolycentropus*. In addition, body length of *Sinopolycentropus* (5.5 mm) is shorter than that of *Pseudopolycentropus* (6.5 to 7.5 mm), but longer than that of *Parapolycentropus* (3.0 mm).

Sinopolycentropus rasnitsyni Shih, Yang, Labandeira & Ren, sp. n.

urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Sinopolycentropus_rasnitsyni
Figs 1,2

Material. Holotype, an almost complete specimen with well-preserved body and wings, female, part and counterpart, No.CNU-MEC-NN-2010044 p/c, is housed in the fossil insect collection of the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China.

Etymology. The specific name is dedicated to Dr. Alexandr Rasnitsyn for his contribution to paleoentomology and his recognition, with M. V. Kozlov, of the first fossil scorpionfly (*Aneuretopsyche rostrata*) with a documented long proboscis in 1990 (Rasnitsyn and Kozlov 1990).

Diagnosis. As for the genus by monotypy.

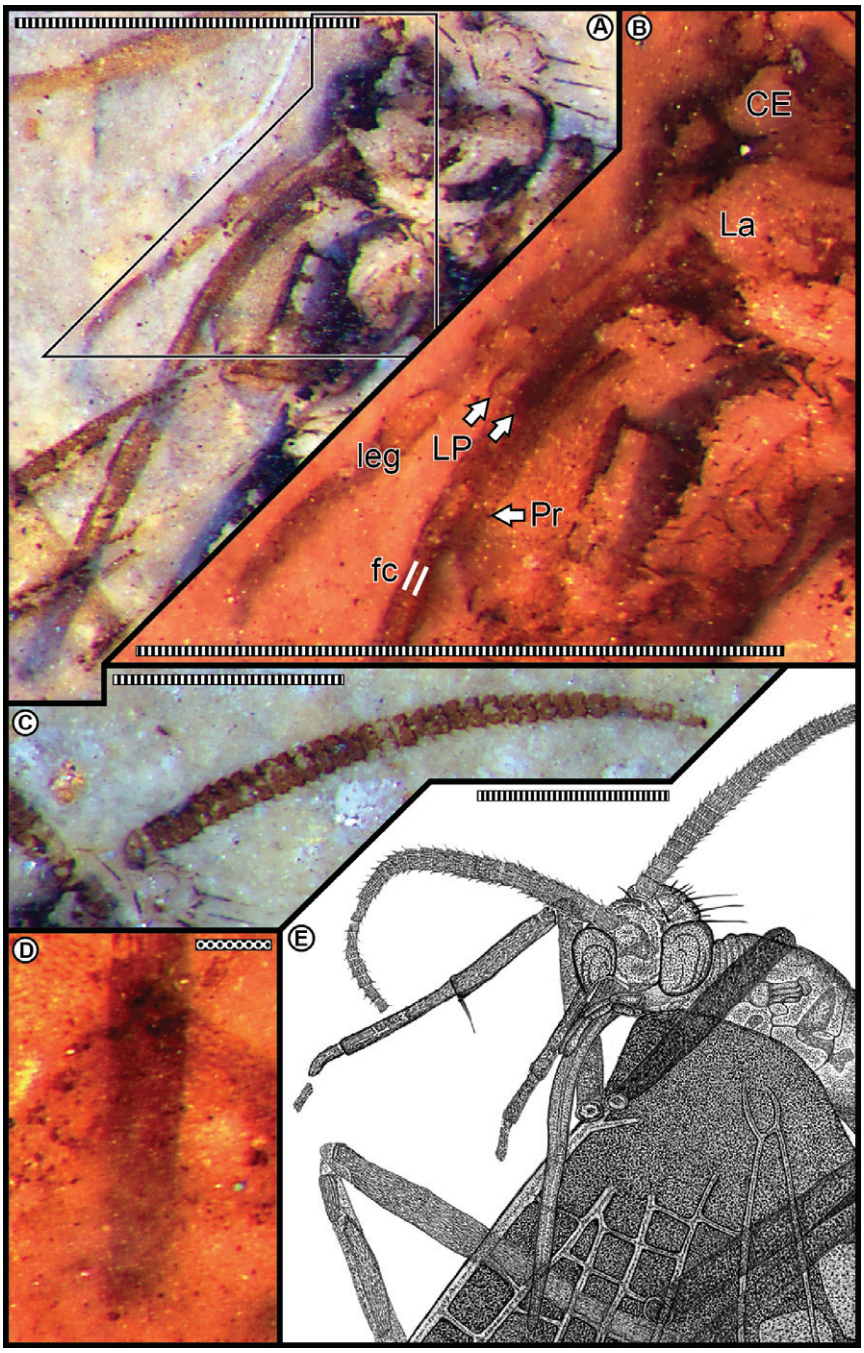

Figure 2. A Head, proboscis, and associated mouthparts **B** Mouthpart detail enlarged from template in **A**, showing base of proboscis (Pr), the tips of both labial palps (LP) at white arrows, labrum (La), and compound eye region (CE) **C** Right antenna **D** Proboscis tip, observed through the wing membrane **E** Camera lucida drawing of head, proboscis and associated mouthparts in **A** using a variety of light sources and angles. Scale bars: stippled, 0.1 mm; striped, 1.0 mm.

Description. A complete, small, female insect (Figs 1A-C); body length (excluding antennae and proboscis) 5.5 mm. Both forewings well-preserved, but hindwings only partially preserved, obscured due to overlap with forewings, thorax and abdomen.

Head and mouthparts. Head capsule spheroidal–prolate, prolonged anteriorly, housing prominent, hemispheroidal, and bulbous compound eyes (Figs 2A, E). Occipital region invested with conspicuously projecting, long bristles and smaller setae. Antennae 2.0 mm long, moniliform, compact and thick, with annulate hairs (Fig. 2C); about same length as proboscis. Each antenna consists of a basal scape and ca. 40 articles; each article bears hairs especially noticeable in profile along its distal annulus; proximal articles about twice as wide as long, distal articles equant. Undefined clypeal region evident below antennal base insertions and above the labrum (Fig. 2B). Mouthparts consistent with previously documented combination for pseudopolycentropodids (but see comments in discussion section below). There is the typical absence of mandibles and maxillary region, and presence of labral and labial elements; in part represented by discernable palps consisting of three articles (Figs 2B, E). Labrum triangular and inconspicuous. A long, decurved, siphonate proboscis 2.0 mm long, labially derived, occurring in an anatomically downturned position that lacks external cuticular ornamentation but bears very fine setae. Proboscis siphon diameter ca. 0.10 mm; housing an inner, eccentrically positioned food canal ca. 0.027 mm in diameter. Proboscis terminus lacks absorptive structures, such as pseudolabellae, related to feeding (Fig. 2D). Two, short labial palps present, adjacent and lateral to the proboscis base, each 0.5 mm long; about one-fourth proboscis length (Fig. 2B). Labial palps composed of three articles, the distal article slightly clavate, with a smooth, rounded terminus, the proximal articles thinner, the proximal-most attached to an enlarged labial area at the ventral base of the head capsule.

Thorax and legs. In lateral aspect pronotum short and neck-like; mesonotum broad, scutellum narrow, metanotum slightly shorter than scutum. Legs entirely covered with pubescence. Right foreleg originating from small, round coxa; long and slender femur (overlapping with thorax) and tibia (overlapping with head); left foreleg (overlapping with mouthparts) intersecting basitarsus of right foreleg and touching left antenna; tibia with at least two apical spurs. Midleg originating from small, round coxa; long and slender femur and tibia; tibia with at least 1 apical spur, tarsi of midleg 5-segmented, basitarsus longest, pretarsus with 1 evident claw. Hindleg originating from round coxa; long and slender femur and tibia; tibia with at least two, long, apical spurs. Tarsi of hindleg 5-segmented, basitarsus longest; length ratio of tibia and basitarsus 1:0.54 for left hind leg. Right hindleg disarticulated between femur and tibia.

Thorax and wings. Forewing broad, 6.1 mm long by 2.4 mm wide; length/width ratio 2.5; apical margin rounded (Figs 1A-D). (By comparison, the forewing length/width ratio is 2.0–2.3 for *Pseudopolycentropus janeannae* and 2.05 for *P. novokshonovi*.) Membrane covered in macrotrichia. Sc short, without anterior branches; base of Sc merging with R apex; Sc reaching C considerably before than Rs origin. Humeral vein absent. Crossvein c–r perpendicular to both R_1 and C, just before wing midsection. R_1 rectilinear at base, slightly arched toward C near wing midsection, coursing into the

distinct pterostigma. Rs stem rectilinear. R_2+R_3 stem abruptly bent at crossvein r–m, then slightly arched toward C, with 2 long branches, R_2 and R_3. R_2+R_3 stem forking earlier than R_4+R_5; R_4 longer than R_2; R_5 longer than R_3. M forking slightly before that of Rs. Thyridium untraceable. M with 5 branches; M_{4+5} forking somewhat before the anterior M_{1+3} branch; M_{2+3} forking at about the same level as R_4+R_5 forking; M_{2+3} stem short and distinct. A crossvein between M_{4+5} stem and CuA, m–cua, near basal dc cell but present after M forking. M+CuA stem distinctly arched. M+CuA forking before R forking into R_1 and Rs. Posterior wing margin almost rectilinear. Hindwing much smaller than forewing, but of similar shape. Right hindwing with only part of R_2+R_3 forking to R_2 and R_3; distal part of R_4 and R_5 preserved and left hindwing with a very short, terminal R_1; basal Rs and part of R_2+R_3 forking to a preserved R_2 and R_3. Distal halves of fore- and hindwings suffused, pterostigma darkened (Figs 1A, 1B, 1D).

Abdomen. Abdomen elongate, tapering apically, with 9 visible segments. Basitergum (T1) fused to metathorax, segments 2-5 distinctly broad. Subgenitalis rectangular in shape and cerci visible (Figs 1B, 1C, 1E).

Locality and stratigraphic horizon. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, middle Jurassic (Bathonian–Callovian boundary interval).

Discussion

Three aspects of this discovery are significant for understanding the ecological roles of Pseudopolycentropodidae with plants in the local ecosystem at Daohugou. First is recognition of the distinct morphological features that separate *Sinopolycentropus* gen. n. from all other coexisting pseudopolycentropodid taxa. Second are the implications that the unique antennal and especially mouthpart modifications have for host-plant use. Last is the importance of rarity in understanding the pollinator associations in an increasingly well-documented, preangiospermous ecosystem from the middle Jurassic.

Distinctiveness of Sinopolycentropus from other Pseudopolycentropodidae

This new, long-proboscid species is distinct from all other members of Pseudopolycentropodidae by several differentiating features. These differences are the base of the Sc vein merging with R vein; the R_2+R_3 vein forking earlier than that of the R_4+R_5 vein; and relatively short, moniliform, and robust antennae bearing hairs on their annulae. To date, all described pseudopolycentropodids have their R_4+R_5 vein forking earlier than that of their R_2+R_3 vein, except for *Pseudopolycentropus triasicus* Novokshonov 1997, which has its R_4+R_5 vein forking at variable levels vs. its R_2+R_3 vein (Papier et al. 1996).

The presence of small, distinctive, three-segmented labial palps is only shared with *Parapolycentropus burmiticus* (Grimaldi et al. 2005). We reinterpret the proboscis sheath and palps of *Parapolycentropus burmiticus* (Grimaldi et al. 2005) as labial, rather than maxillary, in origin (Ren et al. 2009), a tendency in other Antliophora, such as the Diptera (Chaudonneret 1990). However, the proboscis stylets in *Parapolycentropus*, absent in *Sinopolycentropus*, are likely derivatives of maxillary laciniae or galeae.

Typically, pseudopolycentropodids have filiform or moniliform antennae with a relatively high ratio of antenna length to unappendiculate body length. For example, *P. daohugouensis* was reported to have an antenna/body length ratio somewhat greater than 0.37 (2.8/7.5); *P. janeannae* with greater ratios of 0.5 (3.5/7) and 0.57 (4/7); and *P. novokshonovi* with an intermediate ratio of 0.43 (3/7). However, *Parapolycentropus burmiticus* has a distinctively different type of antennae, characterized by a funnel-shaped scape, a scoop-shaped pedicel, the basal five flagellomeres tapered in size and the apical eleven segments significantly more diminutive, forming an arista (Grimaldi et al. 2005), all of which amount to an antenna/body length ratio of 0.4 (1.2/3). By contrast, *S. rasnitsyni* gen. et sp. n. possesses compact, moniliform, and robust antennae, but with a relatively smaller antenna/body length ratio of 0.36. Last, the presence of distinctive, short, three-segmented labial palps, laterally placed at the proboscis base, is a condition not found in other, palpless pseudopolycentropodids, except for *Parapolycentropus* (Grimaldi et al. 2005, Ren et al. 2009).

Significance of Antennal and Mouthpart Modifications

Structural features of the antennae and mouthparts may be relevant for seeking conspecifics and host plants. The unique characteristics of antennal shape, structure and length in *S. rasnitsyni* might be associated with the sensory detection of mates or food sources. The presence of prominent hairs encircling the annular area of each antennal article may be involved in detection of conspecific pheromonal cues or specific chemicals from particular plant hosts. Currently, we cannot draw any conclusions regarding these suggestions, pending scanning electron or high-resolution light microscopy of the antennal hair setal bases and other features. Of more importance are the structure, size, and shape of the proboscis, which indicate that it would have been used for access and imbibition of pollination drops or similar ovulate fluids from a variety of smaller gymnospermous fructifications (Ren et al. 2009, Labandeira 2010). The purpose of comparatively short labial palps, shared only with one other Mid-Cretaceous amber taxon with similar mouthparts and presumed feeding on ovular fluids, could have been for sensory detection of appropriate chemical cues from particular host plants. Such cues would have included fructification exudations or pollination-drop scents, perhaps similar to that of extant insects and their cycad and angiosperm hosts (Pellmyr and Thien 1986, Terry et al. 2004).

The Rarity of Pseudopolycentropodid Pollinators

In the extensive collection of more than 250,000 fossil insect specimens from Daohugou at Capital Normal University, we currently have collected seven specimens of *P. janeannae*, one specimen of *P. novokshonovi*, and a single specimen of *S. rasnitsyni*. This suggests that these three species are extremely rare compared to other, co-occurring insect taxa. Significantly, approximately 20 specimens of small, nonglossate moths also have been found in this collection, of similar size and ecological relationships with plants as the pseudopolycentropodids. This comparison indicates that the ecologically equivalent pseudopolycentropodids are considerably rarer, and by inference, may have had more specialized associations with host plants than those of moths. These low abundances indicate that rarity, indeed, was an important feature of the middle Jurassic Jiulongshan insect fauna and flora, contrary to the viewpoint that rarity was only a feature of angiosperm-dominated biotas from the mid Cretaceous and younger (Vermeij and Grosberg 2010). In addition to the Pseudopolycentropodidae, it also should be noted that two other mecopteran lineages with long-proboscid, siphonate mouthparts—the Mesopsychidae and Aneuretopsychidae—also had likely associations with gymnospermous seed plants, including pollination mutualisms (Ren et al. 2009, Labandeira 2010). The variability of proboscis lengths and widths, diameters of proboscis food canals, and other associated features of the mouthparts, antennae and wings of these three lineages, summarized in Table 1, indicate a similar variety of accessible plant hosts. Although the proboscis of *S. rasnitsyni* is slightly longer than other pseudopolycentropodid species, nevertheless it is within the range of other confamilial taxa, indicating that the Pseudopolycentropodidae were rare, specialized associates of gymnospermous plants during the middle Jurassic at Daohugou.

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Ptychoptera deleta Novák, 1877 from the Early Miocene of the Czech Republic: redescription of the first fossil attributed to Ptychopteridae (Diptera)

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Abstract

The first fossil that was described in Ptychopteridae, *Ptychoptera deleta* Novák, 1877 from the classical Early Miocene locality Mokřina (Krottensee) in western Bohemia is re-examined. The re-description of the holotype including a new line drawing and remarks summarizing the scarce fossil record of this group is provided.

Keywords

Diptera, Ptychopteridae, Ptychoptera, revision, Tertiary, Neogene, Miocene, Ottnangian/Karpatian, Cypris Formation, Cheb Basin, Czech Republic.

Introduction

The family Ptychopteridae is a very small group with about 70 Recent species belonging to two subfamilies (Ptychopterinae and Bittacomorphinae), mostly distributed in the Holarctic, Ethiopian and Oriental Regions. In the Neotropics one species is currently known (Hancock et al. 2006). Ptychopteridae are not present in the Australian and Antarctic Regions. The oldest true representative, *Ptychoptera mesozoica* Kalugina, 1989 was described from the Lower Cretaceous (Neocomian) of Baissa in Buryatia (Siberia, Russia). *Ptychoptera deleta* Novák, 1877, known from the Early Miocene of Mokřina (Krottensee) in western Bohemia (Czech Republic), was the first described fossil representative

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of the family. Handlirsch (1909) supposed that the species did not belong to the genus *Ptychoptera* Meigen, 1803 and created a new genus *Ptychopterula* mainly on the basis of a considerably narrow wing base as present in *Etoptychoptera* Handlirsch, 1909 and a free Sc. However, he emphasized also the common characters present in *Ptychopterula* and the Recent genera *Ptychoptera* and *Bittacomorpha* Westwood, 1835 connection of R and Rs, the position of crossvein r-m, etc. Alexander (1927) also supposed that the species described by Novák did not belong to *Ptychoptera*. Peus (1958), in his monograph on the Ptychopteridae, referred to this species as *Liriope* ("*Ptychopterula*") *deleta* (Novák, 1877). These opinions were based on mistakenly Novak's drawing only, without revision of the holotype (see Fig. 2B). This paper presents a re-description of the holotype including a new line-drawing and photograph. Five other compressed fossil ptychopterid species were described till now: *Ptychoptera miocenica* (Cockerell, 1910) from the Oligocene of Florissant (Colorado, USA) originally placed in genus *Bittacomorpha*; *Brodilka mitchelli* Lukashevich, Coram & Jarzembowski, 2001 and *Zhiganka woolgari* Lukashevich, Coram & Jarzembowski, 2001 both from the Lower Cretaceous of Purbeck and Wealden groups (UK); *Zhiganka comitans* Lukashevich, 1995 from the Lower Cretaceous of Yakutia (Russia), and *Probittacomorpha christenseni* Freiwald & Willmann, 1992 from the lowermost Eocene of Mo-clay (Denmark) (Freiwald and Willmann 1992; Evenhuis 1994; Lukashevich 1995; Ansorge and Schröder 1999; Lukashevich et al. 2001). Two genera, *Zhiganka* and *Probittacomorpha* are attributed to the subfamily Bittacomorphinae and others to Ptychopterinae. A single species, *Ptychoptera eocenica* Podenas, 2007 was described from an Eocene Baltic amber inclusion (Podenas 2007).

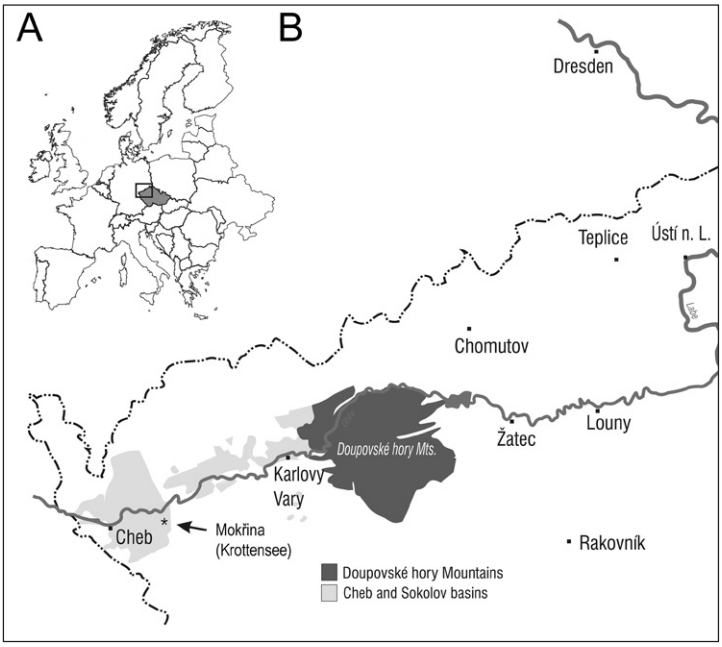

Figure 1. A Geographical position of northwestern Bohemia within Europe **B** detailed map of the Cheb and Sokolov basins with indication of position of Mokřina (Krottensee) locality.

Lukashevich (2008) proposed a new system of Ptychopteroidea and synonymized the family Eoptychopteridae known from the Upper Triassic to Lower Cretaceous with Ptychopteridae. Eoptychopteridae is a considerably variable group of flies with common occurrence throughout the Jurassic up to the Lower Cretaceous (Kalugina 1989; Krzemiński 1992; Lukashevich 1993; Lukashevich et al. 1998; Ren and Krzemiński 2002; Krzemiński and Krzemińska 2003).

Novák (1877) described a fossil entomofauna from Mokřina (Krottensee) located in Cheb county of western Bohemia (Czech Republic) (Fig. 1). This classical Early Miocene locality in Cheb Basin yielded greenish marls of lake sedimentation belonging to the Cypris Formation (Rojík 2004). Fossiliferous layers previously called "Cypris shales" are well known for abundant occurrence of ostracods e.g. *Cypris angusta* (Reuss, 1852) when Cheb and Sokolov basins were interconnected (Obrhelová and Obrhel 1987). Mokřina (Krottensee) locality belongs to biostratigraphic zone MN4 dated by mammals from nearby locality Dolnice (Fejfar 1974), and to ichthyozone IV defined by Obrhelová and Obrhel (1983). Fossil record from Mokřina is also well known by plants and bird remains (Bůžek et al. 1996; Mlíkovský 1996). Novák's collection from Mokřina housed in National Museum in Prague contains 73 insect specimens classified in 10 families of five insect orders (Prokop et al. 2003).

Material and methods

The holotype specimen was observed under stereomicroscope Leica MZFLIII & MZ16 in dry state. The line drawing of the venational pattern was drawn directly using a stereomicroscope and finally readjusted to the photograph scale using image-editing software (Adobe Photoshop CS). Photography was made simultaneously using a digital camera Canon PowerShot S80 attached to the stereomicroscope. The type material referred to as 'NM' is housed at the National Museum in Prague, Czech Republic.

Systematic paleontology

Family Ptychopteridae Osten-Sacken, 1879

Genus *Ptychoptera* Meigen, 1803

http://species-id.net/wiki/Ptychoptera
Figs 2A–C

Ptychoptera deleta Novák, 1877
Ptychoptera deleta Novák, 1877: p. 88, Pl. II, Fig.1.
Ptychopterula deleta (Novák, 1877): Handlirsch (1909): p. 264, 269.
Liriope ("*Ptychopterula*") *deleta* (Novák, 1878): Peus (1958):p. 12, fig. 17.

Type species. *Tipula contaminata* Linnaeus, 1758

Diagnosis. Rs very short; R4+5 five times longer than Rs; R4 nearly as long as R4+5; wing coloration pattern with isolated subapical spot and without spot on R2.

Redescription. Wing with original coloration pattern of dark clouds visible in medial and distal part; Sc rather long, ending opposite proximal third part of R3; R1 long; cross vein r-r (R2) at its about two lengths before tip of R1; Rs very short; R4+5 five times longer than Rs; R4 nearly as long as R4+5; cross vein r-m just before forks of Rs and of M; distal part R5 and most part of medial veins not preserved, cross vein m-cu about its length behind origin of M3+4; A1 rather long, its distalmost section strongly curved to posterior wing margin.

Dimensions. Length of wing fragment about 7 mm, probable total length about 7.1 mm; maximum width about 1.8 mm.

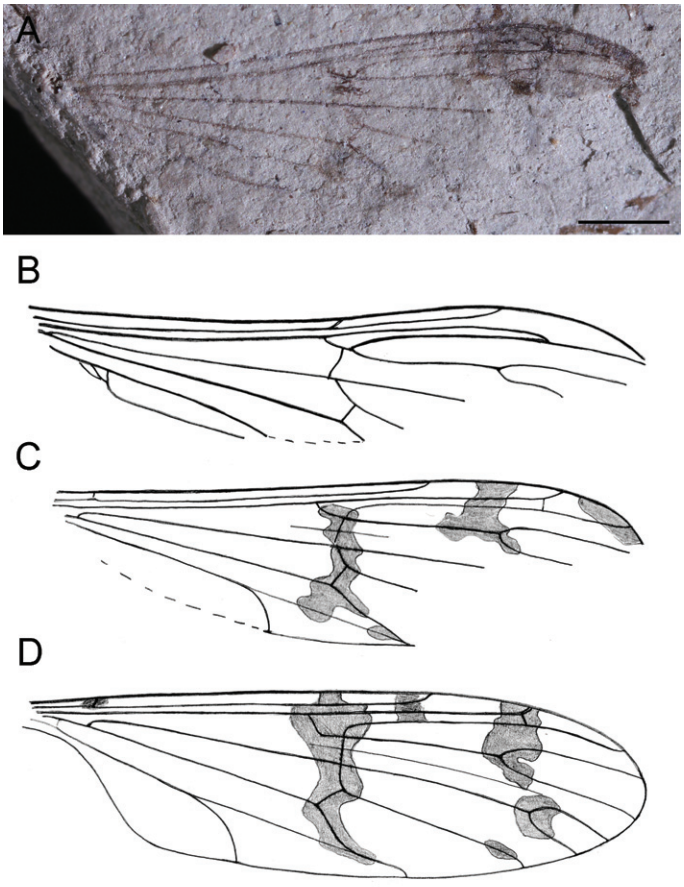

Figure 2 A-C. *Ptychoptera deleta* Novák, 1877 **A** photograph of holotype specimen No. NM-P947 **B** original line drawing of wing venation from Novák (1877) **C** line drawing of wing venation (reconstruction) **D** *Ptychoptera agnes* Krzemiński and Zwick, 1993, drawing of wing venation (scale bar represents 1 mm).

Holotype. No. NM-P947 (imprint of nearly complete wing with medio-apical part missing, posterior wing margin is partially broken, venation well preserved with traces of original pattern of coloration). Specimen is housed in collection of National Museum in Prague, Czech Republic.

Age and layer. Early Miocene (Ottnangian/Karpatian), Cypris Formation (grey claystone) *sensu* Rojík (2004).

Discussion. We provide a re-description of the holotype specimen with several inaccurate characters in wing venation corrected in comparison to the original drawing of Novák, e.g., ending of R1 to anterior wing margin, indication of coloration pattern, A1 basally running parallel to Cu for long distance and ending in posterior wing margin, several missing or present cross-veins. Moreover, we supplement the description by the first photograph of this specimen (unavailable in 1877).

Unfortunately the single diagnostic wing character (M1+2 fork) of the subfamily Ptychopterinae is not preserved. However, the wing venation pattern with very well visible crossvein r-m positioned just before M forking into M1+2 and M3+4, and original color pattern of *P. deleta* show considerable similarities to recent species of *Ptychoptera*. These are distinct apomorphic characters present only in this genus within the family Ptychopteridae. The wing venation of *P. deleta* is somewhat similar to the recent *P. agnes* Krzemiński & Zwick, 1993 described from Hungary (Figs 2C–D). This fact is not surprising due to the Early Miocene age of our fossil (about 18–16 Ma) and considerably high morphological stability of insects (Nel and Prokop 2009; Hörnschemeyer et al. 2009). Finally, our present re-examination of the holotype confirms the great erudition of the Czech pioneer palaeontomologist Dr Ottomar Novák who correctly attributed the fossil species to the otherwise modern genus *Ptychoptera*.

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This paper is devoted to the 75th anniversary of Prof. Alexandr Rasnitsyn, leader of Russian paleoentomological laboratory at Paleontological Institute RAS, Moscow. Authors are grateful to Elena Lukashevich, journal editor Dmitry Shcherbakov (both Palaeontological Institute RAS, Moscow), and anonymous reviewer for their insightful comments and suggestions to the early version of the manuscript. We are grateful to Kamil Zagoršek (National Museum in Praha) for the loan of the holotype specimen and Martin Fikáček (National Museum in Praha) for his kind help with translation from German. Special thank goes to Iwona Kania who kindly helped with scanning of line drawings to digital form. Second author (JP) acknowledges the research support from Grant Agency of the Czech Republic No. 205/08/0643 and Ministry of Education MSM 0021620828.

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New Chironomidae (Insecta, Diptera) with elongate proboscises from the Late Jurassic of Mongolia

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Abstract

Four new species of Chironomidae with well-developed elongate proboscises are described from a Late Jurassic site Shar Teg in SW Mongolia. These are named *Cretaenne rasnicyni* **sp. n.**, *Podonomius blepharis* **sp. n.**, *P. macromastix* **sp. n.**, ? *P. robustus* **sp. n.**

Keywords

Diptera, Chironomidae, fossil, proboscis, feeding, new species, Mongolia, Late Jurassic

Introduction

The present paper continues a series of articles with descriptions of Diptera from the Late Jurassic Shar Teg site (e.g. Kalugina 1992, Lukashevich 2009). The Upper Jurassic lacustrine deposits of Shar Teg Beds outcrop at Ulan Malgait Mt., 4–5 km west of Shar Teg Mt., 100 km ESE of Altai Somon, Gobi-Altai Aimag, SW Mongolia. The fossil assemblage of Shar Teg includes a diverse and abundant complex of flora and fauna (Gubin and Sinitza 1996).

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About 600 identifiable dipteran fossils are known among 3000 fossil insects collected at Shar Teg. Up to now, members of two culicomorph families are described from this locality, Dixidae (Lukashevich 1996) and Chaoboridae (Lukashevich, in press). The representatives of Culicidae and Ceratopogonidae (unknown in Jurassic beds), Simuliidae (rare Jurassic finds) and Thaumaleidae (one fossil from Transbaikalia, J_3–K_1) are not found in Shar Teg.

The Mesozoic records of Chironomidae are numerous, and usually it is the aquatic immatures that are dominant (Kalugina and Kovalev 1985, Jell and Duncan 1986, Kalugina 1993). In Shar Teg, the Chironomidae is one of the most numerically abundant groups: about fifty impressions of adults and twenty pupae and empty pupal exuviae have been collected (undoubted larvae are absent), but due to poor or fragmentary preservation most adults have not been determined even to subfamily. Therefore only several specimens are described herein (pupae will be described later). This chironomid assemblage "very much resembles the stranded corpses of adults and pupae left beside a falling stream, or on the wave swept shore of a lake" (P.S. Cranston, pers. comm.).

The adults of nearly all extant chironomid midges have reduced mouthparts and so their common name is "non-biting midges". However the presence of toothed mandibles in a chironomid midge was recognized first by Downes and Colless (1967), and now they are described in two recent genera of Podonominae, *Archaeochlus* Brundin, 1966 and *Austrochlus* Cranston, 2002 known only from Australia and southern Africa (Cranston et al. 1987, Cranston et al. 2002). Their mandibles closely resemble those of many insectivorous predatory Ceratopogonidae such as *Probezzia* Kieffer, 1906; however, until females are observed feeding, the question will remain unresolved. A culicomorphan of uncertain affinity with a long proboscis is described from the Upper Triassic Cow Branch Formation (Late Carnian) of Virginia, USA (Blagoderov et al. 2007). Recently, functional mandibulate mouthparts are reported in females (and sometimes even in males) of several extinct genera of Chironomidae from Early Cretaceous Lebanese amber (Azar et al. 2008).

New chironomids with biting mouthparts from Shar Teg are described herein. These fossils are housed in the Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). Photographs were made using a Leica MZ 9.5 stereomicroscope with a Leica DFC420 digital camera, with further correction using Adobe Photoshop® CS 9.0 software. Measurements were made with an ocular micrometer in a Leica stereomicroscope. Morphological terminology and measurements mainly follow Sæther (1980). Vein nomenclature is after Wootton and Ennos (1989), followed by Shcherbakov et al (1995): the chironomid veins traditionally named MCu and An are in fact bM_{3+4} (*tb* of Kalugina) and CuP, respectively. For further details regarding the mentioned fossil localities, see Rasnitsyn and Quicke (2002).

Systematics

Family Chironomidae Newman, 1834
Subfamily ?Aenneinae Ansorge, 1999

Genus *Cretaenne* Azar, Veltz & Nel, 2008
http://species-id.net/wiki/Cretaenne

Cretaenne Azar et al. 2008: 688. Type species *Cretaenne kobeyssii* Azar et al. 2008: 689.

The genus was established based on two species from Early Cretaceous Lebanese amber. The specimens under description are assigned to this genus due to functional blade-like laciniae and mandibles in females, postnotum with a longitudinal groove, reduced hind tibial comb, and peculiarities of wing venation (vein C long and reaching wing tip; Sc not terminating in wing margin; R_2 present; cell between divergent R_{2+3} and R_{4+5} very broad; R_{4+5} almost straight; bM_{3+4} present; *r-m*, bM_{3+4} and *m-cu* aligned; *m-cu* connecting CuA proximal to *r-m*). In the new species, tibial spurs are probably present; however, their structure remains unclear due to the state of preservation. The structure of claws is important for the determination of Lebanese species, but claws are not visible in the Mongolian specimens as well as the details of chaetotaxy (e.g., on pedicel) and therefore not mentioned in the description.

***Cretaenne rasnicyni* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Cretaenne_rasnicyni

Etymology. Named in honour of an outstanding Russian palaeoentomologist Dr A.P. Rasnitsyn.

Material examined. Holotype: part and counterpart of well-preserved female PIN 4270/2379±, SW Mongolia, Shar Teg (443/1); Late Jurassic. **Paratypes:** impressions of two females PIN 4270/2367±, 2459, from the same outcrop.

Diagnosis. The new species is distinguished from both known species of *Cretaenne* by the longer proboscis (more than half of the head height and about twice the clypeus height) and the longer Rs stem.

Description. Female. *Measurements* (mm): Total length 2.1–2.7 (holotype 2.3); thorax length ca. 0.8, width ca. 0.4; wing length 2.1–2.3 (holotype 2.1); abdomen length 1.35–1.8 (holotype 1.5). Total length / wing length 1.1.

Holotype (Figs 1a–d, 2b–c). *Coloration*. Thorax dark, abdomen and legs lighter, at least some legs with slightly darker apices of femora and tibiae. *Head* ca. 550 μm wide, ca. 400 μm high to lower eye margin. Scape ca. 100 μm, pedicel ca. 30 μm in diameter. Clypeus ca. 200 μm wide, ca. 250 μm high. Proboscis with visible part ca. 350 μm long

(possibly, without apex), tapering, sclerotized. *Thorax*. Postnotum wider than long, ca. 200 μm long, possibly with longitudinal median groove. *Wing* longer than abdomen, Sc clearly up to Rs level, thinning distally, possibly not reaching C (apical part of Sc not discernible). Vein C and radial veins strong, coloured (R_{2+3} thinner then others), as well as proximal sections of M and CuA, *r-m* and bM_{3+4}. Long stem Rs subequal to *r-m*; R_{4+5} 8–9 times as long as Rs; R_2 distinctly longer than dR_1. VR 1.1. *Legs* (lengths not measurable). Femora (mid- and hind) widened to apex, maximum 120 μm wide, with thin sclerotized ridge ventrally near apex. Tibiae (mid- and hind) apically 80–100 μm wide. Tarsi not preserved. *Abdomen*. Abdominal segments II–V: ca. 200 μm long, 500–600 μm wide. Three large subequal oval sclerotized spermathecae 140–150 μm long, ca. 100 μm wide, with necks (probably, short). Gonapophysis IX distinctly visible, sclerotized, with notum ca. 200 μm long, 15 μm wide at anterior end, with rami ca. 60 μm long. Probable gonocoxites VIII (gonacoxapodemes?) visible as moderately sclerotized small oval lobes near posterior end of notum. Cerci short, hardly visible.

Paratypes (Figs 1e–h, 2a). Visible characters as in holotype, with following additions. *Head* preserved only in PIN 4270/2367, 650 μm wide, 850 μm high with proboscis, ca. 400 μm high to lower eye margin. Eyes with medially narrowing dorsomedial extension, well separated by 60 μm. Coronal triangle ca. 130 μm high, ca. 100 μm wide; coronal suture clear, probably pair of poorly visible ocelli (ca. 30 μm in diameter) adjoining lower part ventrally to eye dorsomedial extension. Scape ca. 100 μm, pedicel ca. 40 μm in diameter. Flagellomeres (five distinctly visible lateral to eye margin) short-oval, 50–70 μm long, 30–40 μm wide. Clypeus ca. 200 μm wide, ca. 300 μm high. Proboscis ca. 550 μm long, sclerotized, stylet-like, pointed, with blade-like tapered laciniae and mandibles, labrum apically more sclerotized. Palpi poorly visible, looking widened (ca. 70 μm in distal parts); visible parts of palpi reaching about 4/5 of proboscis. *Thorax*. Scutum weakly, evenly convex; anterior part ca. 300 μm wide. Antepronotals narrowed medially. Scutellum ca. 120 μm long; postnotum ca. 200 μm long, 300 μm wide, with distinct longitudinal median groove. *Legs*. Measurements (μm). p_1(?): ti 880, ta_{1-5} 1200; p_2: ti 1375, ta_1 750–850, ta_2 ca. 400, ta_{3-5} ca. 700, LR2 0.55; p_3: fe 1000, ti 1450–1500, $ta_{1-5} > 1250$. Tibiae 60–100 μm wide near apex. Apices of mid-, hind tibiae with combs of separate spiniform setae (visible only in PIN 4270/2459): midtibia with no less than 3–4 slenderer setae ca. 50 μm long, hind tibia with no less than 3 thicker setae, longest ca. 50 μm. Hind tibia probably with two spurs, 70 and 50 μm long.

Remarks. The pattern of the female mouthparts is poorly visible in the holotype and unknown in paratype PIN 4270/2459; paratype PIN 4270/2367 has a well-preserved proboscis and its wing venation is very pale and incomplete; the setae at the tibial apices are distinctly visible only in paratype PIN 4270/2459; in both paratypes the spermathecae are not visible. Hence it is possible that these specimens are not conspecific. However, we suggest that all these specimens belong to the same species due to visible peculiarities of venation (particularly the long Rs stem and R_2 position).

The genus *Cretaenne* was described in the subfamily Aenneinae with reservations, due to the vein Sc not terminating in the wing margin and short Rs stem, as distinct from the

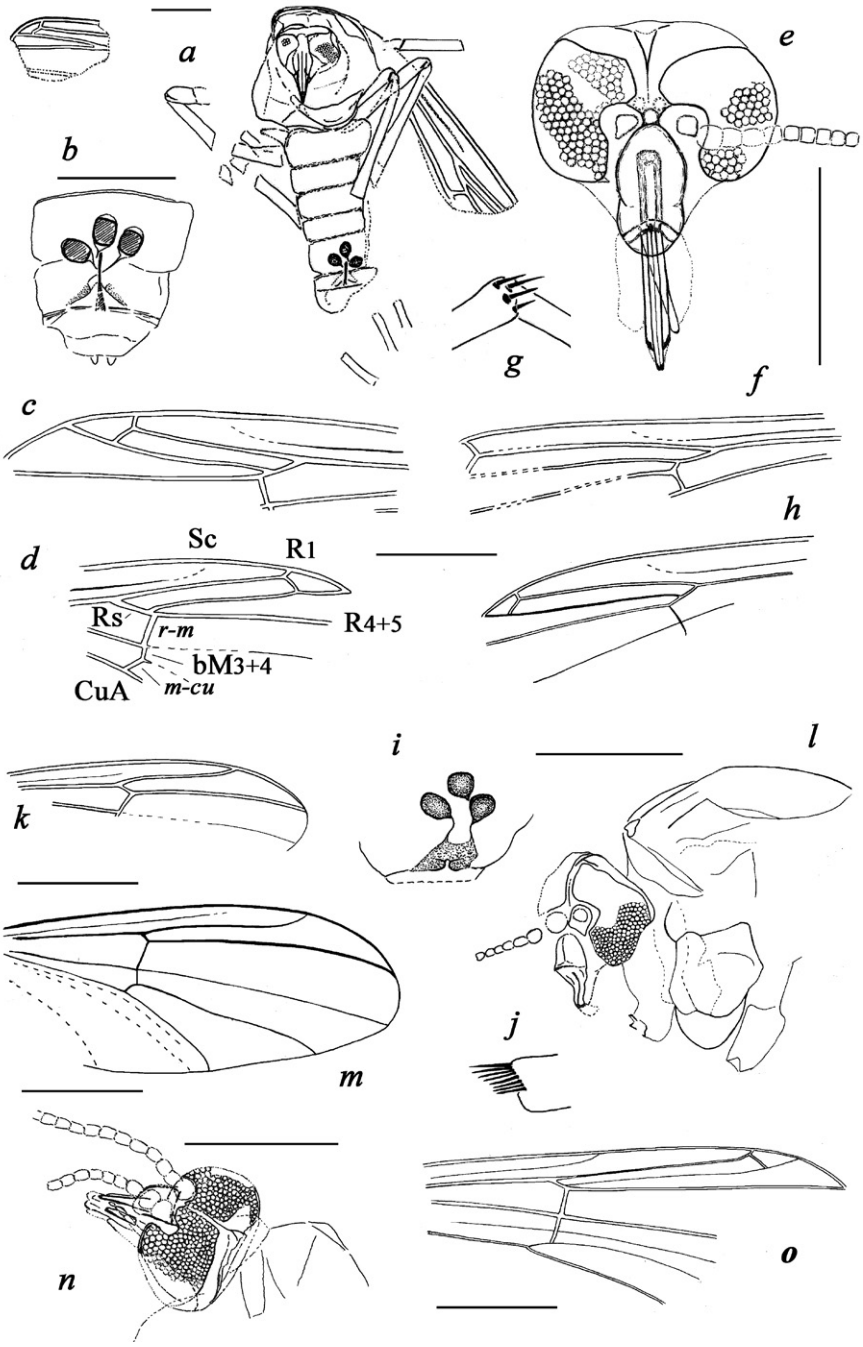

Figure 1. a–h *Cretaenne rasnicyni* sp. n. **a–d** holotype (**a** total habitus **b** abdominal apex **c, d** wings) **e–f** paratype PIN 4270/2367 (head and wing) **g–h** paratype PIN 4270/2459 (apex of midtibia and wing) **i–l** *Podonomius blepharis* sp. n., holotype (**i** abdominal apex **j** hind tibial apex **k** wing **l** head and thorax) **m–n** *P. macromastix* sp. n., holotype (wing and head) **o** Tanypodinae inc. sed., PIN 4270/2324; all from Shar Teg, J_3. Scale bar 0.5 mm except for **g**, **j** without scale.

type genus of the subfamily, *Aenne* Ansorge, 1999 from the Late Triassic and Early Jurassic of Europe (Krzeminski and Jarzembowski 1999, Azar et al. 2008). In the new species from Shar Teg, the stem Rs is long without doubt but Sc is clear only to the level of the first Rs bifurcation, then sharply thins out and possibly does not terminate in C, as seen in *Cretaenne*. We did not reexamine the type material of *Aenne* and *Cretaenne*, but according to the published data, Rs length can vary within species: in *Aenne liasina* Ansorge, 1999, the relatively long Rs is longer or shorter than *r-m* (Ansorge 1999: figs 6–7), whereas the distal thinning of Sc is not recorded. Consequently, the new species is described here as a member of *Cretaenne* due to several features unknown for *Aenne* (described from isolated wings only), viz. a reduced hind tibial comb, the postnotum with a longitudinal groove, the structure of well-developed extended proboscis, and, probably, spurs on middle and hind tibia. Actually, biting mandibles were reported for the Mesozoic *Aenne* with reference to unpublished data of Cranston (Grimaldi and Engel 2005: 504).

Subfamily Podonominae Thienemann & Edwards, 1937

Genus *Podonomius* Kalugina, 1985

http://species-id.net/wiki/Podonomius

Podonomius Kalugina and Kovalev 1985: 101. Type species *Podonomius tugnuicus* Kalugina and Kovalev 1985: 102.

The genus was described for six species from the Early and Middle Jurassic of Siberia, with only two species being attributed with certainty. Later, one more species from the Early Jurassic of Germany was tentatively included (Ansorge 1996). The specimens under description are assigned to this genus due to their broad head, large reniform eyes with dorsomedial projection, short thorax (no longer than its height), narrow scutellum, short postnotum, three rounded sclerotized spermathecae, and peculiarities of venation (vein C long, reaching R_{4+5} tip; Sc not terminating in wing margin; R_{2+3} absent; R_1 long, not thickened distally in female; R_{4+5} straight or only slightly curved down distally; bR_{4+5} and *m-cu* inclined to long wing axis; *r-m*, bM_{3+4} and *m-c*u aligned; *r-m* much longer than bM_{3+4}; cell *ba* and *bp* not symmetrical; *m-cu* connecting Cu proximal to *r-m*; costal and radial veins, stem M and CuA, *r-m*, bM_{3+4} and *m-cu* thickened, other veins very thin and pale; wings without spots).

We re-examined the type material of the six species described by Kalugina (1985) from Siberia (Fig. 2i) but did not examine ?*P. tumidus* Ansorge, 1996 from Grimmen. A postnotum without longitudinal median groove was recorded in the original diagnosis of *Podonomius* (for German species, such information was absent; Ansorge 1996). This feature is known only in Aphroteniinae and Podonominae and unknown in Tanypodinae and Buchonomyiinae (Brundin 1966, Murray and Fittkau 1989, Sæther 1989). Unfortunately it is impossible to see this important character in the new specimens, in particular, due to the lateral position of impressions. Pubescence and setae of their bodies are also not visible on any specimens described here.

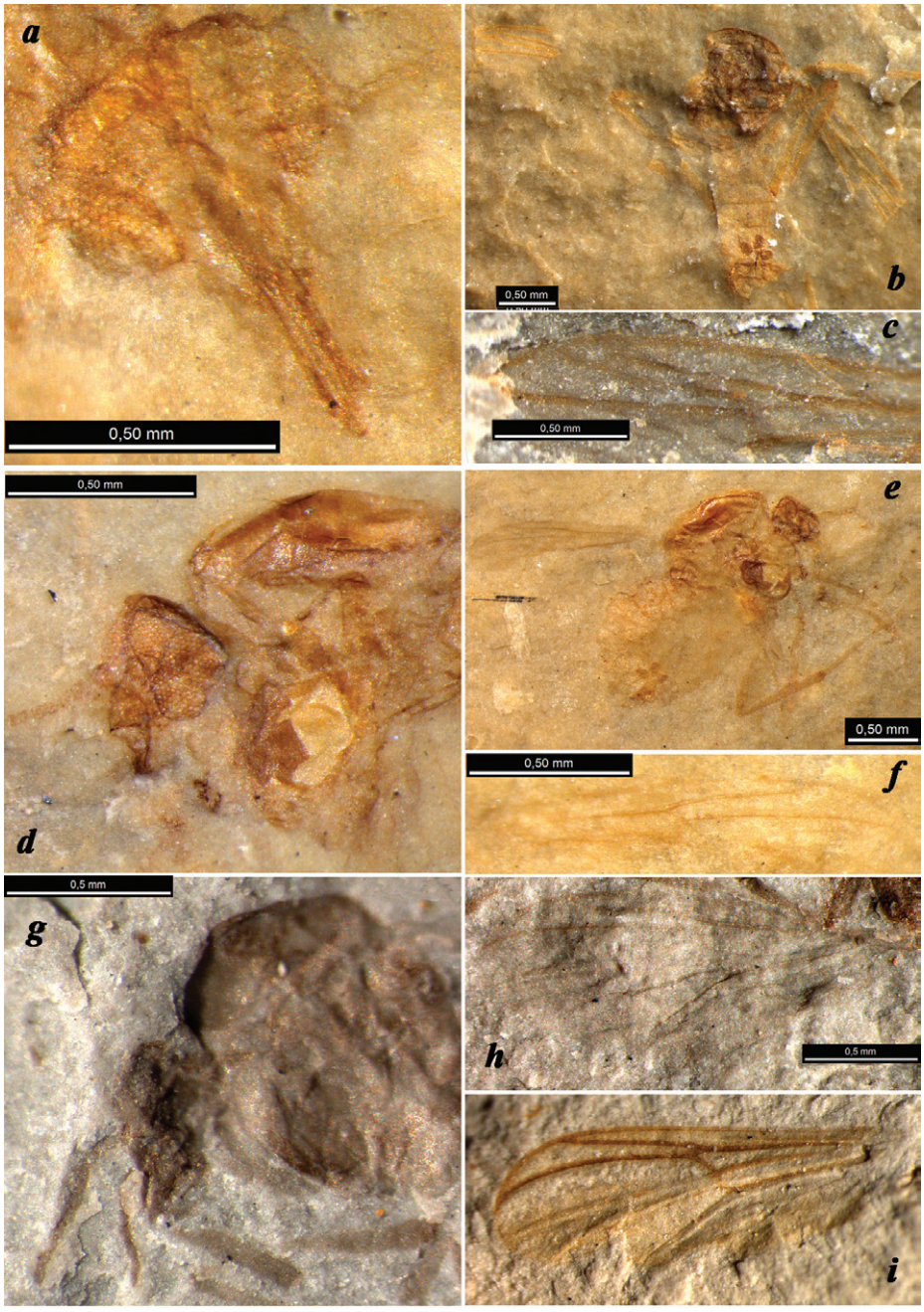

Figure 2. Jurassic Chironomidae: **a–c** *Cretaenne rasnicyni* sp. n. (**a** paratype PIN 4270/2367, female head under alcohol **b–c** holotype **b** female habitus, positive impression under alcohol **c** wing, negative impression) **d–f** *Podonomius blepharis* sp. n., holotype (**d** female head and thorax, negative impression under alcohol **e** female habitus, positive impression under alcohol **f** wing, negative impression under alcohol) **g–h** *P. macromastix* sp. n., holotype (female head and wing); all from Shar Teg, J_3 **i** holotype of ?*P. rotundatus* Kalugina, 1985, Kubekovo, J_2.

***Podonomius blepharis* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Podonomius_blepharis

Etymology. From Greek "blepharis" for eyelash, after the pattern of the tibial comb.

Material examined. Holotype: part and counterpart of well-preserved female PIN 4270/2357±, SW Mongolia, Shar Teg (443/1); Late Jurassic.

Diagnosis. The new species is distinguished by its small size (wing length l.4 mm), well-developed elongate proboscis, weakly convex scutum without a hump, wing with broad cell *c,* and pale legs with darker junction of femur with trochanter and tibia, and with combs of dark closely-spaced spiniform setae at tibial apices.

Description. Female (Figs 1i–l, 2d–f). *Measurements* (mm): Total length 2.0; thorax length 0.8, height 0.9; abdomen length 1.0; wing length 1.4. Total length / wing length 1.4. *Coloration*. Head and thorax dark, abdomen lighter, legs pale with darker junction of femur with trochanter and tibia, with darker apices of tibiae. *Head* no less than 600 μm wide, no less than 550 μm high with proboscis, 380 μm high to lower eye margin. Eyes large, with wide dorsomedial extension, looking narrowly separated by ca. 30 μm. Facets equal. Coronal triangle ca. 100 μm high, coronal suture clear near upper eye margin. Scape 90 μm, pedicel 45 μm in diameter; proximal flagellomeres short-oval to rounded, ca. 35 μm wide and 40–50 μm long. Clypeus ca. 100 μm wide, ca. 150 μm high, possibly with longitudinal groove. Proboscis well-developed, elongate, sclerotized at least in distal part, ca. 200 μm long (projecting distally of clypeus for no less than 120 μm), ca. 30 μm wide at visible apex. *Thorax*. Scutum weakly, evenly convex, without hump or tubercle. Scutellum ca. 150 μm long, not projecting. Postnotum ca. 200 μm long. *Wing*. Vein C probably not produced beyond R_{4+5}; cell *c* at *r-m* level subequal to cell r_1, which only slightly narrower than r_5 cell at level of R_1 tip; R_1 approximately 2/3 as long as almost straight R_{4+5}; *r-m* inclined to M. All veins mentioned strong, coloured. *Legs*. Measurements (μm). p_1(?): ta_1 380, ta_{2-5} ca. 405; p_2: fe 700, ti 680; p_3: fe 560, ti 680, ta_1 ca. 500, ta_{2-5} ca. 650, LR_3 ca. 0.75. Femora maximum ca. 110–120 μm wide, with thin sclerotized ridge ventrally near apex. Tibiae ca. 80 μm wide. Apices of mid-, hind tibiae with combs of dark closely-spaced spiniform setae ca. 50 μm long; in midtibial comb, no less than 10 setae, in hind tibial comb, 8 setae. Spurs not observed. *Abdomen*. Segments III–VII: tergites 150–180 μm long. Three large subequal oval moderately sclerotized spermathecae 100 μm long, ca. 80 μm wide, with necks (probably, long), in compact group. Sternite VIII with posteromedian sclerotized plate, its posterior margin bilobate; probable gonocoxites VIII (gonacoxapodemes?) visible as moderately sclerotized small oval lobes approximating each other. Cerci not visible.

Remarks. The new species is similar to *P. splendidus* Kalugina, 1985 ($J_{1/2}$, Novospasskoye, Transbaikalia) in its venation (C length, ratio R_1/ R_{4+5}), colour pattern of legs and elongated mouthparts, which are visible on paratype PIN 3000/1857 (in the other type specimens of *Podonomius* from Siberia, the mouthparts are not visible due to the state of preservation). *Podonomius blepharis* sp. n. differs from *P. splendidus* in broader cell *c* and smaller size. As for tibial combs, Kalugina noted (1985) that in *P. tugnuicus*

and *P. splendidus* the tibial apices are darkened but without mentioning combs. According to our re-examination of the type material of *P. splendidus*, the hind tibia has a reduced comb consisting of a row of separate dark points, which may be minute setae or possibly bases of missing long bristles (these seem to be visible near the tibial apex in the holotype). In the latter case, a well-developed tibial comb is not unique for *P. blepharis*.

***Podonomius macromastix* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Podonomius_macromastix

Etymology. From Greek "makros" for long and "mastix" for whip, after the long antenna.

Material examined. Holotype: part and counterpart of well-preserved female PIN 4270/2314±, SW Mongolia, Shar Teg (423/6); Late Jurassic.

Diagnosis. The new species is distinguished by its small size (wing length 1.9), well-developed elongate proboscis, strongly convex scutum with a hump, comparatively long wings with R_1 with arched tip and broad cell r_5, and pale legs with darker junction of femur with trochanter and tibia.

Description. Female (Figs 1m–n, 2g–h). *Measurements* (mm): Total length 2.0; thorax length 0.7, height 0.9; wing length 1.9, width 0.8; abdomen length 1.1. Total length / wing length ca. 1.05. *Coloration* pattern as in *P. blepharis* sp. n. *Head* 480 μm wide, no less than 600 μm high with proboscis, 380 μm high to lower eye margin. Eyes large, with wide dorsomedial extension, narrowly separated by ca. 30 μm. Facets slightly increasing to lower eye parts. Coronal triangle ca. 50 μm high, coronal suture ca. 80 μm high. Antenna no less than 600 μm. Scape ca. 80 μm, pedicel ca. 60 μm in diameter; at least 12 flagellomeres, ca. 35 μm wide (proximal 6 flagellomeres moniliform, 40–45 μm long; others cylindrical, 50–70 μm long). Clypeus ca. 130 μm wide, ca. 150 μm high. Proboscis well-developed, elongated, tapering, ca. 180 μm long (about 1/3 of head height), ca. 70 μm wide at visible apex, with pair of separate sclerotized blades. *Thorax*. Scutum strongly convex, with hump before midlength, 700 μm long. Postnotum ca. 200 μm long. *Wing* much longer than abdomen. Vein C only slightly produced beyond $R_{4+5,}$ not reaching wing tip; cell *c* at *r-m* level broader than cell r_1, which is almost half as wide as cell r_5 at R_1 tip level; R_1 with arched tip, 2/3 as long as slightly curved down distally R_{4+5}; *r-m* slightly inclined, bM_{3+4} almost perpendicular to M. *Legs* poorly visible. Measurements (μm). p_2(?): fe ca. 550, ti ca. 700, ta_{1-5} ca. 700; p_3(?): ti ca. 870, ta_{1-5} > 800. Hind femora ca. 110 μm wide; hind tibiae 70–80 μm wide at apex, with sclerotized apical traces, possibly of setae bases. *Abdomen* with three large unequal short-oval sclerotized spermathecae 60–90 μm long, 50–60 μm wide, with necks, in compact group. Cerci ca. 40 μm long.

Remarks. The new species is similar to ?*P. rotundatus* Kalugina, 1985 (J_2, Kubekovo, South Siberia, Fig. 2i) in its venation (length of C, R_1/R_{4+5} ratio, cells r_1/r_5 ratio) and size, but is distinguished by the arched tip of R_1. The new species differs from *P. blepharis* sp. n. in the longer wings with broader cell r_5 and thoracic shape.

? *Podonomius robustus* sp. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Podonomius_robustus

Etymology. From Latin "robustus" for stout, after the total habitus.

Material examined. Holotype: Part and counterpart of partly preserved female PIN 4270/2254±, SW Mongolia, Shar Teg (443/1); Late Jurassic.

Diagnosis. The new species is distinguished by its medium size (wing length 3.7 mm), well-developed, strongly elongate proboscis, wing with C produced beyond R_{4+5} and reaching wing tip, strongly sclerotized abdomen and legs, and one spermatheca situated proximally of other two.

Description. Female (Fig. 3). *Measurements* (mm): Total length 4.1; thorax length 1.5, width ca. 1.0; abdomen length 2.9; wing length 3.7. Total length / wing length 1.1. *Coloration*. Head, thorax, abdomen, legs uniformly dark. *Head* 700 μm wide, no less than 1100 μm high with proboscis, 550 μm high to lower eye margin. Eyes large, with wide dorsomedial extension, well-separated by ca. 100 μm. Facets equal. Frontal strip between eye extensions dark-coloured, long, sclerotized. Coronal triangle ca. 100 μm high, coronal suture ca. 70 μm high. Scape ca. 125 μm, pedicel ca. 40 μm in diameter. Clypeus ca. 200 μm high, ca. 150 μm wide. Proboscis very long, strong (longer than remainder of head), tapering, ca. 550 μm long, ca. 80 μm wide at (visible) apex; apical part with pair of sclerotized blades. Probable palpi no less than 400 μm long, two visible segments elongate, cylindrical, ca. 150 μm long, ca. 30 μm wide. *Thorax*. Scutum 900 μm long; postnotum ca. 250 μm long. *Wing* clearly longer than abdomen. Vein C produced beyond R_{4+5} (costal extension ca. 200 μm), reaching wing tip; cell *c* at *r-m* level broader than cell r_1; cell r_5 at R_1 tip level almost twice as wide as cell r_1; R_1 straight, 2/3 as long as R_{4+5}. Vein C, radial veins, M, *r-m* strong and coloured; other veins thin, pale. *Legs*. Mid- and hind femora ca. 180 μm wide; tibiae 100–120 μm wide near apex. Apex of mid- or hind tibia with traces of at least 5 spiniform setae. *Abdomen*. Segments II–VIII 250–300 μm long, 800–900 μm wide. Three rounded sclerotized spermathecae 70–90 μm in diameter, with long necks, largest spermatheca situated proximally of other two. Gonapophysis IX distinctly visible, sclerotized, with notum ca. 200 μm long and rami ca. 50 μm long. Posterior margin of sternite VIII bilobate: probable gonocoxites VIII (gonacoxapodemes?) visible distal to spermathecae. Cerci distinct, elongate-oval, 150 μm long, ca. 70 μm wide.

Remarks. Adults of this new species are the largest among *Podonomius* (wing length is similar only in ?*P. simplex* Kalugina, 1985 (J_2, Kubekovo, South Siberia), but in the Siberian species R_1 is curved up distally). ?*Podonomius robustus* sp. n. differs from other species from Shar Teg also in the longer costal extension. Such a long costa extending to the wing tip is an important plesiomorphic character (Brundin 1976) and may be a character of generic value. Thus, the new species is only tentatively placed in *Podonomius*.

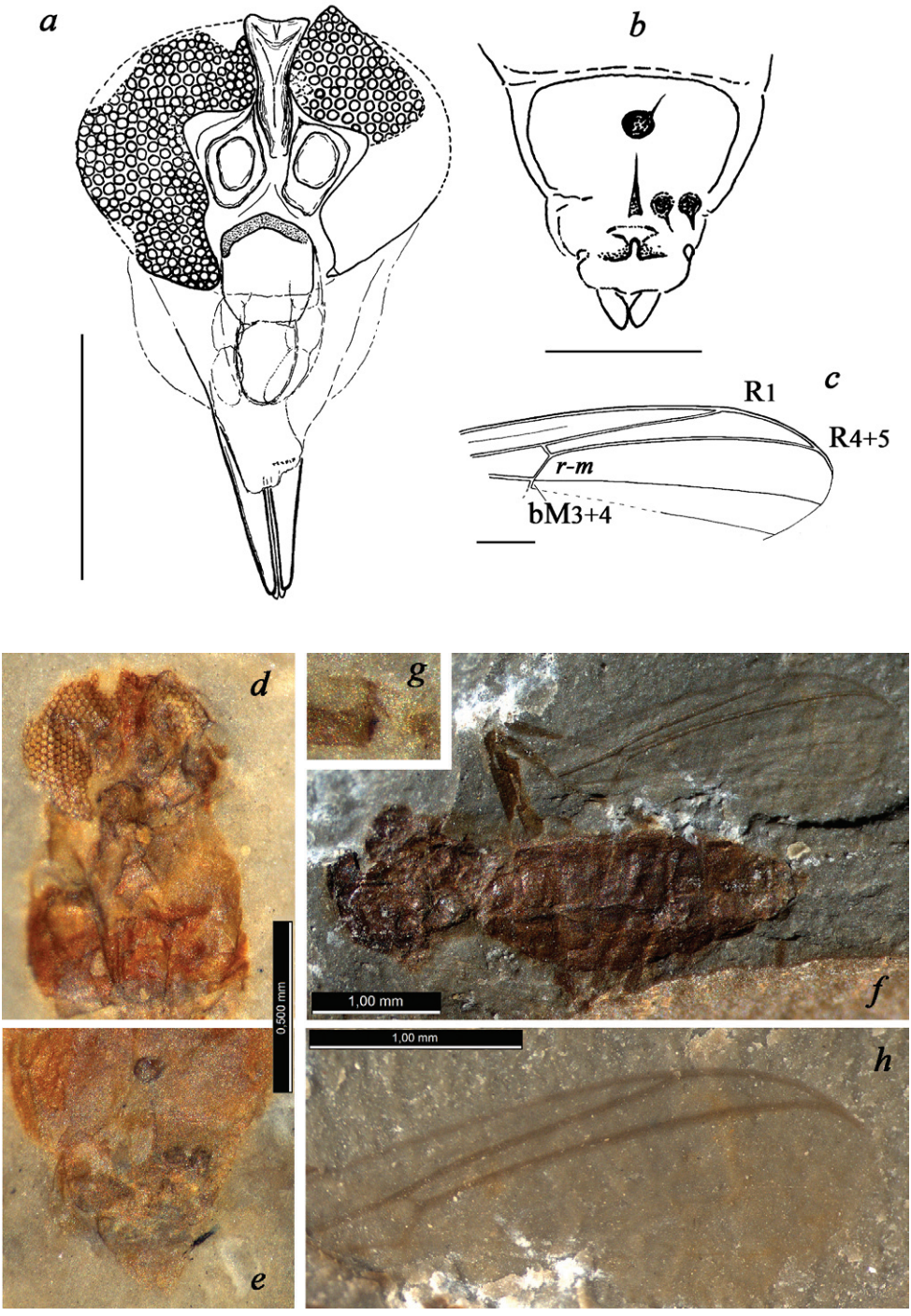

Figure 3. ?*Podonomius robustus* sp. n., holotype (**a, d** head, positive impression **b, e** abdominal apex, negative impression **c, h** wing, negative impression **f** female habitus, negative impression **g** apex of hind tibia, positive impression; all photos made under alcohol except for **f**); Shar Teg, J_3. Scale bar 0.5 mm

Subfamily Tanypodinae Skuze, 1889

Among fifty adult chironomids from Shar Teg, only two incomplete females (PIN 4270/2324±, 4270/2431) and one male (PIN 4270/2384) can be determined as members of this subfamily (all from the same 443/1 outcrop) due to the typical venation on partly preserved wings (Fig. 1o). The poor state of their preservation does not allow us to place the specimens within a genus.

Discussion

The four new species of Chironomidae described in this paper are characterized by the elongate proboscis with well-developed (probably sclerotized) mandibles and/or maxillae. To date, a well-developed piercing proboscis has been described only in two recent and no less than four extinct genera of the Chironomidae (Azar et al. 2008). Among the recent Chironomidae, strongly elongate mouthparts are known also in some Orthocladiinae, namely, in both sexes of the North American species *Pseudorthocladius macrostomus* Soponis, 1980 and *Rhinocladius* Edwards, 1931 (all three species; distributed in South America and Australia). Their proboscis, superficially resembling that of a mosquito, is formed entirely of the extremely elongated labellae, devoid of stylets and presumably used for sipping nectar, not for piercing (Edwards 1931, Freeman 1961, Soponis 1980). Possibly, a poorly described species *Camptocladius nigripectus* Bigot 1888 has a similar type of the proboscis (Edwards 1931).

The proboscises of *Cretaenne rasnicyni* sp. n. and ?*Podonomius robustus* sp. n. are much longer than in any other fossil Chironomidae described to date (possibly except for an undeterminable culicomorphan from the Triassic Cow Branch Formation; Blagoderov et al. 2007). Among the Chironomoidea, similar strongly elongate mouthparts are known in a number of recent species in many genera of Ceratopogonidae belonging to different lineages of this family, such as *Culicoides* Latreille, 1809, *Echinohelea* Macfie, 1940, *Atrichopogon* Kieffer, 1906, *Forcipomyia* Meigen, 1818, *Leptoconops* Skuse, 1889, as well as in extinct species such as the Lower Cretaceous *Protoculicoides skalskii* Szadziewski, Arillo, 1998, *P. punctus* Borkent, 2000, and the Upper Cretaceous *Culicoides filipalpus* Remm, 1976 (e.g. Borkent 2000, Borkent et al. 2009). In nearly all Ceratopogonidae with such mouthparts, females are either insectivorous predators, or blood-suckers on vertebrates, or haemolymph-suckers on insects. However, haemolymph-sucking is restricted to Forcipomyiinae and considered derived feeding mode which appeared in the Cenozoic (Borkent 2000). Nectar-feeding ceratopogonids usually have the stylets more or less reduced, but *Forcipomyia (F.) brevipennis* (Macquart, 1826) considered nectarophagous retains the sclerotized, distinctly toothed mandibles subequal in size to piercing mandibles of its insectivorous congeners (Glukhova 1981). By analogy with Ceratopogonidae we assume that the females of the new chironomid species were entomophagous or haematophagous but secondary nectarophagy cannot be excluded. It is impossible to argue for one of these feeding types, because the fine details of the mouthparts are not discernible in our fossils.

In the general appearance (very long and strong proboscis, body size, shape and proportions; pattern and degree of sclerotization, e.g. strongly sclerotized abdomen and legs) ?*P. robustus* differs from "typical" Chironomidae as well as from other species assigned to the genus *Podonomius* and resembles some "robust" Ceratopogonidae, especially many Palpomyiini, but this advanced tribe is unknown from the Mesozoic (Szadziewski 1996). Unfortunately, the posterior part of the wing is not visible in the holotype of ?*P. robustus*, as well as in the holotype of *P. blepharis* sp. n., and the presence of a forked M_{1+2} (characteristic of Ceratopogonidae) cannot be excluded. Thus, the position of these two species seems to be somewhat uncertain. Similar female wings bare of macrotrichia, with well-developed single radial cell, costal ratio more than 0.9 and vein C produced beyond R_{4+5} and almost reaching wing tip, are known in several Cretaceous species of the ceratopogonid genus *Protoculicoides* Boesel, 1937, such as *P. schleei* (Szadziewski, 1996) and *P. unus* Borkent, 2000 from Lebanese amber (Borkent 2000).

However, in the holotype of ?*P. robustus* the partly visible transverse vein under *r-m* is undoubtedly coloured, that is not recorded for the basal part of vein M_2 in ceratopogonid wing, but typical for bM_{3+4} in podonomine wing (Figs 2h–i). In addition, the venation pattern of the anterior part of the wing is more similar to Podonominae than to Ceratopogonidae (vein R_1 long, cell r_1 long and not narrow) and the vertex of *P. blepharis* as well as ?*P. robustus* possesses a coronal suture, which is a feature of the Chironomidae, absent in Ceratopogonidae (Sæther 2000). Moreover, ?*P. robustus* has a well-developed elongate notum of gonapophysis IX, whereas its absence has been considered as a synapomorphy of the Ceratopogonidae (Sæther 2000), and only some early lineages of Ceratopogonidae have a differently-shaped, short squat notum (vaginal apodeme in Borkent et al. 1987). So we exclude ceratopogonid affinity for both discussed species in spite of the incomplete state of preservation and the strong resemblance to insectivorous predatory or bloodsucking ceratopogonids in the general appearance and consider them as members of Podonominae.

The subfamily Podonominae is shown to be a dominant one in specimen abundance and diversity in the Jurassic deposits of Siberia (Kalugina and Kovalev 1985). No relevant data are available for the other regions. Kalugina stressed the difficulties in differentiation of the Mesozoic Podonominae and Tanypodinae and suggested that often it was possible to classify new taxa with certainty only as members of Tanypodoinae (Tanypodinae + Aphroteniinae + Podonominae) (Kalugina and Kovalev 1985: 82). However, she assigned new genera to subfamilies and explained her choice at every turn. At the same time, Kalugina assumed that some taxa she described in the Podonominae might actually belong to the Tanypodinae, considering that these two subfamilies were less clearly distinguished morphologically in the Jurassic.

Recently, Veltz et al. (2007) have concluded that subfamily identification of Jurassic Chironomidae is impossible and all Podonominae described by Kalugina are Chironomidae *incertae sedis*. Their only argument was rather methodical: Veltz and coauthors found it impossible to assign the different life stages to the same species as well as different species known only as pupae, to the same genus. Veltz and coauthors did not discuss the arguments proposed by Kalugina, e.g. that the larvae with translucent thoracic horns and

pupae with translucent male genitalia were found among the numerous Jurassic impressions of *Oryctochlus* Kalugina, 1985, so the association of larvae with pupae was made with certainty and those of pupae and imago, with some doubts. Kalugina compared every life stage of *Oryctochlus* with those of recent *Trichotanypus* Kieffer, 1906 and drew a conclusion about an undoubted affinity of these two genera of Podonominae (e.g. in pupae of both genera, segment VIII is deeply emarginated posteriorly, which is remarkably similar to segment IX in shape and segment IX with 3 lateral setae, 2 of which are close together in mid-section). According to the time-calibrated molecular data (Cranston et al. 2010), *Trichotanypus* is one of the oldest genera of the subfamily, which split from Parochlini in the Early Cretaceous. The French authors did not discuss substantially any genus described by Kalugina. However, they considered that Podonominae may not be recorded in the Mesozoic (Azar et al. 2008), but that hardly can be true. A transfer of *Libanochlites* Brundin, 1976 (K_1, Lebanese amber) from Podonominae to Tanypodinae made by these authors based on their new data was not supported by other specialists (Cranston et al. 2010).

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RESEARCH ARTICLE

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Palerasnitsynus gen. n. (Trichoptera, Psychomyiidae) from Burmese amber

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Abstract

Palerasnitsynus ohlhoffi **gen. et sp. n.** is described from Burmese amber of late Albian (Lower Cretaceous) age. This is the first record of the family Psychomyiidae from Burmese amber, and the earliest fossil record of the family. The genus *Palerasnitsynus* **gen. n.** differs from all other known psychomyiid genera by the absence of fork III in the forewings.

Keywords

Fossil Trichoptera, fossil insects, aquatic insects, fossil taxonomy, palaeoenvironment

Introduction

Trichoptera are very rare in Burmese amber and previously only two species, *Burminoptila bemeneha* Botosaneanu, 1981 (Hydroptilidae) and *Wormaldia myanmari* Wichard & Poinar, 2005 (Philopotamidae), have been named. Burmese amber from Myanmar is late Albian (late Lower Cretaceous) in age (Ross et al. 2010). Within this paper we describe

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the new genus *Palerasnitsynus* based on a male and a female specimen. The new species *P. ohlhoffi* is described from the male specimen. This taxon constitutes the first record of the family Psychomyiidae from Burmese amber and the earliest fossil record of the family.

Only seven fossil psychomyiid species have been described so far: *Arkharia oblimata* Sukatsheva, 1982 comes from Upper Cretaceous of south-eastern Siberia, originally placed in family Philopotamidae but belonging to the Psychomyiidae (Li and Morse 1997). The extinct psychomyiid *Trichopterodomus leonardi* Erikson, 1983 is described from larval retreats from the Paleocene of North Dakota. Five fossil species of the extant genus *Lype* Mclachlan, 1878 are known from Eocene Baltic amber (Wichard et al. 2009).

Taxonomy

Family Psychomyiidae Kolenati, 1859

***Palerasnitsynus* gen. n.**
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http://species-id.net/wiki/Palerasnitsynus

Type species. *Palerasnitsynus ohlhoffi* sp. n.

Etymology. The new genus is named after Prof. Dr. Alexandr P. Rasnitsyn on the occasion of his 75th birthday, in recognition of his extensive work on Palaeoentomology.

Diagnosis. Genus *Palerasnitsynus* gen. n. differs from all extant genera (*Paduniella* Ulmer, 1913*, Psychomyia* Latreille, 1829*, Psychomyiella* Ulmer, 1908*, Lype* Mclachlan, 1878*, Padangpsyche* Malicky, 1993*, Tinodes* Curtis, 1834*, Trawaspsyche* Malicky, 2004*, Eoneureclipsis* Kimmins, 1955, and *Zelandoptila* Tillyard, 1924) and the extinct genus (*Arkharia* Sukatsheva, 1982) by the absence of apical fork III in the forewing.

Description. Head: Ocelli absent. Antennae filiform, almost as long as forewings; each scapus only slightly longer than each pedicel and individual flagellomeres; flagellomeres cylindrical. Maxillary palps 5-segmented in both sexes, terminal 5th segment flexible, annulated, and at least twice as long as each of the other segments. Labial palps 3-segmented with flexible, annulated, long terminal segments.

Thorax: Mesoscutum with one pair of setal warts. Legs with tibial spurs 2/4/4. Wings elongate, rounded at apex, hind wings narrower than forewings. Forewing subcosta (Sc) simple, terminating into costa (C) at about three quarters the length of wing. Radius R_1 simple; R_{2+3} unforked, R_{4+5} forking into R_4 and R_5 (fork II) close to potential crossvein r; discoidal cell (Dc) short. Media M_{1+2} unforked, M_{3+4} forking into M_3 and M_4 (fork IV); crossvein m indistinct; median cell (Mc) apparently open. Cubitus Cu_1 bifurcated into Cu_{1a} and Cu_{1b} (fork V); Cu_2 simple; crossvein m-cu apparently present, closing thyridial cell (Tc). Forewings with forks II, IV, and V.

***Palerasnitsynus ohlhoffi* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Palerasnitsynus_ohlhoffi
Figs 1–3

Holotype. Male embedded in Burmese amber, late Albian, Myanmar, deposited in the Staatliches Museum für Naturkunde Stuttgart (ex coll. Rainer Ohlhoff, Saarbrücken). The holotype is well preserved in slightly cloudy amber. The forewings cover the hindwings in dorsal view; the hindwing venation is difficult to analyze due to the overlapping hind wings and forewings. The male genitalia are visible in ventral view. The antennae and legs are completely preserved but the left mid leg is broken.

Etymology. The species is named after Rainer Ohlhoff, who kindly made the fossil available for this study.

Diagnosis. The only species of the genus *Palerasnitsynus* which differs from all other known psychomyiid genera by the absence of apical fork III in the forewings. Length of male 1.9mm (intraspecific variation not known).

Description. Length of male (tip of head to tip of abdomen) 1.9 mm; forewing length 1.9 mm; hind wing length 1.7 mm.

Head: Eyes large and bulbous; ocelli absent; antennae filiform, almost as long as forewings, with cylindrical scapes, pedicel and flagellomeres. Maxillary palps 5-segmented, segment 1 short, segment 2 longer than segments 1 and 3, as long as segment 4, segment 5 flexible, annulated, twice as long as segment 4. Labial palps 3-segmented with long terminal segments, nearly as long as segments 1 + 2.

Thorax: Mesoscutum with pair of setal warts. Tibial spurs 2/4/4. Forewings: Subcosta (Sc) simple, Radius: R_1 simple, R_{2+3} unforked, R_{4+5} forked at cross-vein r; discoidal cell short. Media: M_{1+2} simple, M_{3+4} forked. Crossvein m indistinct, median cell (Mc) apparently open. Cubitus: Cu_1 forked; Cu_2 unforked. Crossvein m-cu apparently present, defining thyridial cell (Tc). Forewings apically rounded; venation with apical forks II, IV and V. Light-coloured hindwing venation indistinct. Rs apparently forked into R_{2+3} and R_{4+5}; forks I and II apparently absent. Crossvein r apparently absent. M branched, M_{1+2} unforked, M_{3+4} indistinct.

Genitalia: In ventral view, sternite IX with sinusoidal apical margin, bearing pair of two-segmented gonopods; coxopodite short, broad at basis; harpago long. Harpagones regularly curving mesad, widening at apex. Coxopodites with row of strong hairs along median margins; each coxopodite with brush of short, dark setae at apex. In dorsal view two small black spines about half as long as gonopods, visible through hyaline wings. External structures of male genitalia indistinct in lateral and dorsal view.

Figure 1. *Palerasnitsynus ohlhoffi* sp. n. holotype (male) in ventral view. Scale bar 1mm.

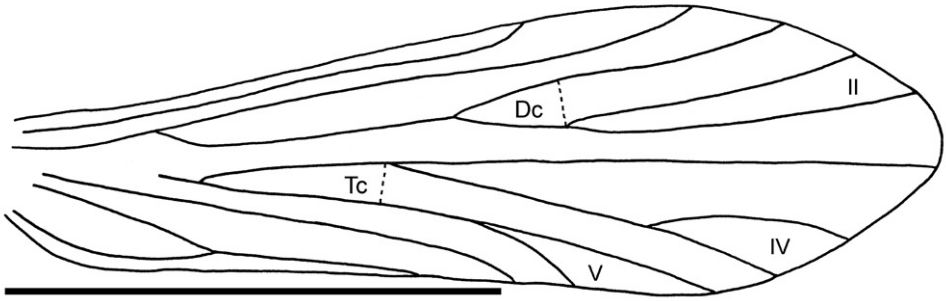

Figure 2. *Palerasnitsynus ohlhoffi* sp. n. male right forewing. Scale bar 1mm.

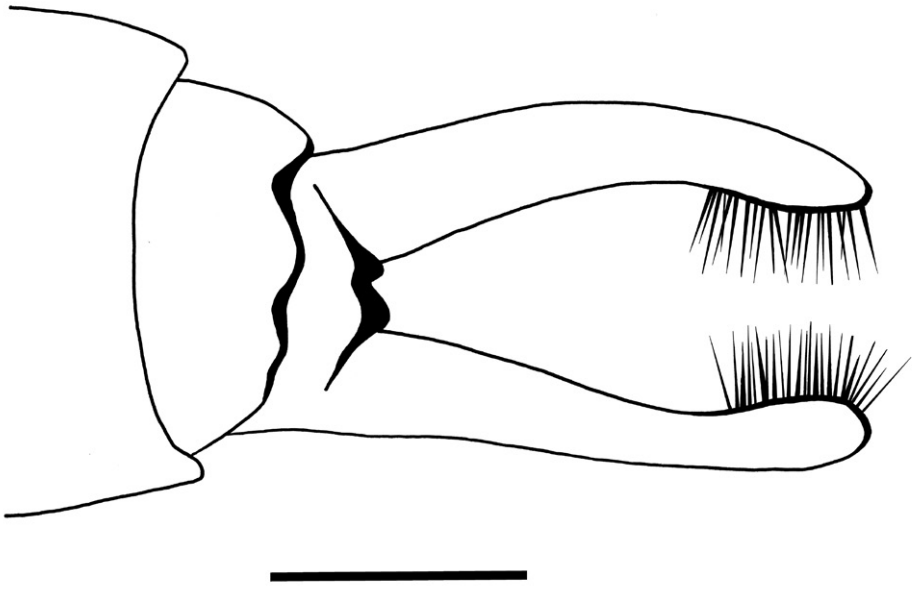

Figure 3. *Palerasnitsynus ohlhoffi* sp. n. male genitalia in ventral view. Scale bar 0.1mm.

***Palerasnitsynus* sp. female**
Figs 4–5

Material. Female imago in Burmese amber, late Albian, Myanmar; deposited in National Museums Scotland, Edinburgh; specimen no. G.2010.20.35 (ex Scott Anderson Coll.).

Description. Length of female (tip of head to tip of abdomen) 2.7 mm; forewing length 2.57 mm.

Head: Length 0.23 mm, width 0.47mm; filiform antennae each with 28 segments (including basal antennal segment), basal antennal segment twice as wide as other segments and twice as long as first segment; eyes large and bulbous, ocelli absent; maxillary palps 5-segmented, terminal segment flexible, annulated, and long (0.31mm), and nearly three times longer than each of the other segments (of similar length to each other); labial palps 3-segmented, also with long, flexible and annulated terminal segment.

Thorax: Mesoscutum with setal warts. Forelegs not easy to see; however, each may have 2 short spurs at end of tibia; mid legs each with 2 long spurs at end of tibia, 1 long preapical spur and possibly the base of a second; hind leg with 2 long spurs at end of tibia and 2 long preapical spurs. Tibial spurs: 2?/4?/4.

Wings with short fringe hairs on the anterior margin and long fringe hairs on posterior margin. Left forewing length 2.57mm; Sc dark and simple, terminating about three-quarters of length of anterior margin; R_1 simple; Rs branching twice, first branch originating at mid-wing, R_{2+3} simple, R_{3+4} branched (= fork II); discoidal cell (Dc) present (crossvein faint); M branching twice, first branch originating at mid-wing, M_{1+2} simple, M_{3+4} branched (= fork IV); Cu branching distally (= fork V); anal veins not visible. Left hindwing apex obscured; Sc dark and simple, terminating about three-quarters of length of anterior margin; R_1 simple, Rs branching once; crossvein r present, discoidal cell present; R_{4+5} connected to M_{1+2} by the crossvein r-m; M branching twice, M_{1+2} ending with short apical fork III, M_{3+4} simple; Cu branching once (= fork V), connected to M by the oblique crossvein m-cu closing thyridial cell apically; anal veins not visible. Forewings each with apical forks II, IV, and V; hind wings each with apical forks III and V.

Genitalia: Length 0.3mm. Typical long and simple ovipositor present; narrow cleft medio-ventrally and a pair of short apodemes apically.

Remarks. Due to the characteristic features (ocelli absent; maxillary palps 5-segmented and with terminal segment flexible and annulated; mesoscutum with one pair of setal warts; and tibial spurs probably 2/4/4), the female probably belongs to the Psychomyiidae. Due to the absence of forewing apical fork III, the specimen belongs to the genus *Palerasnitsynus* gen. n. The female and *Palerasnitsynus ohlhoffi* sp. n. agree in the forewing venation and differ in the hind wing; the discoidal cells are closed and short forks III are present in the female hind wings, but both traits are absent in *P. ohlhoffi* sp. n. There is no evidence to identify this female specimen as *P. ohlhoffi* sp. n.

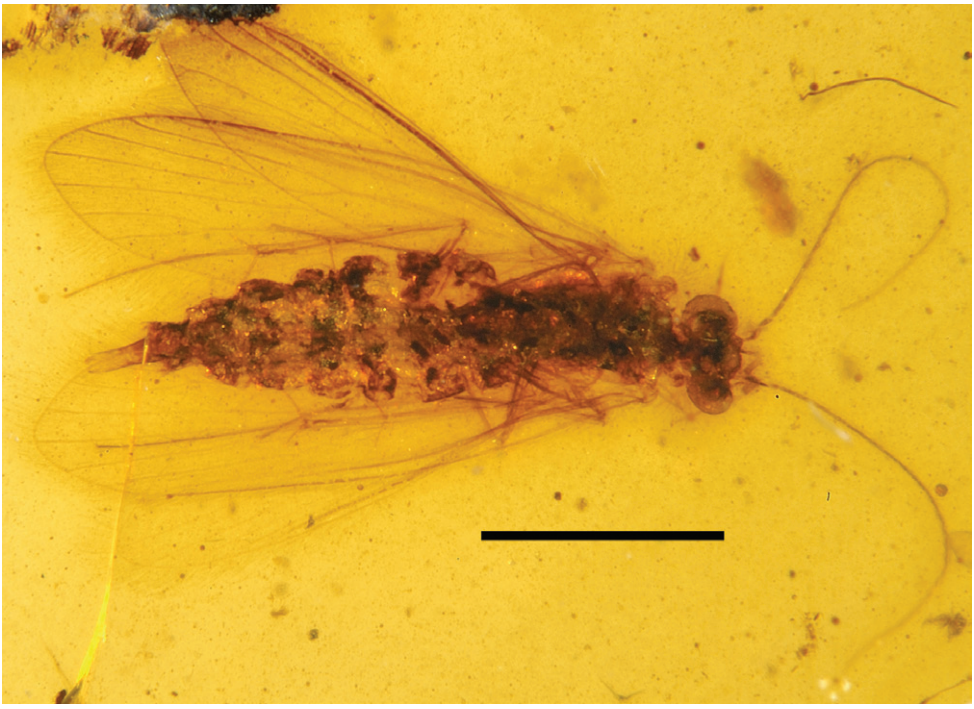

Figure 4. *Palerasnitsynus* sp. female in ventral view. Scale bar 1mm.

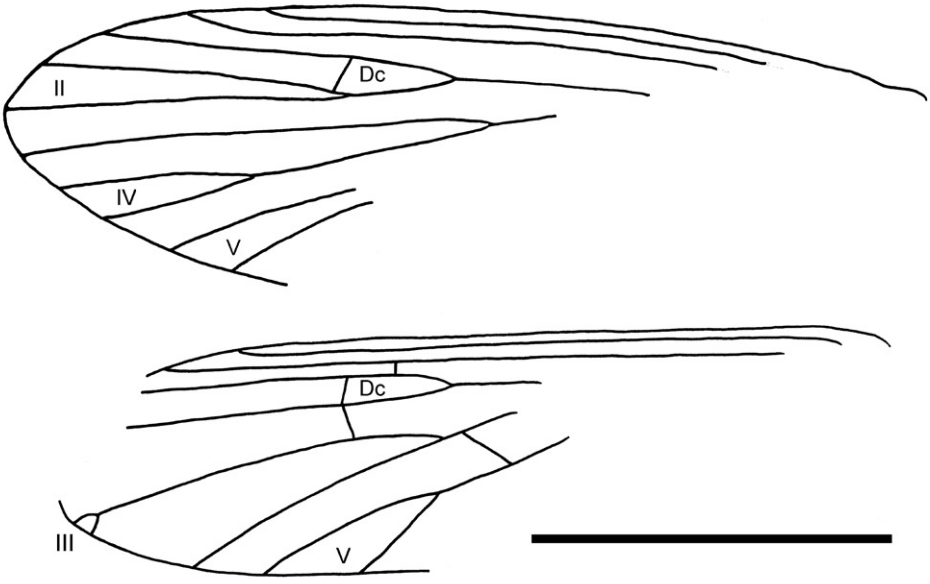

Figure 5. *Palerasnitsynus* sp. female left forewing (part) and left hind wing (part). Scale bar 1mm.

Discussion

The diversity of insects in Burmese amber is high compared with that of other Cretaceous ambers. Ross et al. (2010) listed 228 arthropod species in Burmese amber, but aquatic insects are rare both in number of individuals and number of described species: There are currently two described species of mayflies (Ephemeroptera) (Sinitshenkova 2000; McCafferty and Santiago-Blay 2009), one species of damselfly (Odonata) (Poinar et al. 2010) and an undescribed stonefly (Plecoptera) figured by Grimaldi et al. (2002). True water bugs and water striders are represented by only one species of the family Hydrometridae (Andersen and Grimaldi 2001). More frequent are amphibious flies (Diptera) in the families Ceratopogonidae, Chaoboridae, Chironomidae, Corethrellidae, Culicidae, Limoniidae, Psychodidae, Tanyderidae and Tipulidae (total 28 described species, see Ross et al. 2010). Only three species of caddisflies (Trichoptera) have been described from Burmese amber: *Burminoptila bemeneha* (Hydroptilidae), *Wormaldia myanmari* (Philopotamidae) and *Palerasnitsynus ohlhoffi* gen. et sp. n. (Psychomyiidae).

The low diversity of aquatic insects in Burmese amber might reflect that the late Albian palaeoenvironment had few freshwater habitats. This contrasts with Eocene Baltic amber diversity, comprising 25% amphibious aquatic insects (Wichard et al. 2009). However, the exploration of Burmese amber and its inclusions is continuing and the total diversity is presently uncertain. Extant Trichoptera of Southeast Asia (with Thailand as geographical centre) have been studied in a monograph by Malicky (2010). In this monograph, about 260 species of Hydroptilidae, 180 species of Philopotamidae and 150 species of Psychomyiidae are described today, which contrasts the single fossil species of each family known in Burmese amber.

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RESEARCH ARTICLE

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On the systematic position of *Baltimartyria* Skalski, 1995 and description of a new species from Baltic amber (Lepidoptera, Micropterigidae)

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Abstract

This paper describes a rare case of a male moth in Baltic amber in an excellent position for establishing a species. The moth represents the second species of the genus *Baltimartyria* Skalski, 1995, described herein as *B. rasnitsyni* **sp. n.** The detection of this new species prompts research on the systematic position of the genus within the family Micropterigidae. The genus was found to provide none of the apomorphic characters that would allow placement in one of the monophyletic lineages within the family. The genus is provisionally assigned to the "southern sabatincoid group", a weakly supported assemblage of Southern Hemisphere genera. The sister genus has still to be determined. *Baltimartyria* is the first North Hemisphere representative in this group. Some general aspects of historical biogeography relevant for the group are briefly discussed.

Keywords

Insecta, Lepidoptera, Micropterigidae, fossils, Baltic Amber

Introduction

In comparison with other mega-diverse insect orders preserved in Baltic amber, the Lepidoptera are poorly known (Kristensen and Skalski 1998, Rasnitsyn and Quicke

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2002). The reason for this inadequate knowledge is not the rarity of inclusions, but rather the main morphological feature of lepidopterans – the scales. They cover the whole body and its appendages and hide important diagnostic characters, e. g. wing venation. The scaling provides, however, traits like colour patterns, but these are barely preserved and discernable in amber specimens. The wings are often folded and may frequently obscure features such as the abdomen and its copulatory structures. In many groups the genitalia are also retracted within the distal abdominal segments. Therefore, lepidopterans can rarely be identified at the species level and even assignment to a discrete family may often not be feasible. This applies to the majority of amber Lepidoptera which are usually dominated by micro moths. Only in cases where wings are outspread and genitalia visible can specimens potentially be determined to species.

For many years I had a Baltic amber piece on my desk containing a male moth in a splendid position. The up-held and slightly rubbed wings reveal venational and partial genitalic characters well. The species clearly belongs to Micropterigidae, the most ancestral family of extant Lepidoptera. A number of fossil genera and species were described and assigned to this family (Koslov 1988, Koslov et al. 2002) but their placement in Micropterigidae was rejected by Kristensen and Skalski (1998) because phylogenetically important details were not preserved. Some micropterigid moths described from amber are true and undisputed representatives of the family. The few, hitherto described and named taxa are listed in Table 1 (see Nieukerken et al. in press for the most up-to-date overview of micropterigid fossils and their taxonomic placement). Some further specimens are known, but remained undescribed and unnamed (e.g. Grimaldi and Engel 2005: 562). Considering only described species, the Baltic amber fauna is apparently very poor in individuals of this family. To date, only three inclusions have been reported belonging to three species: *Micropterix proavitella* Rebel, 1936, *Electrocrania immensipalpa* Kuznetzov, 1941 and *Micropterix gertraudae* Kurz and Kurz, 2010. From amber collected in western France only some scales of a presumed but unnamed micropterigid species were discovered and described by Kühne et al. (1973).

Kozlov (1988: 26) synonymised *Electrocrania* Kuznetzov, 1941 with *Micropterix* Hübner, 1815, but this was rejected by Kristensen and Skalski (1998) because of the presence of a mesotibial spur. The holotype of *M. proavitella* was examined by Skalski (1995) who confirmed the placement of the species in Micropterigidae on the basis of wing venation, head morphology, greatly shortened labial palps, the absence of mesotibial spurs and the desclerotised sternum of abdominal segment VIII. However, he realised that the species is not a member of *Micropterix* but represents a separate genus for which he introduced the new name *Baltimartyria* Skalski, 1995. Skalski`s (1995) detailed re-description and illustration of the holotype facilitated the identification of the individual in my possession. At a first glance, it was thought to represent a second specimen of *Baltimartyria proavitella*, because of its similar wing pattern, venation and valvae. A closer inspection, however, revealed some clear differences important enough to regard the specimen as a distinct species, which is described below.

Table 1. Records of Micropterigidae described from amber

species	origin	first revision	current combination
Micropteryx pervetus Cockerell, 1919	Burmese amber	Whalley (1978): *Sabatinca*	*Sabatinca* s.l.
Micropteryx proavitella Rebel, 1936	Baltic amber	Skalski (1995): *Baltimartyria*	*Baltimartyria*
Parasabatinca aftimacra Whalley, 1978	Lebanese amber		*Parasabatinca*
Micropterix gertraudae Kurz and Kurz, 2010	Baltic amber		*Micropterix*

Taxonomy

Family Micropterigidae
***Baltimartyria* Skalski, 1995**

***Baltimartyria rasnitsyni* sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Baltimartyria_rasnitsyni
Figs 1–11

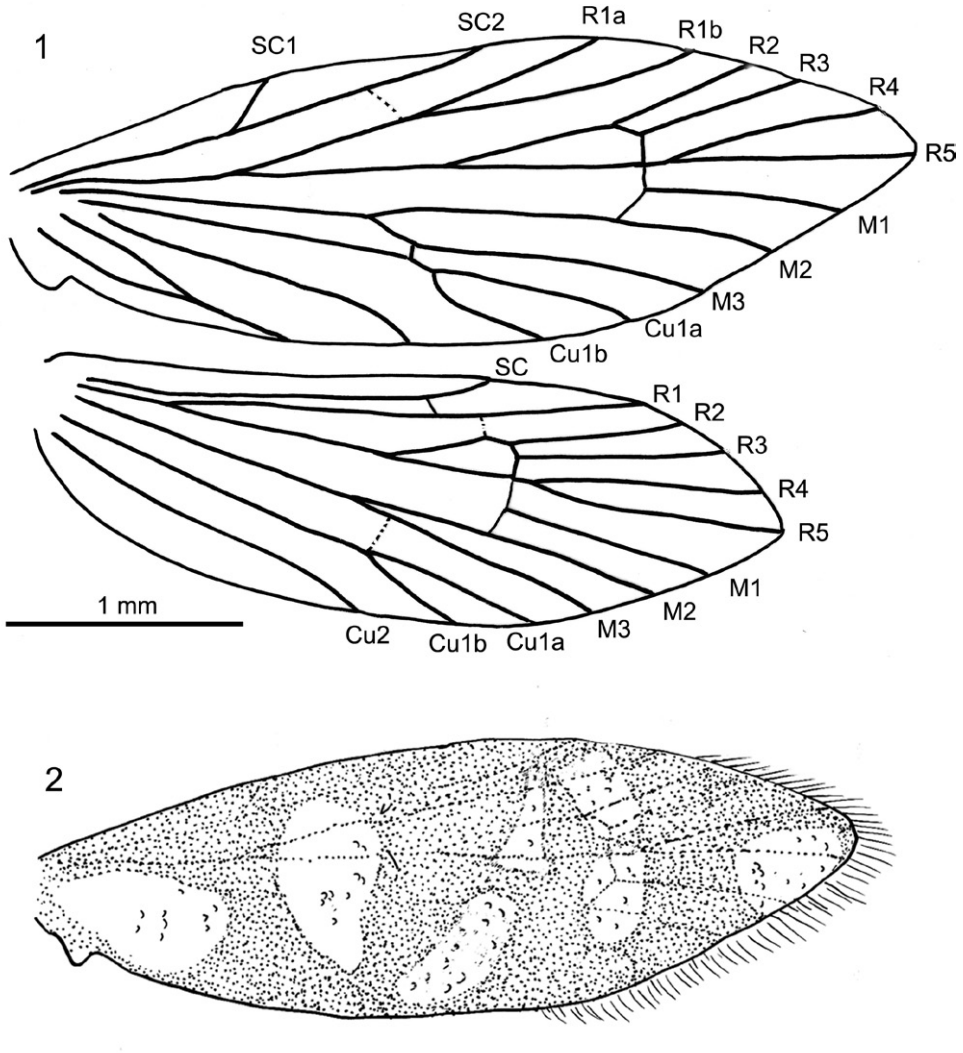
Material. Holotype male, Baltic Amber, MB.I 5950, deposited in Museum für Naturkunde, Berlin.

Preservation. The adult moth is completely preserved and clearly visible from a ventro-lateral view. Right maxillary palps and antenna covered by body, dorsal and inner side of genitalia filled by white emulsion.

Etymology. Named in honour of Alexandr P. Rasnitsyn, the eminent Russian paleoentomologist.

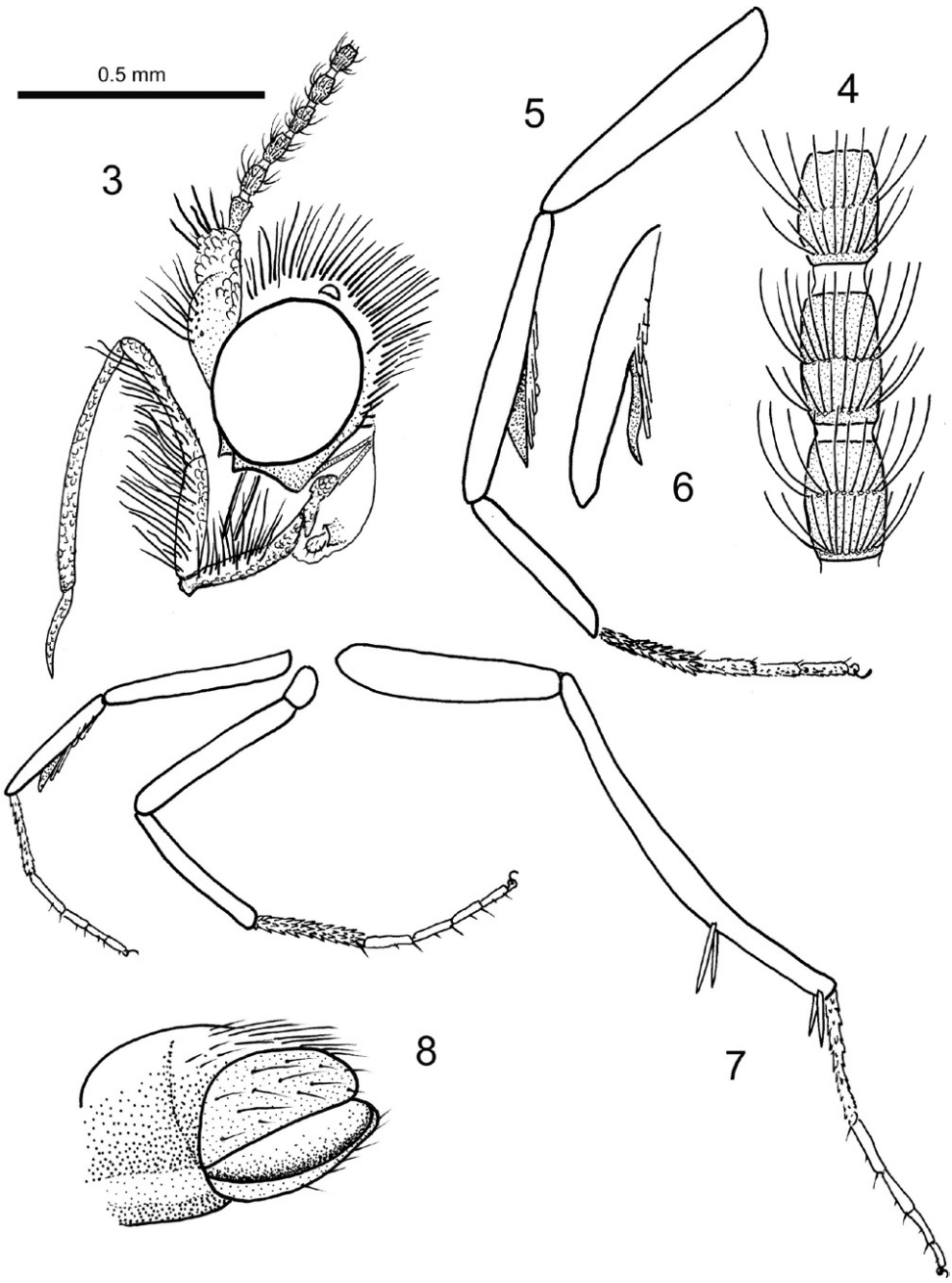
Diagnosis. *B. rasnitsyni* sp. nov. can be separated from *B. proavitella* by segment four of maxillary palps being as long as third and second segment together, and by shortly stalked R4 and R5 in both fore- and hindwings. In *B. proavitella*, the two terminal segments of the maxillary palps are as long as the third segment, and in the fore- and hindwings all terminal R branches originate separately from the cell.

Description. Length of forewing 4 mm, length of body 3 mm; head with erect, piliform scales on vertex, ocelli pale white, scape and pedicel together as long as eye diameter, scaled, 35 barrel-shaped flagellomeres present, basal segments (1–3) with scales, subsequent segments unscaled, each flagellomere with two whorls of long sensilla trichodea, one basal and one at mid-length, ascoids not clearly visible; maxillary palps five segmented, basal segments of equal length, fourth segment longest, terminal segment short, acute and with short bristles; labial palps two-segmented, terminal segment small, rounded; mandibles present (only base visible); fore-tibia with blade-like epiphysis exhibiting an acute tip, spurs 0.0.4, basitarsus of all legs covered with



Figures 1–2. *Baltimartyria rasnitsyni* sp. n. **1** wing venation **2** reconstructed wing pattern.

short, acute and semi-erect scales, tarsal segments with terminal, pair of ventral bristles; reconstructed wing pattern in Fig. 2, venation in Fig. 1, R1 with two branches in forewing, R4 and R5 on a short common stalk from cell in both wings, (anal field of hindwing only partially visible); ventral side of abdominal segment VIII membranous (= pale brown), lateral sides sclerotised (= dark brown), vinculum deeply retracted into segment VIII (segmental limits obsolete by milky nebulae); valvae simple, elliptical and spoon-like, outer surface covered by hairs.



Figures 3–8. *Baltimartyria rasnitsyni* sp. n. **3** head, lateral view **4** flagellomeres from mid-antenna, enlarged **5** foreleg, enlarged **6** tibia of foreleg with epiphysis from different view **7** legs **8** tip of abdomen and genitalia, ventrolateral view.

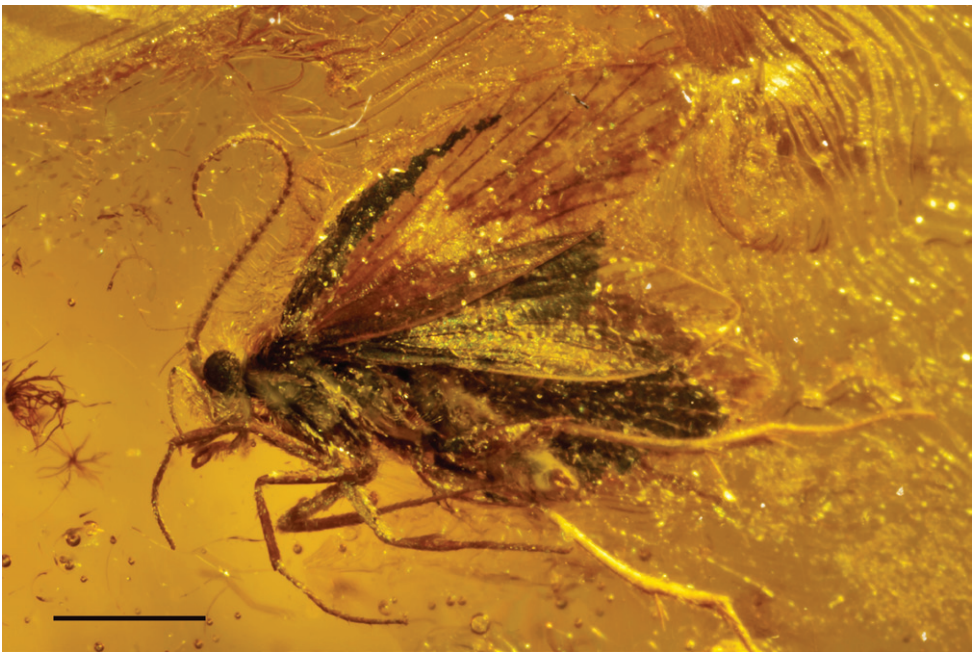


Figure 9. Male holotype of *Baltimartyria rasnitsyni* sp. n. Right hand side position, scale bar 1 mm.

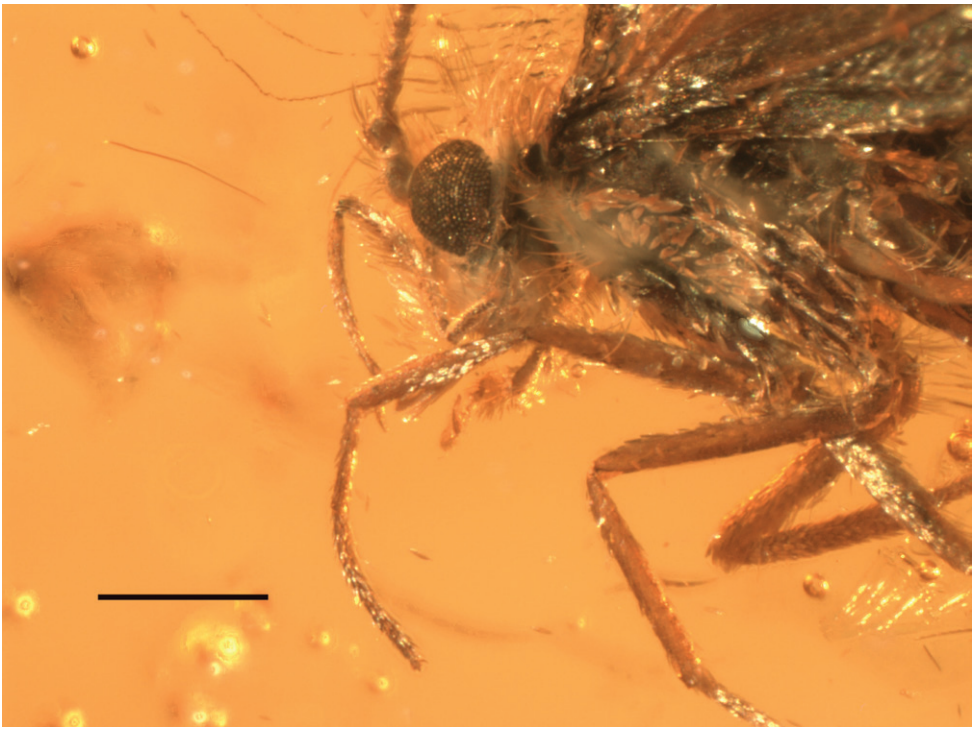


Figure 10. Male holotype of *Baltimartyria rasnitsyni* sp. n. Details of head, scale bar 1 mm.

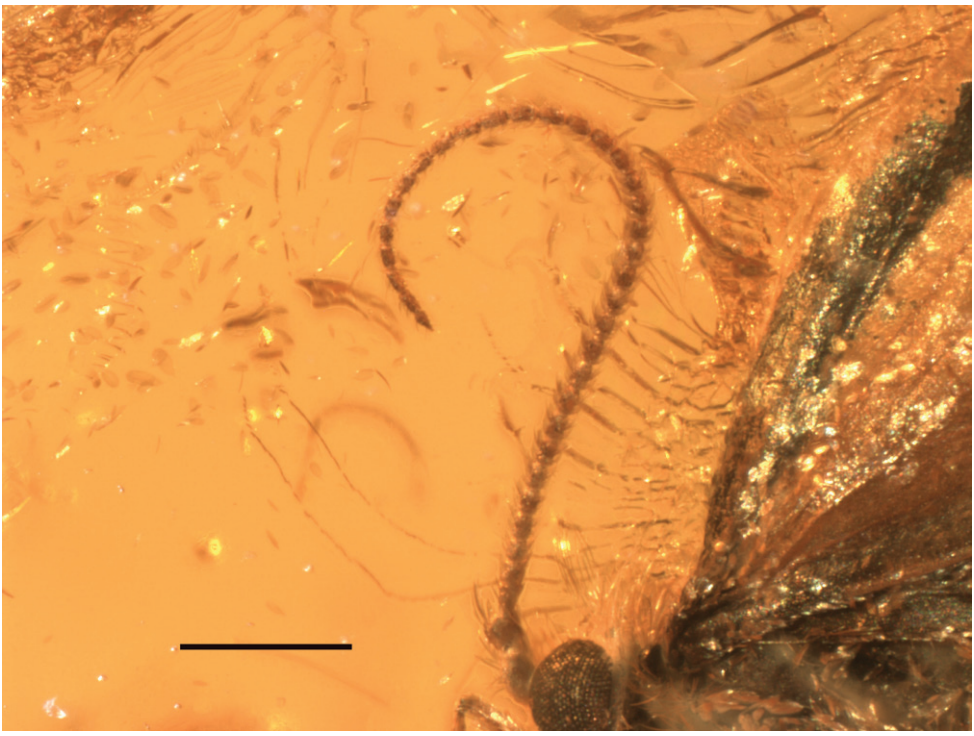


Figure 11. Male holotype of *Baltimartyria rasnitsyni* sp. n. Antenna, scale bar 1 mm.

Systematic position

Skalski (1995) assigned *Baltimartyria* to the so-called *Sabatinca* group of genera on the basis of genital structures and wing venation. The concept of the *Sabatinca* group by 1995 is now obsolete, and the *Sabatinca* group of Gibbs (2010) is more restricted. He noted a resemblance with the Chilean genus *Hypomartyria* (Kristensen and Nielsen 1982) but did not suggest any synapomorphies which could be regarded as evidence of a close relationship. Recently, most genera of the former *Sabatinca* group were revised (Gibbs 2010, Gibbs and Kristensen 2011, Hashimoto 2006, Imada et al. 2011). The phylogenetic significance of a number of morphological characters was re-evaluated and new characters were found to be useful for reconstructing phylogenetic relationships. A molecular analysis of the 16S rRNA gene provided evidence for the separation of Micropterigidae into five monophyletic lineages (Gibbs et al. 2004). Based on the description of this phylogeny (Gibbs 2010: 3) which includes a hypothesized 'Australian group' comprising four genera (Gibbs 2010: 43, fig. 16) a cladogram was constructed (Fig. 12) which, the modest resolution notwithstanding, suffices for the present discussion. Since *Baltimartyria* can be excluded from the *Micropterix* branch, the question arises, where does the genus fit in this topology? Fossil taxa usually have a restricted set of characters which can be

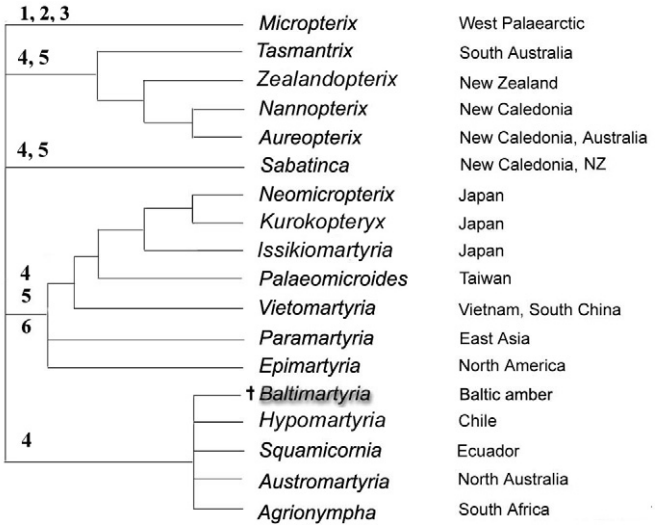


Figure 12. Presumed phylogenetic relationships within Micropterigidae based on Gibbs (2010).

used for placing them together with extant species in a phylogenetic tree. Six informative characters, which can be observed in *Baltimartyria,* were identified. They are described in Table 2, and the distribution of their apomorphic states is indicated by the corresponding numbers in the cladogram of Fig. 12. Hindwing venation (5) and modified antennae (6) exclude the genus from three lineages. The remaining lineage, the "southern sabatincoid group" (comprising *Hypomartyria, Austromartyria* and *Agrionympha*; the assignment of *Squamicornia* to this assemblage is conjectural) is based on resemblances in the structure of sternum V gland protuberances, presence of both dorsal and ventral valve muscles from segment IX and morphology of early instar larvae. These characters may be plesiomorphic within the family (Gibbs and Kristensen 2011). Unfortunately, the abdomen of the holotype of *B. rasnitsyni* sp. n. is covered by numerous hairs that do not allow discerning structures on segment V. This was the only character which could be observed on fossil specimens. Thus, no apomorphies have been identified which would support the monophyly of this assemblage. But only this weakly supported group yields no characters conflicting with placement of *Baltimartyria* within. Therefore, the genus is here provisionally assigned to the "southern sabatincoid group". The sister genus of *Baltimartyria* thus remains to be identified. According to wing venation, the "southern sabatincoid group" members have largely retained the plesiomorphic states ascribed to the Lepidoptera ground plan (Kristensen 1984). All other micropterigid lineages have developed a few apomorphic characters in the wings. It seems quite likely therefore that this "southern sabatincoid group" contains the extant genus which is most overall similar to the last ancestor of the family.

Table 2. Characters of Micropterigidae observable in *Baltimartyria* and relevant for its placement

	character	**plesiomorphic state**	**apomorphic state**
1	R in forewing	all branches to costa	R5 to wing apex
2	R1 in forewing	forked	simple, unforked
3	male segment IX	caudal margin simple and straight	caudal margin with processes
4	male venter VIII	sclerotised	more or less membranous
5	R in hindwing	complete vein to costal margin	more or less coalescent with Sc
6	antenna	filiform, flagellomeres barrel-shaped	flagellomeres modified

Historical biogeography

Given the uncertainty about the placement of *Baltimartyria* any discussion on aspects of its historical biogeography is premature. However, the following, general remarks might be useful for considering in future discussions.

According to the geographic distribution of extant Micropterigidae (Gibbs 1983), *Baltimartyria* was initially expected to belong to the Northern Hemisphere genera of the *Sabatinca* group. Morphological characters, however, suggest a placement in an assemblage comprising Southern Hemisphere genera. The distribution pattern of these Southern genera points to a Gondwanan origin of the ancestor of the group and its subsequent splitting into several evolutionary lines, following the disintegration of the Gondwana palaeocontinent. However, if the "southern sabatincoid group" including *Baltimartyria* is indeed a monophylum, this hypothesis would be challenged, and the notion of a world-wide distribution prior to the splitting of Gondwana favoured. Eskov (2002) has compiled and discussed similar examples of alleged South Hemisphere species (in Plecoptera, Mecoptera, Diptera, etc) found as fossils in Eurasia and concluded, that many of these presumed Gondwana elements had a much wider distribution in earth history but eventually survived in refuge areas in Southern Hemisphere continents only. Thus, their Gondwanan origin is questionable.

However, in Eskov`s discussion on Gondwanan vs. non-Gondwanan origin of taxa the role of drifting terranes is not considered. In South East Asia a series of terranes were identified, which were attached to the Asian continent during the Paleozoic and Mesozoic. They all arrived from the south and had their origin on the northern margin of Gondwana (Metcalfe 1998, 2001, Hall 2001). A permanent, sub-aerial drift of these terranes, inhabited by plant and animal species, allowed their survival during the passage and is considered to have imported them finally into the Asian biota. This passive transport is one of the mechanisms which has contributed to a wider distribution of taxa in the Mesozoic and Cenozoic. During the passage from southern to northern latitudes the biota on drifting terranes had to cope with a change in climatic conditions. Crossing the equator and the Inter-Tropical Convergence Zone in the Mesozoic was probably not

as dramatic as it was today because of a generally warmer climate and less pronounced temperature gradient along latitudes. Nonetheless, species had to adapt to changing climatic and ecological conditions. The presence of mountain ranges on terranes could have facilitated survival by vertical shifts of distribution ranges. The Mesozoic equatorial crossing of Gondwanan terranes certainly affected the biota in several ways. Its significance can be investigated today by comparing the distribution of endemic taxa in Madagascar and India. India collided with Asia in the early Tertiary (Hall 2001). In the Mesozoic the Indian plate was united with Madagascar. The recent discovery of Micropterigidae in Madagascar allows the inference, that the family was present on the Indian plate as well. If species survived the northward drift they evolved in isolation and should be today the closest relatives of the Madagascan taxa. Up to now species of the *Sabatinca* group were not found to occur on the Indian subcontinent. Either they became extinct, or they escaped discovery until now. A distinctive clade of *Micropterix* has been described for India (Lees et al. 2010) but is attributed to the Palearctic radiation on the basis of morphological and molecular evidence. Extinction of the *Sabatinca* group might point to the significance of changing conditions during drift. Discovery in India is plausible since the species on Madagascar were detected only recently (Lees et al. 2010), despite intensive research on Lepidoptera (including microlepidopterans) in the decades before.

There are undoubtedly more undetected micropterigid species, fossil and extant, on the globe. Each discovery provides new information and throws new light on current phylogenetic and biogeographic reconstructions.

Acknowledgements

The paper was presented at the workshop on Baltic Amber during the DGaaE (= Deutsche Gesellschaft für allgemeine und angewandte Entomolgie) conference in Berlin in March 2011. The organiser of the workshop, W. Wichard, invited me to talk on amber Lepidoptera and proposed to submit the present paper for the Festschrift. C. Neumann took a photo of the inclusion and provided the inventory number. H.C. Zeller-Lukashort gave some important hints. Jason Dunlop corrected the English text. N.P. Kristensen and D.C. Lees reviewed the manuscript and suggested many corrections and improvements. I sincerely thank all of them for their input and help.

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RESEARCH ARTICLE

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Head capsule characters in the Hymenoptera and their phylogenetic implications

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Abstract

The head capsule of a taxon sample of three outgroup and 86 ingroup taxa is examined for characters of possible phylogenetic significance within Hymenoptera. 21 morphological characters are illustrated and scored, and their character evolution explored by mapping them onto a phylogeny recently produced from a large morphological data set. Many of the characters are informative and display unambiguous changes. Most of the character support demonstrated is supportive at the superfamily or family level. In contrast, only few characters corroborate deeper nodes in the phylogeny of Hymenoptera.

Keywords

Hymenoptera, morphology, phylogeny, head anatomy

Introduction

Phylogenetic research on Hymenoptera has been pursued for more than a century (see Sharkey 2007 for an overview). However, only for the past forty-odd years have this effort been more focused by the application of cladistic methodology and active search for characters that might be useful for elucidating hymenopteran evolution. Rasnitsyn (1969, 1980, 1988) made ground breaking advances in the field by surveying characters across the entire Hymenoptera, extant as well as extinct. His culminating effort was a widely cited phylogenetic hypothesis for the order (Rasnitsyn 1988). Although the analyses were not performed in a strictly cladistic context, the phylogenetic treat-

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ment presented in this paper formed a landmark. It served as an inspiration as well as a characters source for the first more stringent analyses of hymenopteran relationships (Ronquist et al. 1999; Carpenter and Wheeler 1999; Dowton and Austin 2001). Not all the relationships proposed by Rasnitsyn (1988) have been corroborated by these and later efforts, and the phylogenetics of Hymenoptera continuously evolve as morphological character systems are re-evaluated and expanded (e.g., Vilhelmsen et al. 2010a) and molecular data sets are developed (e.g., Castro and Dowton 2006; Sharanowski et al. 2010; Heraty et al. 2011). However, the hypotheses presented by Rasnitsyn continue to be relevant when comparing and discussing the results of more recent analyses.

Characters from the head capsule have long been included in attempts to make phylogenetic inferences across the Hymenoptera. Ross (1937) discussed some of the variation in this region among basal Hymenoptera, in particular the different configurations of ventral sclerotisations occurring between the occipital and oral foramina. However, as he was not working in a cladistic context, he was unable to establish putative transformation series and character support for different clades. In contrast, Rasnitsyn (1988) explicitly employed head capsule characters, among others. This was continued in the first stringently cladistic analyses performed for the basal hymenopteran lineages by Vilhelmsen (1997, 2001) and Schulmeister (2003a, b). These analyses included additional characters discussed in Vilhelmsen (1996, 1997, 1999). In the latter paper, the variation within the ventral sclerotisations among especially basal Hymenoptera was discussed at length and the difficulties with establishing homologies and inferring transitions between different conditions in this particular feature was highlighted.

In the present paper, I review characters from the head capsule from previous treatments as well as introducing some new ones. The characters are scored from a taxon sample closely matching that of Vilhelmsen et al. (2010a), which used a comprehensive data set from the skeleto-musculature of the mesosoma to analyse phylogenetic relationships broadly across the Hymenoptera. This data set was assembled as part of the US National Science Foundation Hymenoptera Assembling the Tree of Life project. Indeed, the characters presented here will be included in forthcoming combined analyses of molecular and morphological data. In the present paper, the characters scored will be mapped on a phylogeny from Vilhelmsen et al. (2010a) and their possible phylogenetic implications discussed.

Materials and methods

Heads of the taxa examined were detached from the rest of the body and the antennae and mouthparts were removed. The heads were examined in a dissection microscope and bisected in a parasagittal plane to allow the observation of internal features. In addition, SEM images of anterior and posterior views of the head of a number of taxa (see below) were downloaded from MorphBank (http://www.morphbank.net/) for a

number of taxa and used to score as well as illustrate characters (see Figs 1-6). The data set was assembled in Mesquite (Maddison and Maddison 2007) and traced in the same program on a phylogeny of Hymenoptera produced by Vilhelmsen et al. (2010, fig. 69). A slightly modified version of this tree with the terminals collapsed at the family or superfamily level is used to illustrate the evolution of selected characters (Fig. 7).

Material examined

Taxa for which Morphbank SEM images were available are indicated with 'MB' in the list below, followed by the image numbers.

Outgroup

Neuroptera, Chrysopidae: *Chrysopa perla* (Linnaeus, 1758). Mecoptera, Panorpidae: *Panorpa communis* (Linnaeus, 1758). Lepidoptera, Micropterigidae: *Micropterix calthella* (Linnaeus, 1761).

Hymenoptera

Xyeloidea, Xyelidae: *Macroxyela ferruginea* (Say, 1824) MB 102882, 102884, 102885.

Tenthredinoidea, Tenthredinidae: *Athalia rosae* (Linnaeus, 1758) MB 102486-88; *Notofenusa surosa* (Konow, 1905). Diprionidae: *Monoctenus juniperi* (Linnaeus, 1758). Pergidae: *Heteroperreyia hubrichi* Malaise, 1955.

Pamphilioidea, Pamphiliidae: *Onycholyda amplecta* (Fabricius, 1804) MB 102834, 102837.

Cephoidea, Cephidae: *Cephus pygmeus* (Linnaeus, 1767) MB 102672, 102946.

Siricoidea, Anaxyelidae: *Syntexis libocedrii* Rohwer, 1915. Siricidae: *Tremex columba* (Linnaeus, 1763) MB 102749, 134704; *Urocerus gigas* (Linnaeus, 1758).

Xiphydrioidea, Xiphydriidae: *Xiphydria camelus* (Linnaeus, 1758); *Xiphydria prolongata* (Geoffroy, 1758) MB 102708-9, 134719.

Orussoidea, Orussidae: *Orussobaius minutus* Benson, 1938; *Orussus abietinus* (Scopoli, 1763) MB 134672, 134675.

Ceraphronoidea, Ceraphronidae: *Ceraphron* sp. MB 78643, 78654. Megaspilidae: *Lagynodes* sp. MB 79001, 79018; *Megaspilus fuscipennis* (Ashmead, 1888); *Megaspilus* sp. MB 134646, 134648.

Chalcidoidea, Aphelinidae: *Cales noacki* Howard, 1907 MB 101253, 101256, 101328, 101330; *Coccophagus rusti* Compere, 1928 MB 101454, 101458. Chalcididae: *Acanthochalcis nigricans* Cameron, 1884; *Acanthochalcis* sp. MB 134808, 134812. Eulophidae: *Cirrospilus coachellae* Gates, 2000 MB 101190, 101192. Eurytomidae: *Eurytoma gigantea* Walsh, 1870 MB 101509, 101511. Mymaridae:

Gonatocerus ashmeadi (Girault, 1915) MB 101615, 101617; *Gonatocerus morrilli* (Howard, 1908). Pteromalidae: *Cleonymus* sp. MB 101374-75, 101380-81; *Nasonia vitripennis* (Walker, 1836) MB 101734, 101736, 101738; *Spalangia nigripes* Curtis, 1839. Torymidae: *Megastigmus transvaalensis* (Hussey, 1956) MB 101672, 101672, 101709.

Cynipoidea, Cynipidae: *Diplolepis rosae* (Linnaeus, 1758) MB 71826-27; *Periclistus brandtii* (Ratzeburg, 1832) MB 72041-42. Figitidae: *Anacharis* sp.; *Melanips opacus* (Hartig, 1840) MB 75299; *Melanips* sp. MB 75329; *Parnips nigripes* (Barbotin, 1964) MB 80037, 80053. Ibaliidae: *Ibalia leucospoides* (Hochenwarth, 1785); *Ibalia rufipes* Cresson, 1879 MB 77314-15.

Evanioidea, Aulacidae: *Aulacus impolitus* Smith, 1991 MB 103222, 103243; *Pristaulacus strangaliae* Rohwer, 1917 MB 103739, 103747. Evaniidae: *Brachygaster minuta* (Olivier, 1792) MB 103249, 103257; *Evania albofascialis* Cameron, 1887 MB 134630, 134632; *Evaniella semaeoda* Bradley, 1908 MB 103427, 103443. Gasteruptiidae: *Gasteruption* spp. MB 103453; *Pseudofoenus* spp. MB 103788, 103810.

Ichneumonoidea, Braconidae: *Aleiodes terminalis* Cresson, 1869 MB 103161, 103186; *Doryctes erythromelas* (Brullé, 1846) MB 103274, 103330; *Orgilus gracilis* (Brues, 1908) MB 103649, 103655; *Rhysipolis* sp. MB 103818, 103843; *Urosigalphus* sp.; *Wroughtonia ligator* (Say, 1824) MB 103109, 103126, 134714, 134716. Ichneumonidae: *Dusona egregia* (Viereck, 1916) MB 103363, 103366, 134625, 134627; *Labena grallator* (Say, 1836) MB 103512, 103524; *Lymeon orbum* (Say, 1835) MB 103559, 103562; *Pimpla aequalis* (Provancher, 1880) MB 103694, 103718; *Zagryphus nasutus* (Cresson, 1868) MB 103134, 103149.

Megalyroidea, Megalyridae: *Dinapsis* spp.; *Megalyra fasciipennis* Westwood, 1832 MB 103568, 103589, 134657, 134660.

Mymarommatoidea, Mymarommatidae: *Mymaromma anomalum* (Blood & Kryger, 1922) MB 101797-98, 101800.

Platygastroidea, Platygastridae: *Archaeoteleia mellea* Masner, 1968 MB 101920, 101922, 103191, 103211; *Isostasius* sp. MB 103486, 103503; *Proplatygaster* sp. MB 103760, 103776, 134687, 134690; *Sparasion formosum* Kieffer, 1910 MB 103049, 103068; *Telenomus podisi* Ashmead, 1893 MB 103079, 103096.

Proctotrupoidea, Diapriidae: *Belyta* sp. MB 101879-80, 101882; *Pantolytomyia ferruginea* (Dodd, 1915) MB 79029; *Poecilopsilus* sp. MB 79100. Heloridae: *Helorus anomalipes* (Panzer, 1798); *Helorus* sp. MB 78665, 104116, 134637, 134639. Maamingidae: *Maaminga rangi* Early et al., 2001. Monomachidae: *Monomachus antipodalis* Westwood, 1874 MB 80081-82. Pelecinidae: *Pelecinus polyturator* (Drury, 1773) MB 79061, 134682-85. Proctotrupidae: *Austroserphus albofasciatus* Dodd, 1933 MB 78510, 103974, 103978; *Phaenoserphus* sp. MB 80116, 80121, 80147; *Proctotrupes* sp. Roproniidae: *Ropronia garmani* (Ashmead, 1898) MB 78872, 134697, 134700. Vanhorniidae: *Vanhornia eucnemidarum* Crawford, 1909 MB 78898, 134709, 134711.

Stephanoidea, Stephanidae: *Megischus* spp. MB 103607, 103620, 134650, 134653; *Schlettererius cinctipes* (Cresson, 1880).

Trigonaloidea, Trigonalidae: *Orthogonalys pulchella* (Cresson, 1867) MB 103661, 103682, 134678, 134680; *Taeniogonalos gundlachii* (Cresson, 1865) MB 103032, 103043.

Apoidea, Ampulicidae: *Ampulex compressa* (Fabricius, 1781) MB 134606, 134608; Crabronidae: *Pison chilense* Spinola, 1851 MB 102586-88; Sphecidae: *Stangeella cyaniventris* (Guérin-Méneville, 1831).

Chrysidoidea, Bethylidae: *Cephalonomia stephanoderis* Betrem, 1961 MB 102530-31, 102534. Chrysididae: *Chrysis angolensis* Radoszkowski, 1881. Plumaridae: *Plumarius* sp. Scolebythidae: *Ycaploca evansi* Nagy, 1975.

Vespoidea, Pompilidae: *Aporus niger* (Cresson, 1867). Rhopalosomatidae: *Rhopalosoma nearcticum* Brues, 1943. Sapygidae: *Sapyga pumila* Cresson, 1880 MB 102635, 102637. Vespidae: *Metapolybia cingulata* (Fabricius, 1804).

Results and discussion: annotated character list

1. Ocellar corona

(0) absent (e.g., Figs 1A-C, 2B-D)

(1) present (Figs 1D, 2A)

The presence of a circlet or semicirclet of cuticular teeth around the median ocellus is a ground plan feature of both Orussidae (Vilhelmsen 2003) and Stephanidae (Aguiar 2001). Given the phylogenetic position in Vilhelmsen et al. (2010a) of these two families as successive outgroups to the remainder of the Apocrita and all Apocrita, respectively, it is equally parsimonious to assume that the ocellar corona has evolved independently in Orussidae and Stephanidae or in the common ancestor of Orussidae + Apocrita, subsequently to become lost in most of the latter (see also Vilhelmsen and Turrisi 2011).

2. Supraantennal grooves or depressions

(0) absent (e.g., Figs 3A-B, 4B, D)

(1) present (Figs 3C, 4A)

Grooves or depressions, also called scrobes, are prominent above the antennal foramina in many Chalcidoidea and apparently belong to the ground plan of the superfamily. However, they were not observed in *Gonatoceros* (Mymaridae). The Mymaridae have been suggested to be the sister group of the remainder of the Chalcidoidea (e.g., Gibson 1986, Gibson et al. 1999), a result that was recently corroborated by Heraty et al. (2011), but not by Davis et al. (2010) or Vilhelmsen et al. (2010a), were the Mymaridae were nested deeply within Chalcidoidea. The scrobes serve to accommodate the scapes of the antennae. Less well developed depressions are observed in a number of apocritan taxa, especially among the Ichneumonoidea, where they also seem to be a ground plan feature. They have been assigned the same character state as the more prominent grooves in Chalcidoidea.

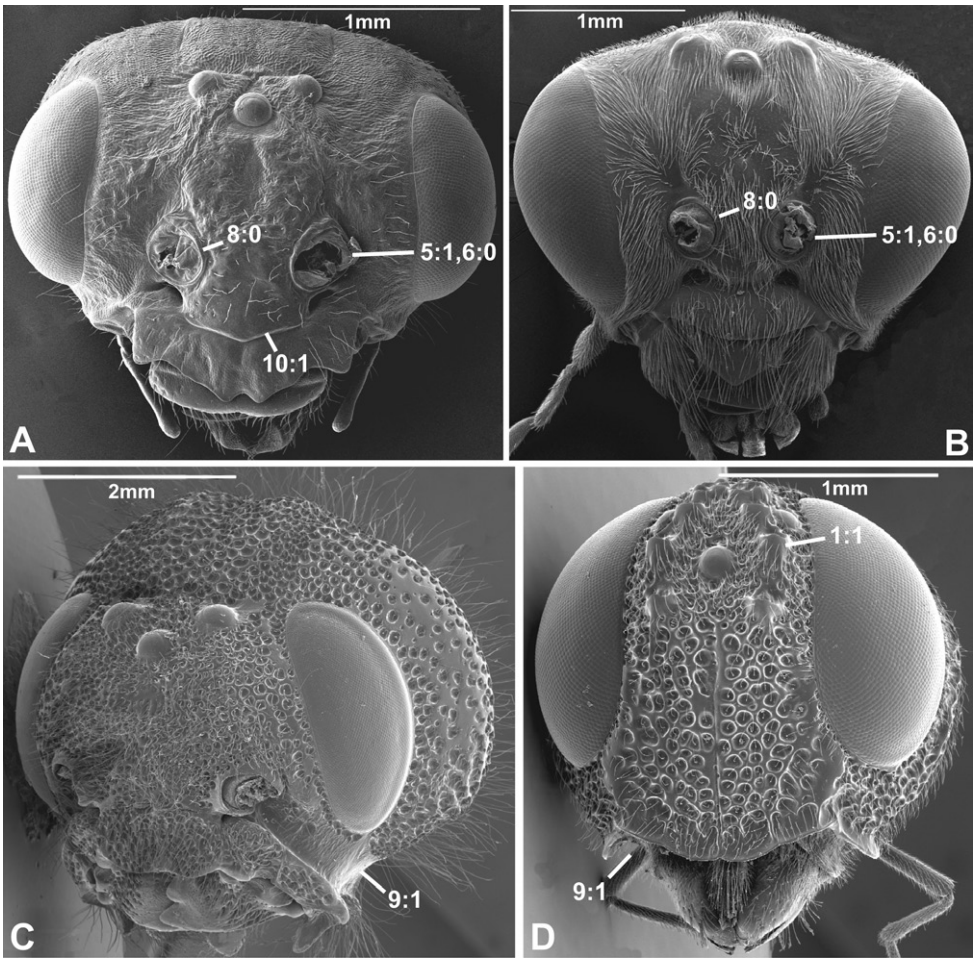

Figure 1. Anterior view of head capsule of **A** *Macroxyela ferruginea* (Xyeloidea, Xyelidae); modified from MB 102882 **B** *Athalia rosae* (Tenthredinoidea, Tenthredinidae); modified from MB 102486 **C** *Tremex columba* (Siricoidea, Siricidae); modified from MB 134704 **D** *Orussus abietinus* (Orussoidea, Orussidae); modified from MB 134672. Numbers indicate character numbers:character states.

3. Notch on the inner margin of the eye

(0) absent (e.g., Figs 3A, C-D)

(1) present (Fig. 3B)

A prominent notch is present on the inner margin of the eye in some Aculeata (especially Vespoidea) and Ichneumonoidea, but does not seem to be a ground plan feature of either of these taxa.

4. Hairs on eyes

(0) absent or indistinct, as most as long as diameter of ommatidium (e.g., Figs 3B, C)

(1) distinct setae longer than ommatidium present on at least part of eye (Figs 3A, D)

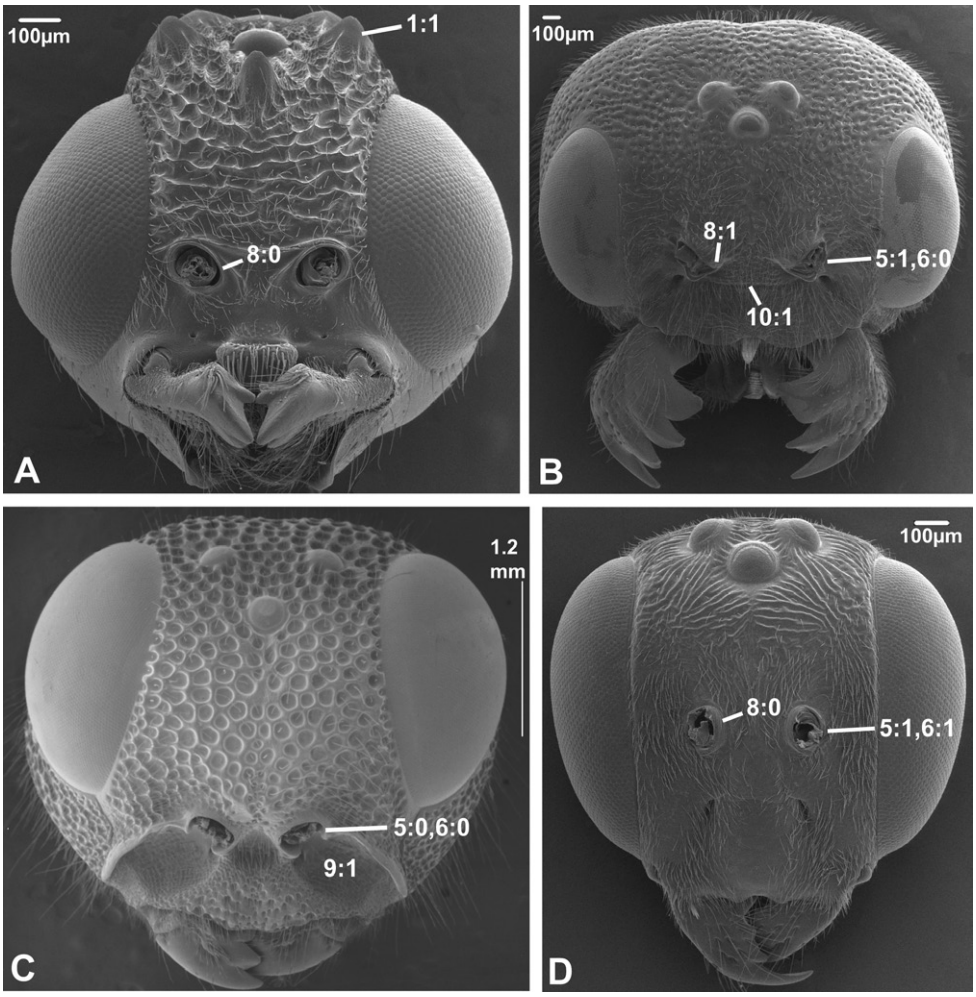

Figure 2. Anterior view of head capsule of **A** *Megischus* sp. (Stephanoidea, Stephanidae), modified from MB 103607 **B** *Taeniogonalos gundlachii* (Trigonaloidea, Trigonalidae); modified from MB 103032 **C** *Megalyra fasciipennis* (Megalyroidea, Megalyridae); modified from MB 103568 **D** *Pseudofoenus* sp. (Evanioidea, Gasteruptiidae); modified from MB 103788. Numbers indicate character numbers:character states.

Among the non-apocritan lineages, distinct hairs on the eyes (between the ommatidia) were only observed in *Cephus* (Cephidae). In contrast, hairs are present in many apocritan taxa, especially among the Chalcidoidea and the Proctotrupomorpha s.str. (Vilhelmsen et al. 2010a). They probably evolved independently in these taxa as they are not present in *Maaminga* (Maamingidae) and *Mymaromma* (Mymarommatidae).

5. Position of antennal foramina relative to eyes

(0) below or level with ventral margin of eyes (Figs 2C, 3A, 4D)

(1) above ventral margin of eyes (Figs 1A, B, 2B, D, 3B, D, 4C)

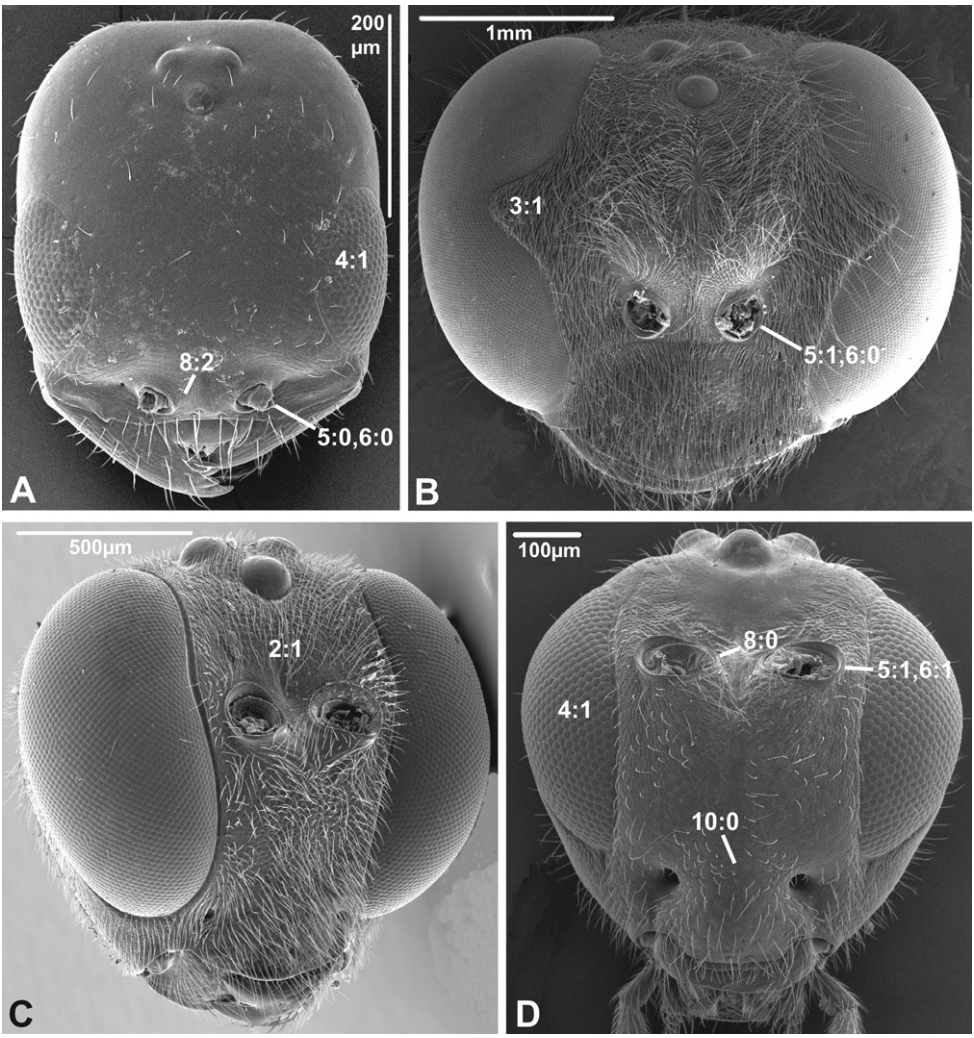

Figure 3. Anterior view of head capsule of **A** *Cephalonomia stephanoderis* (Chrysidoidea, Bethylidae); modified from MB 102531 **B** *Pison chilense* (Apoidea, Crabronidae); modified from MB 102586 **C** *Dusona egregia* (Ichneumonoidea, Ichneumonidae); modified from MB 134625 **D** *Orgilus gracilis* (Ichneumonoidea, Braconidae); modified from MB 103649. Numbers indicate character numbers:character states.

6. Position of antennal foramina relative to clypeus

(0) equal or closer to clypeus than its own diameter (Figs 1A, B, 2B, C, 3A, B, 4D)

(1) further from clypeus than its own diameter (Figs 2D, 3D, 4C)

These two characters are partly overlapping, but it was decided score them separately to partition the information as finely as possible. Both characters are quite variable across the Hymenoptera, also within many superfamilies. Having the antennal foramina below the ventral margins of the eyes is apparently apomorphic for Orussidae and Platygastroidea, and possibly synapomorphic for Megalyridae + Ceraphronoidea.

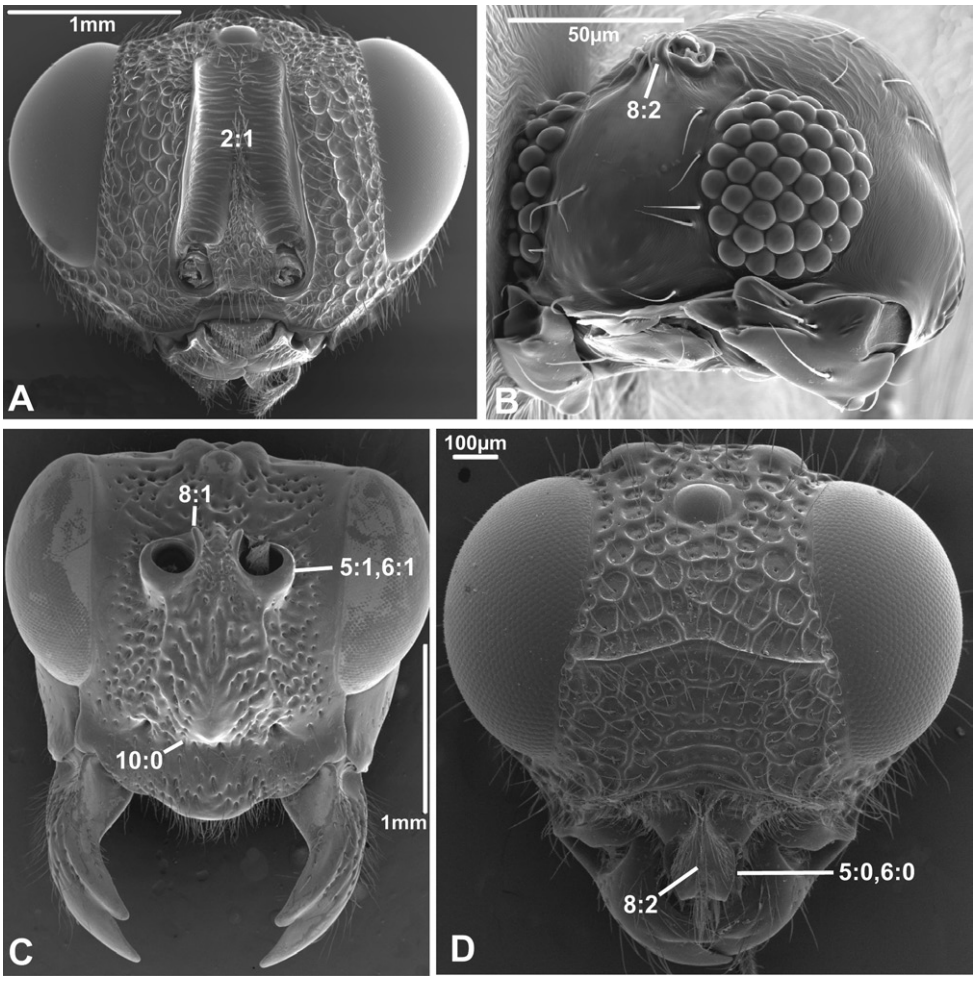

Figure 4. Anterior view of head capsule of **A** *Acanthochalcis* sp. (Chalcidoidea, Chalcididae), modified from MB 134808 **B** *Mymaromma anomalum* (Mymarommatoidea, Mymarommatidae); modified from MB 101797 **C** *Pelecinus polyturator* (Pelecinidae); modified from MB 79061 **D** *Sparasion formosum* (Platygastridae); modified from MB 103049. Numbers indicate character numbers:character states.

7. Frontal shelf

(0) absent

(1) present, antennal foramina facing upwards (Early et al. 2001: fig. 6)

Early et al. (2001) proposed the presence of a prominent extension in lateral view of the frons to form a distinct shelf below the antennal foramina to be a putative synapomorphy of Diapriidae and Maamingidae; they noticed that a similar structure is also present in Monomachidae, Embolemidae (not included here) and some Ichneumonoidea. Furthermore, the shelf is absent from some Diapriidae (e.g., *Ismarus*). Vilhelmsen et al. (2010a) did not retrieve Diapriidae + Maamingidae in any of their analyses; however, Heraty et al. (2011) found support for a clade comprising Maamingidae,

Monomachidae and at least part of the Diapriidae, Maamingidae and Monomachidae being sister groups within this clade.

8. Inner margin of antennal foramen (ordered)

(0) not distinctly raised compared to outer margin (Figs 1A, B, 2A, D, 3D)

(1) with distinct projection, raised compared to outer margin (Figs 2B, 4C)

(2) area between projections raised as well forming interantennal process (Figs 3A, 4B, D)

The presence of raised inner margins on the antennal foramina that might or might not be connected medially (states 1&2) are of scattered occurrence throughout the Hymenoptera. Having just the margins raised might be apomorphies of the Orussidae and Trigonalidae, as well as occurring in the groundplan of the Platygastroidea; within the latter, the projections have fused medially in *Archaeoteleia*, *Sparasion* and *Telenomus* (formerly placed in a separate family, the Scelionidae; see Sharkey 2007).

9. Subantennal groove

(0) absent or weakly developed (e.g., Figs 1A, B, 2A, D)

(1) present, distinct (Figs 1C, D, 2C)

The presence of a well developed groove extending from the antennal foramen and ventrally of the eye for accommodating the proximal part of the antenna is a putative apomorphy of Siricidae (Vilhelmsen 1997) and Megalyridae (Vilhelmsen et al. 2010b); it is also observed in many Orussidae (Vilhelmsen 2003) and Aulacidae (Turrisi and Vilhelmsen 2010), but it is not a ground plan feature of any of these families. Less developed subantennal grooves are observed in Stephanidae and Xiphydriidae (Vilhelmsen 1997), but these have been scored as state 0. There seems to be a strong correlation between the presence of well developed subantennal grooves and the adult having to emerge from a pupal chamber within wood (Vilhelmsen and Turrisi 2011).

10. Epistomal sulcus (unordered)

(0) absent or reduced, internal ridge absent (Figs 3D, 4C))

(1) present, distinct, usually with internal ridge (e.g., Figs 1A, 2B)

(2) present, not continuous medially, extends dorsally to antennal foramen

The epistomal sulcus and corresponding internal ridge separates the clypeus from the frons. Having these structures well developed and continuous medially is apparently a hymenopteran ground plan feature. The epistomal sulcus has been reduced a number of times within the Hymenoptera, notably in many Chalcidoidea and Cynipoidea, although it is uncertain whether the absence is a ground plan feature of either of these superfamilies. Having the sulcus well developed laterally, but discontinuous medially (state 2) is a putative apomorphy of Evaniidae.

11. Clypeus

(0) not inflected

(1) inflected, covering base of labrum (Figs 5A, C; Vilhelmsen 1996: figs 11-13)

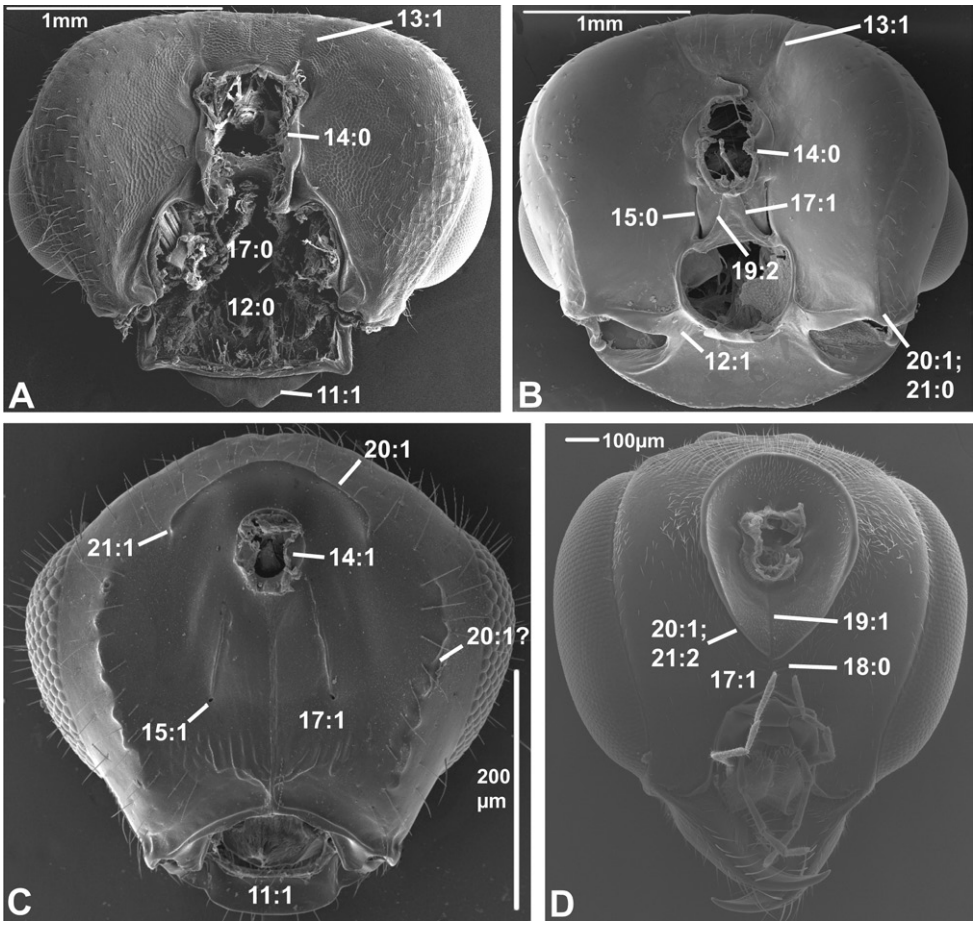

Figure 5. Posterior view of head capsule of **A** *Macroxyela ferruginea* (Xyeloidea, Xyelidae)¸ modified from MB 102885 **B** *Onycholyda amplecta* (Pamphilioidea, Pamphiliidae); modified from MB 102837 **C** *Ceraphron* sp. (Ceraphronoidea, Ceraphronidae); modified from MB 78643 **D** *Pseudofoenus* sp. (Evanioidea, Gasteruptiidae); modified from MB 103810. Numbers indicate character numbers:character states.

In all Hymenoptera where this feature could be observed, the ventral margin of the clypeus is sclerotised also on its posterior, internal side, and the labrum is situated slightly posterior to it (Fig. 1A). Vilhelmsen (1996) stated this to be an autapomorphy for the Hymenoptera; this is corroborated here.

12. Mandibular foramen

(0) oral and mandibular foramen continuous (Fig. 5A)

(1) mandibular and oral foramina separated by subgenal sclerotisation (Fig. 5B)

The separation of the mandibular and oral foramina by sclerotisations continuous with the head capsule is a long established apomorphy of the Pamphilioidea (e.g.,

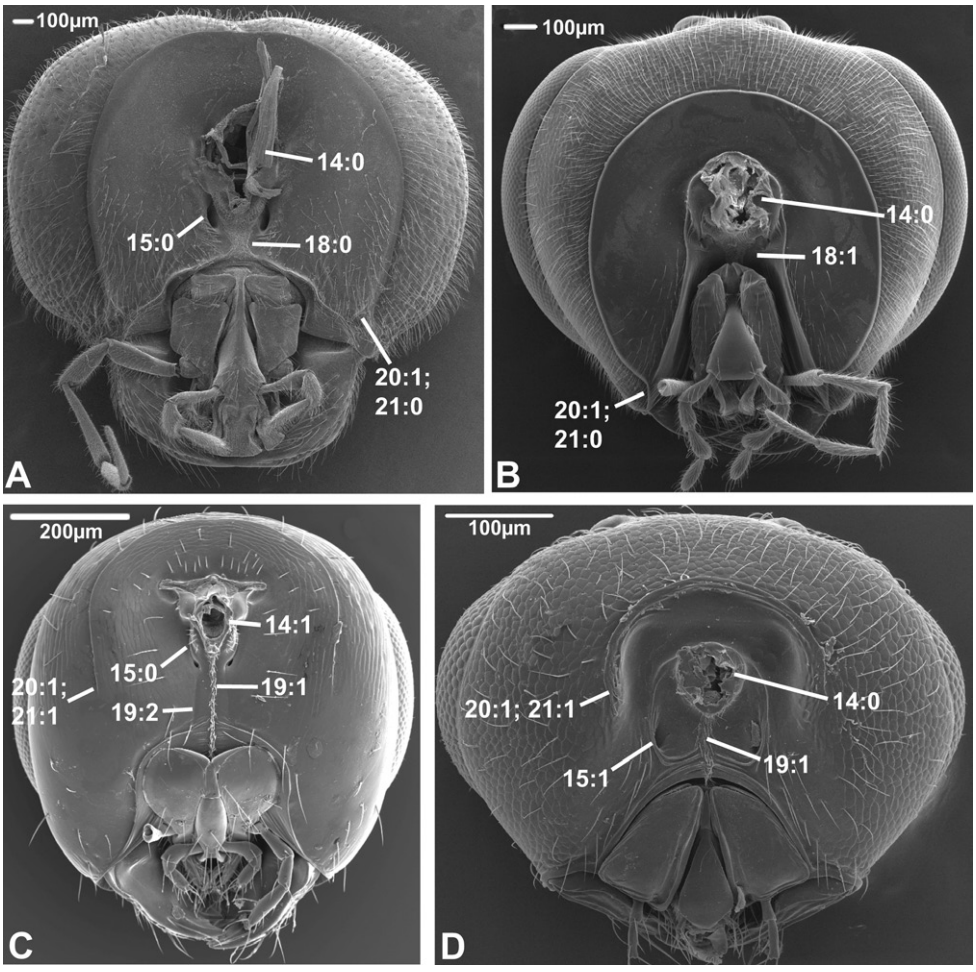

Figure 6. Posterior view of head capsule of **A** *Taeniogonalos gundlachii* (Trigonaloidea, Trigonalidae); modified from MB 103043 **B** *Dusona egregia* (Ichneumonoidea, Ichneumonidae); modified from MB 103363 **C** *Megastigmus transvaalensis* (Chalcidoidea, Torymidae); modified from MB 101672 **D** *Isostasius* sp. (Platygastroidea, Platygastridae); modified from MB 103503. Numbers indicate character numbers:characters states.

Königsmann 1977). A few of the apocritan taxa examined here also display this feature: *Ampulex* (Ampulicidae); *Mymaromma* (Mymarommatoidea).

13. Occipital sulcus and ridge

(0) absent (e.g., Figs 5C, 6B, D)

(1) present (Figs 5A, B)

The occipital sulci are present above the occipital foramen in the basalmost lineages of Hymenoptera and is definitely a ground plan feature of Hymenoptera (Vilhelmsen 1999). It is absent in Xiphydriidae, Orussidae and Apocrita, a putative synapomorphy for these taxa (Vilhelmsen 2001).

14. Position, occipital foramen

(0) approx. halfway between top of head and oral foramen (Figs 5A, B, 6A, B, D)

(1) distance from top of head to occipital foramen half or less than distance to oral foramen (Figs 5C, 6C)

The dorsally displaced occipital foramen is apparently an apomorphy of the Ceraphronoidea (Fig. 5C). It is also observed in a few other apocritan taxa (e.g., some Chalcidoidea).

15. Position, posterior tentorial pits

(0) adjacent/at level with occipital foramen/condyles (Figs 5B, 6A, B)

(1) considerably ventral to occipital foramen (Figs 5C, 6D)

The posterior tentorial pits are considered level with the occipital foramen when at least their dorsal ends reach the level of the ventral margin of the foramen (e.g., Fig. 5B). The ventrally displaced posterior tentorial pits are of scattered occurrence across the Apocrita. The trait is prominent in some Ceraphronoidea (Fig. 5C), where it is perhaps correlated with the dorsal position of the occipital foramen (see previous character). The ventrally placed tentorial pits also occur in the Pelecinidae, Platygastridae, Proctotrupidae, Ropronidae and Vanhornidae and might be interpreted as a ground plan feature/synapomorphy of a larger clade within the Proctotrupomorpha (see Fig. 7), but then the condition has to have reversed within the Heloridae and *Archaeoteleia*, *Sparasion* and *Telenomus* (Platygastroidea).

16. Postoccipital bridge

(0) absent

(1) present (Vilhelmsen 1999: figs 2D, 5C)

In contrast to the ventral sclerotisation (see character 17), this is an internal structure, formed by a sclerotisation between the insertion points of the ventral profurcopostoccipital muscles ventrally of the tentorial bridge (see Vilhelmsen 1999). Among the taxa examined here, it has only been observed in *Cephus* (Cephidae) and *Syntexis* (Anaxyelidae) and has probably evolved convergently in these two taxa.

17. Sclerotisation between occipital and oral foramina

(0) absent, foramina confluent (Fig. 5A)

(1) present, foramina separate (Figs 5B-D)

The various configurations of the ventral head sclerotisations in basal Hymenoptera were discussed at length in Vilhelmsen (1999). The external ventral head sclerotisation might take the form of either a hypostomal bridge, which is inferred to have formed by sclerotisation in situ of the area between the posterior tentorial pits (see Fig. 5B: 15:0) or a postgenal bridge (e.g., Fig. 6C), formed by the median extension of the genae into the hypostomal area, replacing the hypostomal bridge (Snodgrass 1960; Rasnitsyn 1969, 1988). These hypothetical transformation series seems to be based not so much on ontogenetic data as on observations of differences in the detailed configuration of various anatomical landmarks in the area between the occipital and oral

foramina. The postgenal bridge is thus characterised by having the posterior tentorial pits separated from the oral foramen by a considerable distance and sometimes also by the presence of a median longitudinal, often hairy line (see Fig. 6C: 19:1) interpreted as the fusion line between the postgenae. In contrast, the hypostomal bridge does not display a narrow fusion line, although a broader hairy area might be present (Xiphydriidae; see Vilhelmsen 1999: figs 3C, D), and the posterior tentorial pits extend ventrally to close to the oral foramen. Given the variability of these landmarks across the Hymenoptera (see below) and the hypothetical nature of the transitions between them, it was decided not to differentiate between the two types of ventral sclerotisations here, but score just absence/presence of a sclerotisation. The variation in the configuration of lines on the ventral sclerotisation is coded in character 19. In this way, it is attempted to deal with the putatively phylogenetically relevant information from this region in a more objective way.

As it is scored here, the presence of a ventral head sclerotisation is optimized as a ground plan feature of the Hymenoptera, contrary to the inference of Vilhelmsen (1999); the absence of the sclerotisation in Xyeloidea and Tenthredinoidea is inferred to be secondary. However, this interpretation relies heavily on the condition of the selected outgroup taxa, most of which have a sclerotisation.

18. Ventral sclerotisation configuration

(0) at most oblique ventral to tentorial pits, not extending anteriorly (Figs 5D, 6A)

(1) horizontal ventral to pits and extending anteriorly (Fig. 6B)

This character has been scored inapplicable when the ventral sclerotisation (see previous character) is absent. The sclerotisation is inflected just below the tentorial pits in some apocritan taxa, forming the dorsal and anterior parts of a trough that accommodates the labiomaxillary complex. This condition was already noticed by Ross (1937) to be present in many Ichneumonoidea and is apparently an apomorphy of the superfamily, but it is also observed in Heloridae, Pelecinidae, Proctotrupidae, and Ropronidae.

19. Longitudinal sulci on ventral head sclerotization (ordered)

(0) none

(1) one median sulcus or hair line present, at least ventrally (Figs 5D, 6C, D)

(2) two sublateral sulci present, not merging ventrally (Figs 5B, 6C)

This character has been scored inapplicable when the ventral sclerotisation (see character 17) is absent. When a narrow median hair line is present, it has been scored state 1. In some cases (e.g., *Megastigmus* (Torymidae) Fig. 6C) both a median hair line and two sublateral sulci are present; these instances were scored as polymorphic (1&2). These longitudinal sulci and hair lines are some of the anatomical landmarks used to differentiate between the different types of ventral sclerotisations (see character 17), state 1 being indicative of a postgenal bridge, state 2 of a hypostomal bridge. This character is highly variable throughout the Hymenoptera. If treated as ordered, there is an unambiguous change from state 2 to state 1 in the common ancestor of Siricidae,

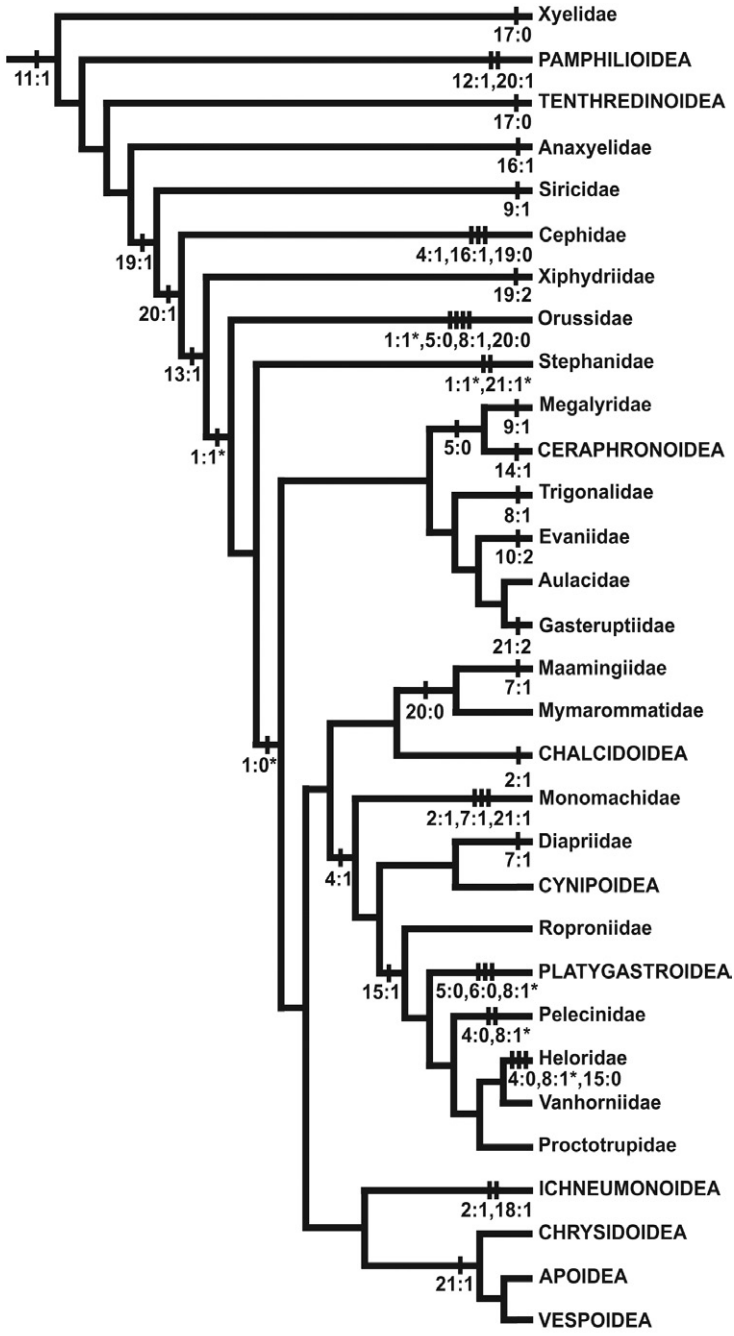

Figure 7. Selected character state changes mapped onto a phylogeny of Hymenoptera. Tree modified from Vilhelmsen et al. 2010a, fig. 69. Outgroup taxa have been removed and terminals have been collapsed to the family or superfamily level; Aulacidae, Diapriidae, Chrysidoidea and Vespoidea are treated as monophyletic. Not all character state changes shown; changes marked with a * have equally parsimonious alternative optimisations.

Cephidae (which has state 0), Xiphydriidae (which has state 2 derived secondarily), Orussidae, and Apocrita (in which this character is very variable and displays few unambiguous changes). This corroborates the suggestion of Rasnitsyn (1988) that the postgenal bridge replaces the hypostomal bridge among basal Hymenoptera, albeit only once (with secondary reversals), not twice as he proposed (in the Siricidae and Vespina = Orussidae + Apocrita, respectively).

20. Occipital carina

(0) absent (Fig. 5A)

(1) present (Figs 5B-D, 6A-D)

The occipital carina extends dorsally and laterally of the occipital foramen, usually reaching the ventral margin of the head capsule close to the mandibular bases (but see following character). The presence of the occipital carina is not a ground plan character of the Hymenoptera but apparently evolved at least twice among the basal Hymenoptera, in the Pamphilioidea and (with reversals, e.g., in Maamingidae + Mymarommatidae) in the common ancestor of Cephidae, Xiphydriidae, Orussidae (where it is not a ground plan character, at least for the extant members of the family, see Vilhelmsen 2003) and Apocrita.

21. Occipital carina configuration (unordered)

(0) reaching ventral margin of head capsule (Figs 5B, 6A, B)

(1) not reaching ventral margin and not continuous medially (Figs 5C, 6C, D)

(2) continuous ventrally of occipital foramen (Fig. 5D)

This character has been scored inapplicable when the occipital carina is absent. In most Hymenoptera that have an occipital carina it reaches the ventral margin of the head capsule. Some taxa have the ventral ends of the occipital carina terminating before this, notably the Aculeata and Stephanidae. In a few apocritans, the ventral ends of the occipital carina joins medially below the occipital foramen, forming a continuous rim around the latter; this condition is a putative apomorphy of the Gasteruptiidae (Fig. 5D).

Conclusion

The characters explored in the present paper show considerable variation across the Hymenoptera. For many of the characters, there is considerable variation within as well as between the families and superfamilies. The most unequivocal character support is usually displayed toward the distal ends of the tree as autapomorphies of families or superfamilies (the presence of a medially interrupted epistomal sulcus (char. 10:2) in Evaniidae; the presence of a dorsally displayed occipital foramen (char. 14:1) in Ceraphronoidea; the impression of the ventral sclerotisation below the occipital foramen to form a cavity for the labiomaxillary complex (char. 18:1) in Ichneumonoidea; having the occipital carina continuous ventrally of the occipital foramen (char. 21:2) in Gasteruptiidae); or autapomorphies of the Hymenoptera (the inflection of the

clypeus; char. 11:1). Characters that corroborate more inclusive clades above the superfamily level are much rarer. An example of one such character is the absence of the occipital sulcus and ridge (char. 13:1) which has been lost in Xiphydriidae, Orussidae and Apocrita.

This pattern was even more obvious in the analyses of the much more comprehensive mesosomal data set assembled by Vilhelmsen et al. (2010a, fig. 67), where most relationships between the superfamily and ordinal levels were poorly, if at all, supported. This again emphasises the need to build comprehensive data sets for combined analyses to make progress with complicated phylogenetic problems like the higher level relationships of the Hymenoptera. The process of developing hymenopteran phylogenetics that Alexandr P. Rasnitsyn has done so much to further is continuing today, providing ever expanding insights into the evolutionary history of this megadiverse group.

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RESEARCH ARTICLE

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A molecular phylogeny of the Cephinae (Hymenoptera, Cephidae) based on mtDNA COI gene: a test of traditional classification

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Abstract

Cephinae is traditionally divided into three tribes and about 24 genera based on morphology and host utilization. There has been no study testing the monophyly of taxa under a strict phylogenetic criterion. A molecular phylogeny of Cephinae based on a total of 68 sequences of mtDNA COI gene, representing seven genera of Cephinae, is reconstructed to test the traditional limits and relationships of taxa. Monophyly of the traditional tribes is not supported. Monophyly of the genera are largely supported except for *Pachycephus.* A few host shift events are suggested based on phylogenetic relationships among taxa. These results indicate that a more robust phylogeny is required for a more plausible conclusion. We also report two species of *Cephus* for the first time from Turkey.

Keywords

Hymenoptera, phylogeny, Cephidae, COI, host shift.

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Introduction

The Cephidae is a small family of Hymenoptera with a thin integument, usually black or dark colored and commonly with narrow yellow bands on the abdomen. It comprises approximately 160 species in three subfamilies and about 24 genera and is primarily Holarctic (Benson 1935, 1946; Smith and Schmidt 2009; Taeger et al. 2010). Two of the subfamilies, Athetocephinae and Australcephinae are represented by only four species and are restricted to Madagascar and the Australian Region (Benson 1935, 1946; Smith and Shinohara 2002a; Smith and Schmidt 2009). The majority of species are included in the Holarctic subfamily Cephinae. Although several faunal treatments (Ries 1937; Middlekauff 1969; Zhelochovtsev and Zinovjev 1988; Calmasur and Ozbek 2010; Korkmaz et al. 2010) and a single world review (Muche 1981) have been published, and a number of cephid species have been described in recent years (Smith and Solomon 1989; Smith 1997; Smith and Shinohara 2002a,b; Smith and Schiff 2005; Wei 2007; Smith and Schmidt 2009; Wei and Smith 2010), their phylogenetic relationships have not been investigated.

Cephidae can be easily identified since they are morphologically intermediate between the hymenopteran suborders Symphyta and Aculeata. Because of several apocritan-like characters, such as a weak constriction between the first and second abdominal segments, the lack of cenchri and the rough area on fore wing, and the form of male genitalia, they were once considered as a likely sister group of Apocrita (Königsmann, 1977). However, considerable evidence from both morphological and molecular data strongly support a sister group relationship between Orussidae and Apocrita, and the Cephoidea, containing the only family Cephidae, appears as to share a last common ancestor with a lineage leading to the Siricoidea (e.g., Rasnitsyn 1980,1988; Basibuyuk and Quicke 1995; Vilhelmsen 1997, 2001; Ronquist et al. 1999; Schulmeister et al. 2002; Sharkey 2007).

Ries (1937) suggested that *Janus* is the most primitive genus of Cephinae based on its filiform and many segmented antennae and tarsal claws. Benson (1946) divided the Cephinae into three tribes, Cephini, Hartigiini and Pachycephini based both on morphology and host utilization. The larvae of Cephini bore in the stems of Poaceae, those of Pachycephini live in the stems of Papaveraceae and Poaceae, and those of Hartigiini bore in the twigs of Rosaceae or other arborescent plant families (Benson 1946; Middlekauff 1969). Numerous morphological characters and color patterns that traditionally have been used for separation of the taxa within the family are claimed to be either variable or display phenotypic plasticity (Ries 1937; Benson 1946, 1968; Korkmaz et al. 2010). Current classification is mainly based on morphology and host usage and therefore necessitates a close examination under the phylogenetic approaches.

Phylogenetic studies of taxa that exhibit adaptive phenotypic variation provide valuable insights into the evolutionary forces driving the origins of diversification (Zhang et al. 2008). Research on phytophagous insects has confirmed that adaptation and specialization to different plant species are central to generating diversifica-

tion at all hierarchical levels (Mopper and Strauss 1998; Berlocher and Feder 2002; Funk et al. 2002; Nosil et al. 2002; Eubanks et al. 2003; Lozier et al. 2007). However, host specialization in the Cephinae, as observed in most phytophagous insect groups, might have led to evolutionary shift between higher taxonomic groups. Host shift probably has taken place many times at different periods, and therefore the classification based on host use may not reflect the true phylogenetic relationship within the Cephinae.

Here, we selected the mitochondrial cytochrome oxidase subunit I (COI) gene to reconstruct the phylogenetic relationships of the Cephinae and identify systematic position of its tribes and genera by applying phylogenetic inference methods. The selected COI gene region is informative for estimating relationships at both intra- and interspecies level due to possession of both completely conserved and variable regions and having a heterogeneous evolutionary rate across the gene (Lunt et al. 1996; Dowton and Austin 1997; Caterino et al. 2000; Roe and Sperling 2007; Bacci et al. 2009) This region is also utilized as DNA–based bio-identification system for animals at the global level (Hebert et al. 2003). *Cephus parvus* (Dovnar-Zapolskij, 1931) and *C. runcator* Konow, 1896, are recorded for the first time from Turkey.

Material and methods

Sixty-eight specimens representing three tribes and seven genera of the subfamily Cephinae were collected from localities presented in Table 1. All specimens are deposited in the Entomological Collection of Cumhuriyet University, Sivas (ECCUS). A specimen of *Arge* sp. (Argidae) was included as an outgroup in the phylogenetic analyses. Several keys were used to identify the specimens (Benson 1946, 1951, 1968; Muche 1981; Zhelochovtsev and Zinovjev 1988). The taxa names, the voucher specimens, and GenBank accession numbers are presented in Table 1.

DNA extraction, amplification, and sequencing

Alcohol-preserved specimens were allowed to dry on filter paper, and DNA was extracted from left legs of the specimens using the High Pure PCR Template Preparation Kit (Roche Diagnostics, Mannheim, Germany) following the protocol for DNA isolation from mammalian tissue. Each DNA sample was dissolved in 200 µl elution buffer and stored at -20°C. The partial mitochondrial COI gene (750 bp) was amplified by using the conserved COI primers with the following sequence: COI–s1859, 5' – GGAACIGGATGAACWGTTTAYCCICC – 3' and COI–a2590 5' – GCTCCTATTGATARWACATARTGRAAATG – 3' (Simon et al. 1994). PCR reactions were conducted with 10 µl of extracted DNA in 50 µl reaction mixture. Amplification conditions were as follows: denaturation for 5 min at 94°C, followed by 37 cycles of denaturation at 94°C for 30 s, annealing at 59°C for 45 s, extension at 72°C for 30 s

Table 1. List of taxa and voucher specimens used for sequencing.

Genus	Species	Voucher no.	GenBank accession no.	Location	Col. date
Arge	sp.	ECCUS 201	JF901916		
Calameuta					
	filiformis (Eversmann, 1847)	ECCUS 210	JF901849	İçel	12.04.2009
	filiformis	ECCUS 211	JF901850	Sivas	04.06.2009
	haemorrhoidalis (Fabricius, 1781)	ECCUS 212	JF901852	Kütahya	20.05.2009
	haemorrhoidalis	ECCUS 213	JF901853	Isparta	17.05.2009
	haemorrhoidalis	ECCUS 214	JF901855	Kocaeli	04.05.2010
	haemorrhoidalis	ECCUS 215	JF901856	Kocaeli	04.05.2010
	haemorrhoidalis	ECCUS 216	JF901857	Bayburt	05.06.2010
	haemorrhoidalis	ECCUS 217	JF901858	Uşak	19.05.2009
	haemorrhoidalis	ECCUS 218	JF901859	Isparta	17.05.2009
	idolon (Rossi, 1794)	ECCUS 219	JF901851	Konya	17.05.2009
	pallipes(Klug, 1803)	ECCUS 220	JF901854	Sivas	13.05.2010
	pallipes	ECCUS 221	JF901860	Hakkari	11.06.2003
	pygmaea (Poda, 1761)	ECCUS 222	JF901848	Hatay	09.04.2009
	sp.	ECCUS 223	JF901861	Sivas	17.06.2007
Cephus					
	brachycercus Thomson, 1871	ECCUS 230	JF901871	İstanbul	08.05.2010
	brachycercus	ECCUS 231	JF901872	Sivas	10.05.2010
	fumipennis Eversmann, 1847	ECCUS 232	JF901873	Ardahan	07.06.2010
	nigrinus Thomson, 1871	ECCUS 233	JF901874	İstanbul	08.05.2010
	parvus (Dovnar-Zapolskij, 1931)	ECCUS 234	JF901875	Sivas	17.05.2010
	parvus	ECCUS 235	JF901876	Sivas	26.05.2010
	pulcher Tischbein, 1852	ECCUS 236	JF901877	Erzurum	06.06.2010
	pygmeus (Linné, 1767)	ECCUS 237	JF901911	Denizli	18.05.2009
	pygmeus	ECCUS 238	JF901912	Hatay	09.04.2009
	pygmeus	ECCUS 239	JF901913	Hatay	09.04.2009
	pygmeus	ECCUS 240	JF901914	Bayburt	07.06.2008
	pygmeus	ECCUS 241	JF901915	Bayburt	07.06.2008
	rjabovi Dovnar-Zapolskij, 1926	ECCUS 242	JF901878	Kırıkkale	20.06.2009
	rjabovi	ECCUS 243	JF901879	Kırıkkale	20.06.2009
	runcator Konow, 1896	ECCUS 244	JF901880	Edirne	07.05.2010
	runcator	ECCUS 245	JF901881	Edirne	07.05.2010
	sareptanus Dovnar-Zapolskij, 1928	ECCUS 246	JF901882	Erzurum	06.06.2010
	sareptanus	ECCUS 247	JF901883	Erzurum	06.06.2010
	sp.	ECCUS 248	JF901884	Bilecik	05.05.2010
	sp.	ECCUS 249	JF901885	Bilecik	05.05.2010
	sp.	ECCUS 250	JF901886	Çanakkale	06.05.2010
	sp.	ECCUS 251	JF901887	Amasya	02.05.2010
	sp.	ECCUS 252	JF901888	Amasya	02.05.2010
	sp.	ECCUS 253	JF901889	Tekirdağ	08.05.2010
	sp.	ECCUS 254	JF901890	Sivas	18.05.2010
	sp.	ECCUS 255	JF901891	Erzurum	06.06.2010

Genus	Species	Voucher no.	GenBank accession no.	Location	Col. date
	sp.	ECCUS 256	JF901892	Kars	07.06.2010
	sp.	ECCUS 257	JF901893	Kars	07.06.2010
	sp.	ECCUS 258	JF901894	Bolu	04.05.2010
Trachelus					
	iudaicus (Konow, 1907)	ECCUS 260	JF901865	Bayburt	05.06.2010
	iudaicus	ECCUS 261	JF901866	Bayburt	05.06.2010
	libanensis (André, 1881)	ECCUS 262	JF901867	İçel	13.04.2009
	libanensis	ECCUS 263	JF901868	İçel	13.04.2009
	sp.	ECCUS 264	JF901862	Sivas	12.06.2010
	sp.	ECCUS 265	JF901863	Sivas	30.05.2010
	tabidus (Fabricius, 1775)	ECCUS 266	JF901869	İçel	12.04.2009
	tabidus	ECCUS 267	JF901870	Çanakkale	06.05.2010
	troglodyta (Fabricius, 1787)	ECCUS 268	JF901864	Zonguldak	03.05.2010
Hartigia					
	linearis (Schrank, 1781)	ECCUS 270	JF901896	Ardahan	07.06.2010
	linearis	ECCUS 271	JF901897	Kırşehir	03.06.2003
	linearis	ECCUS 272	JF901898	Kırşehir	03.06.2003
	nigra (M. Harris, 1779)	ECCUS 273	JF901899	Konya	17.05.2009
	sp.	ECCUS 274	JF901900	Sivas	17.05.2010
	sp.	ECCUS 275	JF901901	Sivas	13.05.2010
	xanthostoma (Eversmann, 1847)	ECCUS 276	JF901902	Zonguldak	03.05.2010
	xanthostoma	ECCUS 277	JF901903	Zonguldak	03.05.2010
Syrista					
	parreyssii (Spinola, 1843)	ECUUS 280	JF901906	Sivas	26.05.2007
	parreyssii	ECUUS 281	JF901907	Adana	05.06.2003
Characopygus					
	sp.	ECCUS 290	JF901895	İçel	13.04.2009
Pachycephus					
	cruentatus (Eversmann, 1847)	ECCUS 300	JF901904	Sivas	06.06.2009
	smyrnensis J.P.E.F. Stein, 1876	ECCUS 301	JF901908	Edirne	07.05.2010
	smyrnensis	ECCUS 302	JF901909	Edirne	07.05.2010
	smyrnensis	ECCUS 303	JF901910	Sivas	11.06.2010
	sp.	ECCUS 304	JF901905	Sivas	12.06.2010

and a 5 min final extension at 72°C. The purification and sequencing of amplification products were performed using a commercial sequencing company (Macrogen Ltd., Seoul, Korea.). Sequencing reactions were carried out in both directions using the same primers as in PCR reactions. The forward and reverse nucleotide sequences were assembled and edited by eye using the CodonCode Aligner v 3.5.6 (CodonCode Corporation) and aligned by using CLUSTAL W version 1.83 (Thompson et al. 1994), using the default parameters of the program. Finally, all the sequences obtained are deposited in GenBank (Table 1).

Data analysis

Estimates of evolutionary divergence analyses were conducted in MEGA5 (Tamura et al. 2007) using the Kimura 2-parameter model (Kimura 1980) over sequence pairs between genera. The rate variation among sites was modeled with a gamma distribution (shape parameter = 0.87). The presence of substitution saturation was determined with DAMBE version 4.5.18 (Xia and Xie 2001). The genetic distance versus the number of transitions and transversions at first, second and third codon position in all taxa was plotted to examine the saturation at a partial COI gene sequences.

In order to investigate the phylogenetic relationship of Cephinae, phylogenetic trees were constructed using maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) methods. Nucleotides were used as discrete and unordered characters. The best-fit model of DNA substitution and the parameter estimates used for tree constructions were chosen according to the Akaike Information Criterion (AIC) as implemented in Modeltest version 3.7 (Posada and Crandall 1998). The phylogenetic signal in the data partitions was estimated by maximum likelihood mapping method (Strimmer and von Haeseler 1997) using TREE-PUZZLE version 5.2 program (Schmidt et al. 2002). MP phylogenies were estimated, with characters unordered and equally weighted, under the heuristic search algorithms 'simple' and 'TBR' using PAUP version 4.0b10 (Swofford 2002). Bootstrap estimates were calculated from 100 replicates under the above search options. This whole procedure was also applied to the data after removal of the third codon position. ML analyses (Felsenstein 1981) were conducted using RAxML-VI-HPC v. 4.0.0 (Stamatakis 2006)f. The AIC results from Modeltest provided the GTR + I + G model as the best-fit for substitution model. BI analysis was performed with the software BEAST v. 1.5.2 (Drummond and Rambaut 2007). The analysis was run with four chains for 5×10^7 generations, sampling from the chain every 5.000 generations. This generated an output of 10^4 trees. All analyses were performed assuming a Yule process of diversification. In order to confirm that the chains had achieved stationary, we evaluated "burn-in" plots by plotting log-likelihood scores and tree lengths against generation number using the software Tracer v. 1.5 (Drummond and Rambaut 2007). After determining convergence, we discarded all samples obtained during the first five millions generations as "burn-in". The percentage of samples recovering any particular clade in a BI analysis represents that posterior probability of a clade (Huelsenbeck and Ronquist 2001). A majority rule consensus tree (Bayesian tree) was then calculated from the posterior distribution of trees, and the posterior probabilities calculated as the percentage of samples recovering any particular clade. The BI tree built with TREEANNOTATOR, discarding the initial 10% of samples as burn-in [Fig-TREE v. 1.3.1] (Rambaut 2008) was used to visualize the results. For the sake of a better presentation, branches representing individuals belonging to same species were collapsed if the species is recovered as monophyletic (Fig. 4).

Results

Evaluation of the material collected after publication of Korkmaz et al. (2010) and Calmasur and Ozbek (2010) revealed that there are two additional species of *Cephus* occur in Turkey. The examined material is presented below.

Cephus parvus **(Dovnar-Zapolskij, 1931)**

Material examined. Turkey: Sivas [39°42.71'N, 37°01.30'E] 1300 m, 26.05.2010, 1♀, 17.05.2010, 1♂.

Distribution. Palearctic region

Cephus runcator **Konow, 1896**

Material examined. Turkey: Edirne [40°39.32'N, 26°17.82'E] 50 m, 07.05.2010, 6♀, 1♂.

Distribution. Turkey, S. E. Europe

The complete alignment of the partial mitochondrial COI gene sequences from 68 cephid specimens, including representatives of these two new records, resulted in a fragment containing 658 base pairs, among which 287 nucleotide positions were variable and 223 sites of which were parsimony-informative. The analyzed sequences correspond to a functional mitochondrial gene region because of the presence of singular peaks in each chromatograph and absence of in–del and premature stop codons, and presence of the highest nucleotide substitutions at the third codon position (Avise 1994). The percentages of nucleotide composition at each codon position are variable (Fig. 1). The mean frequency of COI sequences used in the analyses showed a bias of A + T (T 37.0%, C 15.2%, A 33.9% and G 16.0%), which is similar to other reported members of Hymenoptera (Jermiin and Crozier 1994, Dowton and Austin 1995,1997, Leys et al. 2000, Danforth et al. 2003). The A + T content at the third, second and first codon positions are 90.7%, 59.8%, and 61.9%, respectively. The nucleotide G has lowest (1.0%) and the A highest content (52.8%) at the third codon positions. The distribution of polymorphic sites for all cephid species shows that the majority of substitutions are at synonymous sites. The vast majority of synonymous substitutions are also found at third codon positions with a rate of 87.88% for the Cephinae. The first and the second positions are relatively more conserved in comparison with the third position.

The numbers of base substitutions per site from averaging over all sequence pairs between genera are shown in Table 2. The least diverged genera appears to be *Chara-*

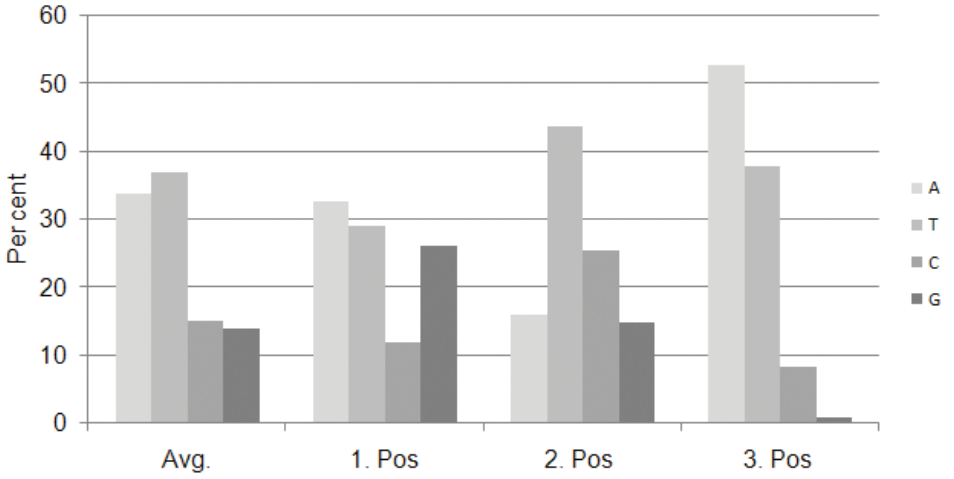

Figure 1. Percentage of nucleotide composition at each codon position.

copygus and *Pachycephus* (p= 0.062) and, the most are *Hartigia* and *Syristra* (p= 0.161) also with highest standard error value of 0.017.

All three codon positions in the partial COI gene were analyzed for saturation, achieved by plotting the number of observed substitutions against the model TN93 genetic distance estimates. The scattergrams (Fig. 2a–c) showed that transitions and transversions for the first, second and third codons of the partial COI gene increased with the genetic distance, but considerable scattering was also observed. In addition, a similar plot of the third codon transition of the COI gene (Fig. 2d) suggested that saturation of transition occurred between certain pairs of the taxa, which may lead to higher levels of homoplasy (Kumar et al. 2001; Zhang et al. 2008).

Table 2. Estimates of evolutionary divergence over sequence pairs between genera. The number of base substitutions per site from averaging over all sequence pairs between groups are shown. Standard error estimates are shown above the diagonal.

Genera	1	2	3	4	5	6	7	8
1.Calameuta		0.010	0.011	0.010	0.013	0.012	0.015	0.025
2.Trachelus	0.110		0.010	0.009	0.013	0.012	0.014	0.025
3.Cephus	0.108	0.119		0.007	0.013	0.010	0.016	0.026
4.Characopygus	0.078	0.094	0.069		0.012	0.007	0.012	0.028
5.Hartigia	0.136	0.146	0.143	0.114		0.013	0.017	0.029
6.Pachycephus	0.116	0.125	0.113	0.062	0.137		0.013	0.029
7.Syrista	0.124	0.145	0.156	0.102	0.161	0.125		0.030
8.Outgrup	0.248	0.263	0.256	0.249	0.292	0.278	0.279	

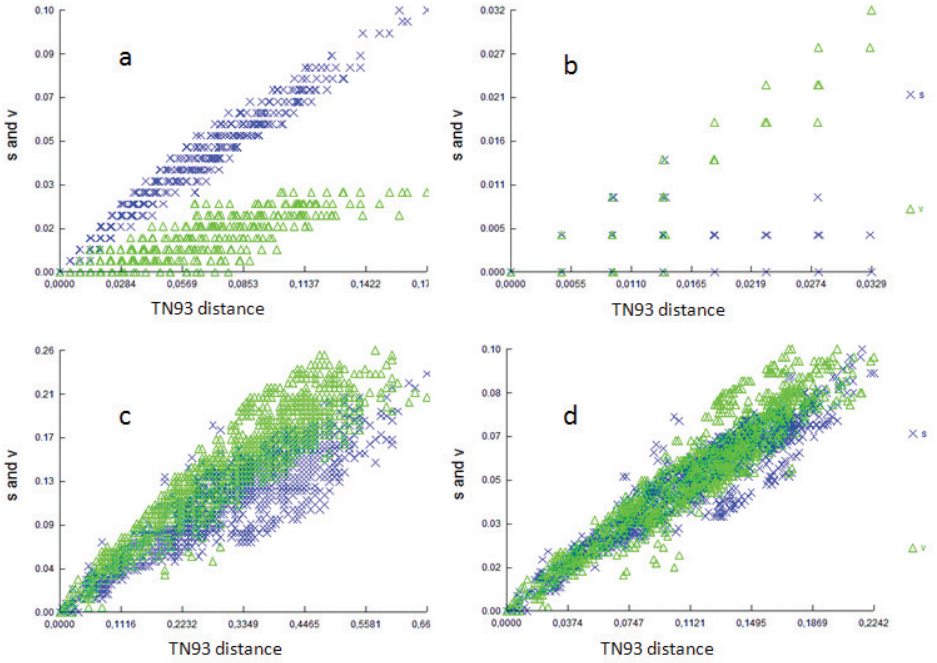

Figure 2. Saturation plots of transversion and transition rates against JC69 distance at **a** first codon position **b** second codon position **c** third codon position, and **d** sum of data.

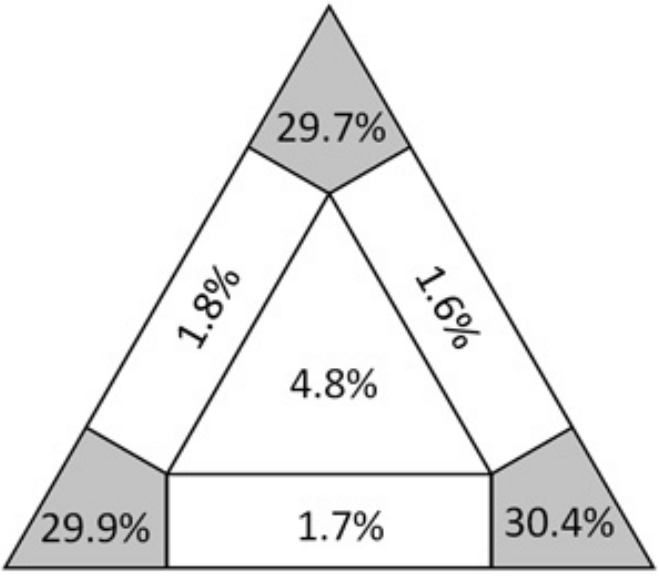

Figure 3. Likelihood mapping analysis of the sequence alignments of COI gene present in the Cephinae. The regions at the corners of the triangles correspond to the three possible tree topologies for a quartet; the lateral regions to partly resolved trees and the central region to unresolved trees. The numbers indicate the percentage of quartets falling in each region.

Result of likelihood mapping is presented in Fig. 3. High dichotomic phylogenetic signal was detected in the dataset. The percentage of the quartets suggesting a star- or network- like phylogeny is 9.9%, indicating that data are reliable for a dichotomic phylogenetic analysis (Schmidt 2009). For ML analysis GTR+I+G models showed a significantly better fit than the other less complicated models for the COI dataset. Maximum likelihood analyses under the same model of evolution resulted in topologies with lnL = – 5570.6831 in RAxML, which were very close to the BI tree. Bayesian inference under the GTR+I+G model resulted in a topology with mean lnL = – 5347.963. Posterior probability values from the BI were congruent with ML bootstrap support. ML and BI analyses generated a tree with almost the same overall topology (Fig. 4). Equally weighted parsimony analysis of the 287 parsimony-informative characters produced 12 most parsimonious trees with a length of 1065 steps (Homoplasy Index = 0.608, Retention Index = 0.392 and Consistency Index = 0.392). These equally parsimonious solutions were due to differences in terminal branches. However, the branching pattern of bootstrap tree was comb-like and recovered almost no original branches. Considering that this may be due to many synonymous changes in the third codon position, we run an analysis excluding the third codon position from the data. The analysis produced 60 equally parsimonious trees with a length of 200 and the bootstrap application was also resulted with no support to branching pattern of original trees. This may be partly attributed to the nature of data and relatively a short sequence not sufficient to detect phylogenetic signal under parsimony interference. Therefore, we do not present any MP trees here.

Discussion

Currently, the Cephinae is divided into three tribes based on morphology and feeding habits of larvae. The recovered mitochondrial gene trees substantially conflict with the current taxonomic arrangement, particularly the tribe level. Trees constructed under ML and BI methods supported monophyly of each genus except *Pachycephus* but failed to recover monophyly of any tribes. However, it should be noted that monophyly of most genera were supported by low posterior values (Fig. 4). This is probably due to the strongly biased nucleotide composition and the saturation at the third codon position (Fig. 2). The BI tree suggests that the most basal clade of Cephinae is the genus *Cephus* making the Cephini paraphyletic with respect to rest of Cephini and other tribes. Occurrence of *Syrista* within Pachycephini rather than Hartigiini makes both tribes polyphyletic and paraphyletic respectively (Fig. 4). Otherwise, Pachycephini and Hartigiini appear as sister groups. However, we do not propose a new classification as the present phylogeny is generated from a single gene fragment.

Evolution of phytophagy has occurred many times in insects, and is often accompanied by a significant increase in rates of speciation (Mitter et al. 1988). Phytophagous insects are also notable for their high degree of host-plant specialization; probably over 75% of species feed only on members of one plant family (Bernays and Chap-

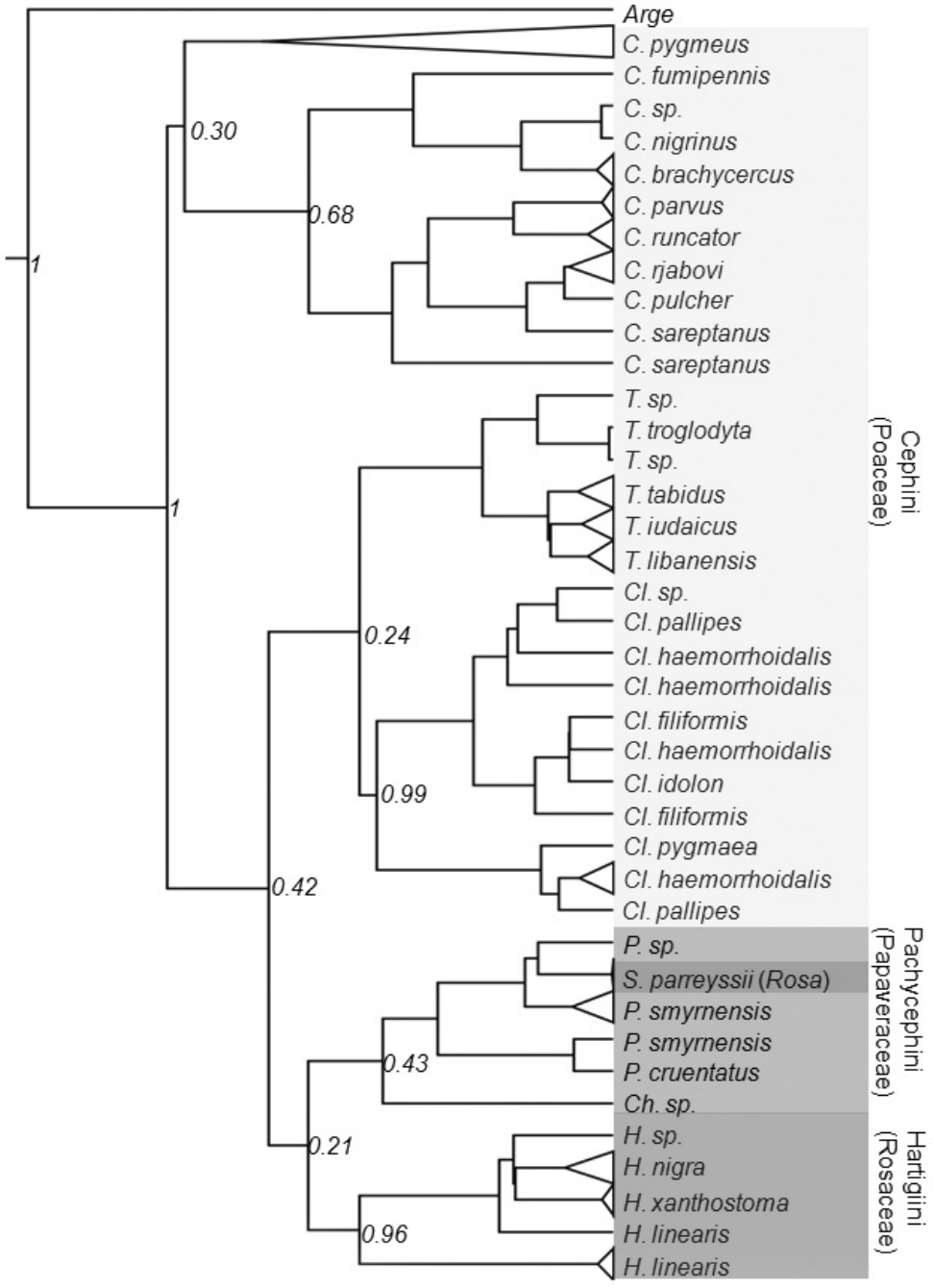

Figure 4. Bayesian interface tree based on the mitochondrial COI gene sequences of the Cephinae. Host plants are indicated in parentheses. Numbers at nodes indicate the posterior values.

man 1994), and many insect species feed only on a single plant species (Scheffer and Wiegmann 2000). *Syrista* which is considered in the tribe Hartigiini, occurred within Pachycephini clade (see Fig. 4) and this placement is questionable as larvae of *Syristra* feed on *Rosa.* However, if this placement is considered to be true than it suggests a host shift event from Papaveraceae to Rosaceae. Occurrence of *Cephus* at most basal clades also suggests two later shifts from Poaceae to Rosaceae and Papaveraceae (Fig. 4). Considering relationships among genera and species of Cephini inferred from the present phylogenetic hypothesis, several host shift events are also evident. However, we are reluctant for further discussion until a more robust phylogeny become available derived from analyses of several gene sequences of both nuclear and mitochondrial genomes.

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RESEARCH ARTICLE

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Lytopylus Förster (Hymenoptera, Braconidae, Agathidinae) species from Costa Rica, with an emphasis on specimens reared from caterpillars in Area de Conservación Guanacaste

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Abstract

Twelve species of Costa Rican *Lytopylus* are treated; these include all species reared from Lepidoptera caterpillars in Area de Conservación Guanacaste, Costa Rica, over 32 years of caterpillar inventory, as well as two species recorded in the literature as occurring in Costa Rica. Ten new species are described, i.e., *Lytopylus bradzlotnicki, Lytopylus colleenhitchcockae, Lytopylus gregburtoni, Lytopylus jessicadimauroae,*

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Lytopylus jessiehillae, Lytopylus mingfangi, Lytopylus rebeccashapleyae, Lytopylus robpringlei, Lytopylus sandraberriosae, Lytopylus vaughntani. The following species are transferred to *Lytopylus*: *Metriosoma flavicalcar* Enderlein 1920 to *Lytopylus flavicalcar* **comb. n.**; *Bassus macadamiae* Briceño and Sharkey 2000 to *Lytopylus macadamiae* **comb. n.**; *Metriosoma bicarinatum* Enderlein 1920 to *Lytopylus bicarinatum* **comb. n.**; *Metriosoma brasiliense* Enderlein 1920 to *Lytopylus brasiliense* **comb. n.**; *Bassus tayrona* Campos 2007 to *Lytopylus tayrona* **comb. n.**; *Microdus femoratus* Cameron 1887 to *Lytopylus femoratus* **comb. n.**; *Microdus melanocephalus* Cameron 1887 to *Lytopylus melanocephalus* **comb. n.**; *Bassus pastranai* Blanchard 1952 to *Lytopylus pastranai* **comb. n.**; *Agathis nigrobalteata* Cameron 1911 to *Lytopylus nigrobalteatus* **comb. n.** Two keys to species of *Lytopylus* are presented, one interactive and the other static.

Keywords
parasitoids, biology, endoparasitoids, koinobiont, Lepidoptera

Introduction

This is the first of a series of articles to revise the species of Agathidinae reared from lepidopteran caterpillars as part of the inventory of the caterpillars and their parasitoids of Area de Conservación Guanacaste (ACG), northwestern Costa Rica (http://janzen.sas.upenn.edu; http://www.acguanacaste.ac.cr; Janzen et al 2009). It includes keys, in traditional and interactive formats, to the reared species of *Lytopylus* Förster and to the two species of *Lytopylus* previously recorded from Costa Rica. This is not meant to be a comprehensive treatment of the Costa Rican fauna of *Lytopylus*. A conservative estimate, based on extensive collections at INBio, the Universidad de Costa Rica, and the University of Kentucky, is that there are a minimum of 50 species occurring in the country. Here we treat only 12.

Lytopylus, though proposed in 1862, has spent most of its existence as a junior synonym of *Bassus* Fabricius, *Microdus* Nees, and *Agathis* Latreille. Sharkey et al. (2009) removed it from synonymy in their revision of the Oriental genera of Agathidinae. New World members of the genus may be distinguished from other agathidines by the sculpture of the third metasomal median tergite and by the structure of the propodeal foramen. See the first couplet of the key included in this publication for specifics. The sistergroup to *Lytopylus* is *Braunsia* Kriechbaumer which is restricted to the Old World and is mostly tropical or subtropical (Sharkey et al. 2006).

The source files for the keys, descriptions, illustrations, DNA sequence and distributional data are all freely available to future researchers who may wish to build on this beginning. The detailed specimen records are available by search of the individual specimen DHJPARxxxxxxx voucher codes at http://janzen.bio.upenn.edu/caterpillars/database.lasso. DNA trace files and primer information are available through the Barcode of Life Datasystem (BOLD) [Ratnasingham and Hebert 2007] at http://www.boldsystems.org.

Methods

Phenetic and phylogenetic trees, using 658 base pairs of cytochrome *c* oxidase (COI) data, were constructed using neighbor-joining (NJ), maximum parsimony (MP) and Bayesian methods. MP was performed using TNT (Goloboff et. al, 2008). A traditional search with 100 random addition sequences followed by branch-swapping, saving 100 trees per replication, was performed. 1000 bootstrap replications were used to estimate branch reliability. The Bayesian analysis was performed using MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). Best-fitting DNA substitution models were determined using MrModeltest2.2 (Nylander 2004). The general time reversible model of evolution with a parameter for invariant sites and rate heterogeneity modeled under a gamma distribution (GTR+I+G) was determined as the best-fitting model.

The Bayesian analysis consisted of two independent Bayesian MCMC runs initiated from different random starting trees. The analysis ran for 2,000,000 generations, reaching a topological similarity criterion of 0.01; trees were sampled every 500 generations. 25% of the trees from each run were removed as burn-in upon topological convergence.

The NJ tree was produced from PAUP* (Swofford 2002) using default settings.

Sequence data, trace files, and field data are available on BOLD (www.barcodinglife.org). Additional collection information is deposited at http://janzen.sas.upenn.edu, and all sequences have been deposited in the GenBank database.

The dichotomous key, descriptions, and the interactive key (Appendices 1–3) were generated using DELTA Editor Dallwitz et al. (1999), DELTA Dallwitz et al. (1993), and Intkey Dallwitz et al. (1995).

This set of 10 species of ACG *Lytopylus*, represented by 76 specimens, is the yield from rearing 498,000+ wild-caught caterpillars of about 6,000 species from ACG dry forest, cloud forest, and rain forest, and a variety of intergrades, over 32 years, beginning 1978 (Janzen et al 2009). At least 90% of these caterpillars were, in some instar, large enough to host a larva of *Lytopylus*. The names of the caterpillars, from which the degree of host-specificity mentioned below is determined, is the collective contribution of more than 100 taxonomists and parataxonomists working with both caterpillar morphology and food plant biology, and correlated adult morphology; additionally, nearly all of the caterpillar species have now had their adults DNA-barcoded as yet another check on identification (Janzen et al 2009, 2011).

Abbreviations and codes. There are numerous codes in the text. Codes beginning with an "H" and followed by numbers are unique identifiers used for specimens in the Sharkey lab at the University of Kentucky, and in the specimen database (http://sharkeylab.org/taxabank/home.php), e.g., H6408. Codes beginning with DHJPAR, e.g., DHJPAR0036705, are used by Janzen as unique identifiers for the parasitoids reared by the ACG caterpillar inventory. Some of the Lepidoptera hosts are incompletely identified; however, they also have unique names such as *Desmia* Solis19 (which is an interim name for *Desmia* species 19 as determined by M. Alma Solis of the USDA Systematic Entomology Laboratory, Washington, D.C.). These

names will be updated in the Janzen database (http://janzen.sas.upenn.edu/caterpillars/database.lasso) when the species is baptized with a formal scientific name, but the interim name, in this case *Desmia* Solis19, will remain searchable in that database. Host caterpillars are uniquely identified by their own voucher code system, which is recognizable by YY-SRNP-XXXXX where "YY" is the two digit year and "XXXXX" is a unique number within that year. DNA barcodes associated with each specimen via the DHJPAR code also each have a searchable accession on BOLD (e.g. ASBC979-07 for DHJPAR0021167).

Abbreviations used for specimen depositories are as follows:

AEI American Entomological Institute, Gainesville, Florida, USA.

HIC Hymenoptera Institute Collection, University of Kentucky, Department of Entomology, Lexington, Kentucky, USA.

INBio National Biodiversity Institute, Santo Domingo de Heredia, Costa Rica.

Results

Phylogeny and Biology: *Lytopylus* is an unusual genus of Agathidinae in that it has a cosmopolitan distribution and a wide range of host higher taxa. Most genera of Agathidinae found in the neotropics are restricted to the New World. When there are exceptions to this rule, they are in the form of Holarctic genera that appear to have dispersed into cool, high altitude areas in the northern neotropics, e.g., *Agathis*, which is found at high altitudes in Costa Rica (Sharkey, unpublished). Most genera of Agathidinae also seem to be restricted to one or a few closely-related families of Lepidoptera; however, the collective set of *Lytopylus* species attack a wide range of host families. Even within the small sample of ten reared species of *Lytopylus* represented here, five host families are attacked, i.e., Crambidae, Elachistidae, Pyralidae, Thyrididae, and Tortricidae. However, all of these are leaf-rolling and leaf-tying small caterpillars. *Lytopylus* are conspicuous in not using species of caterpillars that feed exposed on leaf surfaces (e.g., butterflies and macro-moths), and in not using large caterpillars. However, their absence from leaf-nest-occupying Hesperiidae (over 500 species reared from ACG, Janzen et al. 2011) remains a puzzle, especially since *Bassus brooksi,* a reasonably close relative to *Lytopylus*, attacks a very specific, large subset of ACG Hesperiidae (Janzen et al. 1998).

Figure 1 presents the NJ tree, which was much more resolved than were the phylogenetic trees produced by MP and Bayesian analyses. However all three methods were congruent with each other, both in that individuals of what are believed to be a single species grouped together, and the groups bear the same relative position to each other. We mapped the support values of the Bayesian and MP analyses on the NJ tree. Branches without values are those that collapsed in the phylogenetic analyses.

Individual species of *Lytopylus* tend to be rather host-specific. Of the species treated here all but one, *L. jessiehillae*, are found on a single host species. And even the hosts of

L. jessiehillae are very similar to each other. Moreover, the results of our phylogenetic analyses (Fig. 1) show that host family is directly correlated to phylogenetic history, with sister species of *Lytopylus* sharing the same host family in every case (three). For members of *Lytopylus,* as with most other closely examined genera of Agathidinae in ACG, the regular use of multiple species of hosts by a single species is the exception and host range is phylogenetically constrained, albeit at a lower taxonomic level than appears to be the case with other Agathidinae.

Taxonomy: Sharkey *et al.* (2009) distinguished *Lytopylus* from *Bassus* and removed it from synonymy, however only three Neotropical species were formally transferred, i.e., *L. boliviensis* (Szepligeti), *L. bicristatus* (Enderlein), and *L. facetus* (Enderlein). The following is a list of all of the non-Costa Rican Neotropical species of *Lytopylus* known to MJS that are not treated above or elsewhere in this paper; all are new combinations: *Metriosoma bicarinatum* Enderlein 1920 = *Lytopylus bicarinatum*; *Metriosoma brasiliense* Enderlein 1920 = *Lytopylus brasiliense; Bassus tayrona* Campos 2007 = *Lytopylus tayrona*; *Microdus femoratus* Cameron 1887 = *Lytopylus femoratus*; *Microdus melano-*

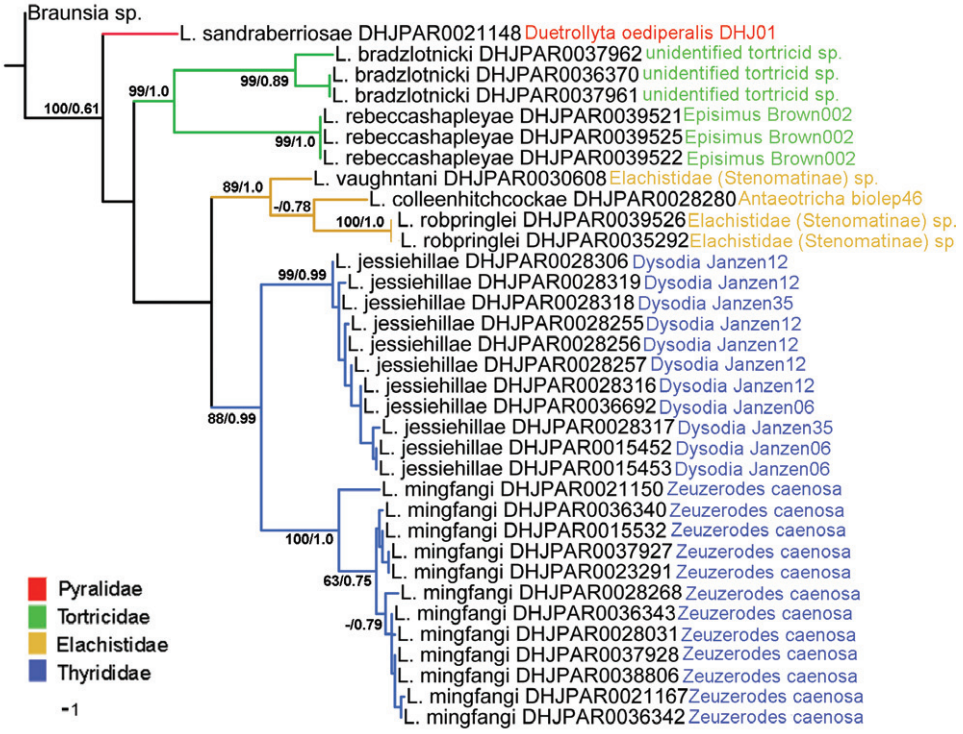


Figure 1. NJ tree of the COI barcode region for eight of the 10 *Lytopylus* treated here. Branch support = parsimony bootstrap/Bayesian posterior probabilities (bootstrap values less than 60 are not illustrated). Branches and host names are colored to reflect host family.

cephalus Cameron 1887 = *Lytopylus melanocephalus*; *Bassus pastranai* Blanchard 1952 = *Lytopylus pastranai*; *Agathis nigrobalteata* Cameron 1911 = *Lytopylus nigrobalteatus.*

Members of *Lytopylus* can be distinguished from other agathidines in the New World with two characters. Most species (90%) of *Lytopylus* have some sculpture (rugosity, striae, etc.) on the third median tergite (Fig. 2c, T3), whereas other New World agathidines have T3 completely smooth or rarely with some very weak coriaceous sculpture (Fig. 2d). The 10% of *Lytopylus* that lack sculpture on T3 can be distinguished by the position of the cavity on the mesosoma (MC) into which the metasoma inserts. In species of *Lytopylus* (Fig. 2a) it is positioned completely above the coxal cavities of the hind leg and separated from them by a straight transverse carina (TC). In other agathidines (except *Braunsia*, an Old World genus) the ventral margin of MC is positioned below the dorsal margin of CC and a straight transverse carinae is lacking (Fig. 2b).

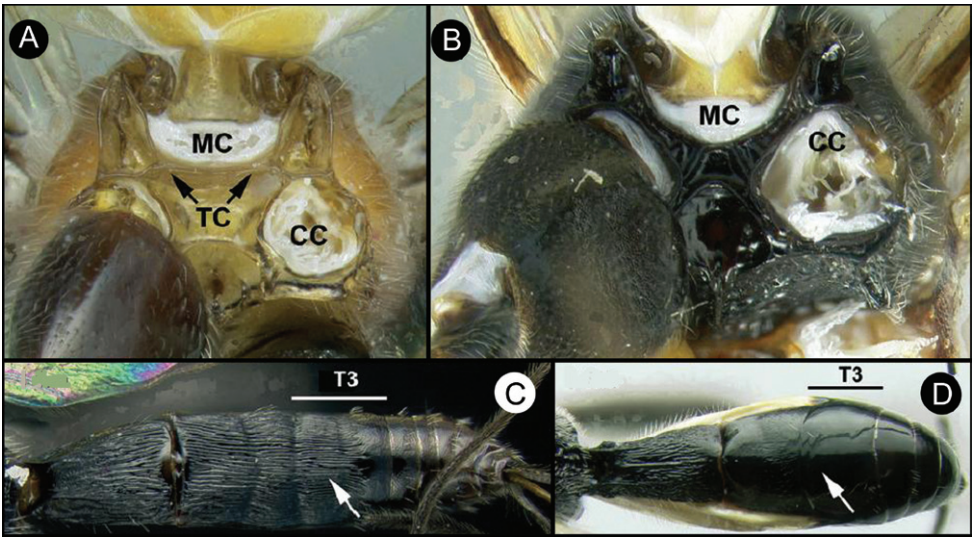
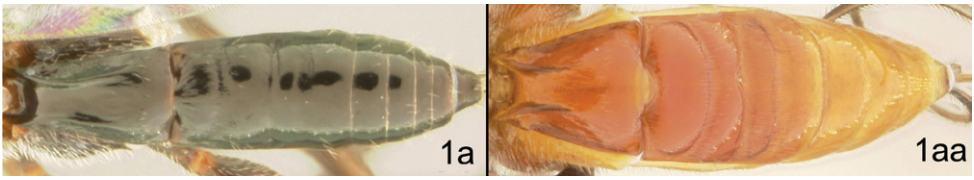


Figure 2. a *Lytopylus* sp. Metasomal cavity (MC) situated entirely dorsal to coxal cavities (CC); a wide, high, straight, transverse carinae (TC) between MC and CC **b** *Therophilus* sp. MC situated partly between CC **c** *Lytopylus* sp. median tergite 3 (T3) showing extensive striae in anterior half **d** *Therophilus* sp. T3 smooth.

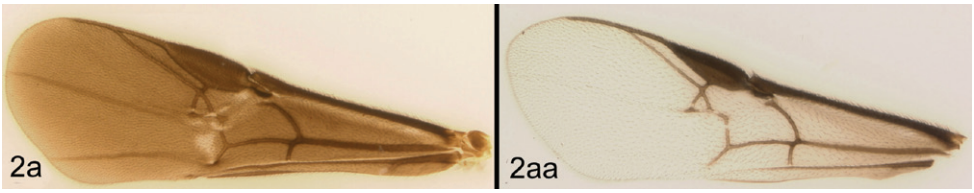
Key to Costa Rican species of *Lytopylus* (♀ and ♂)

Note: This key is restricted to those species reared in ACG and those that are recorded in the literature as occurring in Costa Rica. Since there are a minimum of 50 species of (mostly undescribed) *Lytopylus* occurring in Cost Rica, users of this key should compare specimens with the descriptions and images after identification using the key below or the interactive key found here.

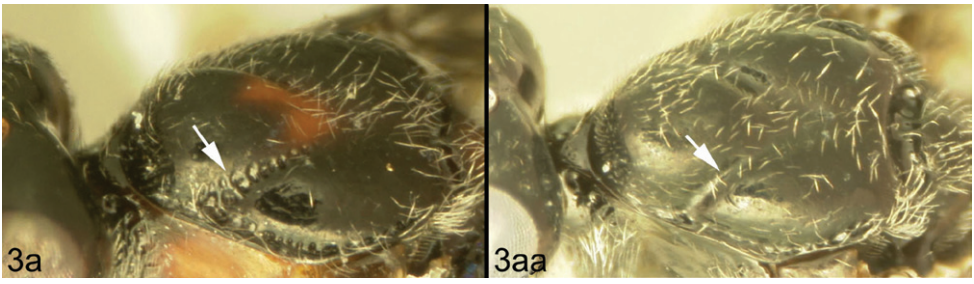
1a Metasoma mostly or entirely melanic.....**2**
1aa Metasoma mostly or entirely pale, yellow, orange, or reddish brown.....**4**



2 Forewing evenly and deeply infuscate ..... ***L. vaughntani* sp. n.**
2aa Forewing mostly hyaline, sometimes weakly infuscate basally **3**

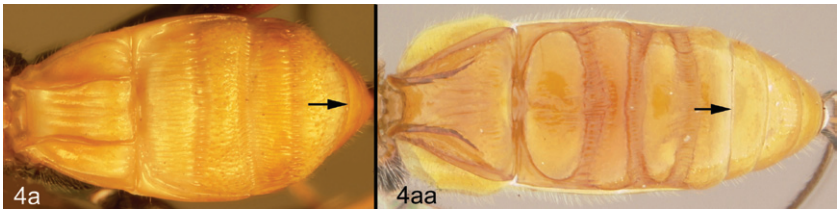


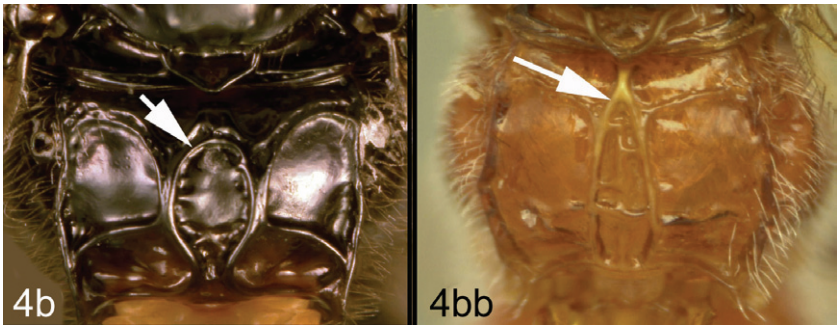
3a Notauli sculptured with crenulae in anterior half.....***L. bradzlotnicki* sp. n.**
3aa Notauli mostly or entirely smooth in anterior half.....
.....***L. rebeccashapleyae* sp. n.**



4a Median syntergite 2+3 forming a carapace that almost covers all more posterior terga; posterior margin of median syntergite 2+3 convex; 4b. median areola of propodeum well-defined and smooth with a rounded anterior border.... **11**

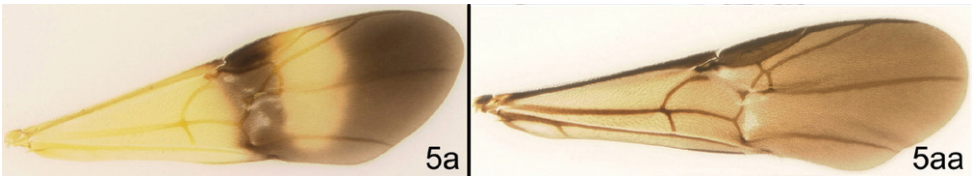
4aa Median syntergite 2+3 not forming a carapace that almost covers all more posterior terga; posterior margin of median syntergite 2+3 straight; 4bb. median areola of propodeum not as above, either pentagonal or triangular with sharp angles, or absent **5**





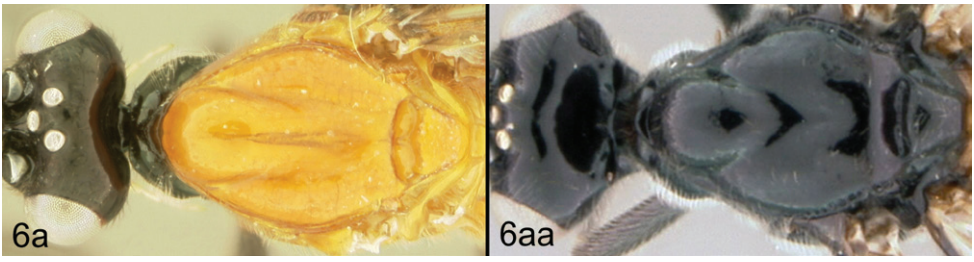
5a Forewing banded ..... ***L. sandraberriosae* sp. n.**

5aa Forewing not banded, mostly or entirely infuscate **6**

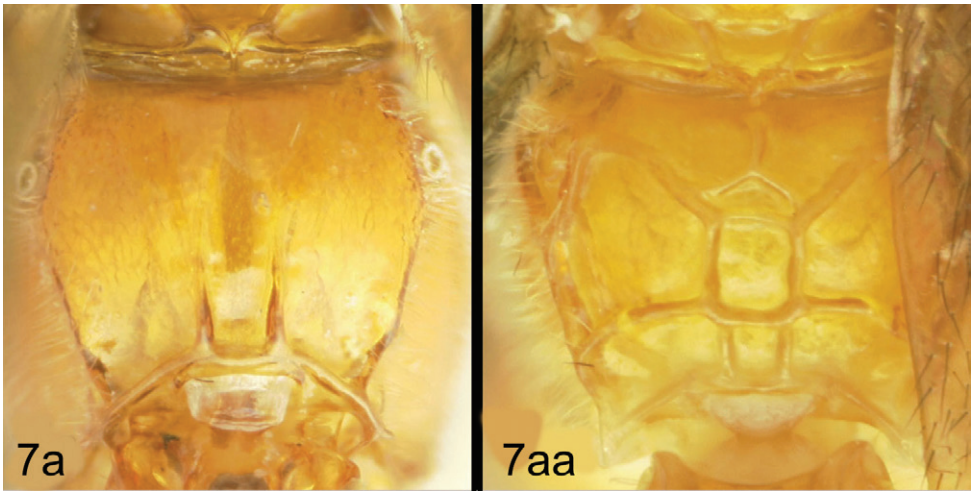


6a Mesoscutum mostly or entirely pale, orange or reddish yellow 7

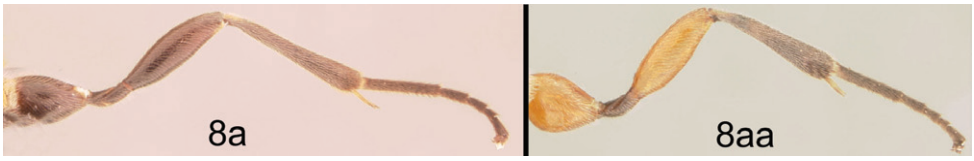
6aa Mesoscutum mostly or entirely melanic **8**



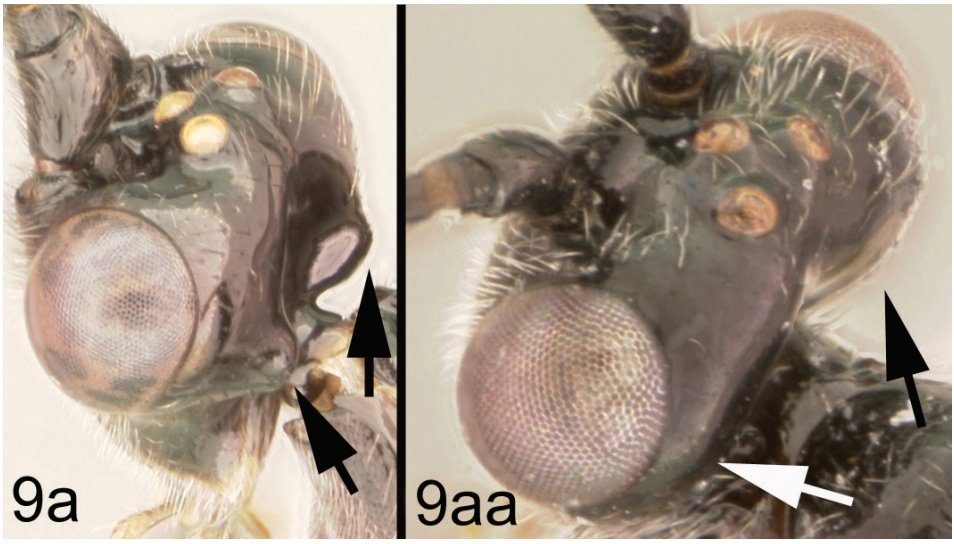
7a Propodeum mostly smooth, lacking areolae .....***L. flavicalcar*** **(Enderlein)**
7aa Propodeum sculptured with areolae .....***L. robpringlei*** **sp. n.**



8a Hind leg almost entirely black **9**
8aa Hind leg reddish in large part, either coxa or femur or both reddish **10**

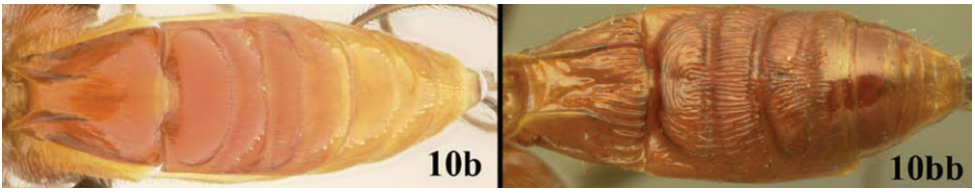


9a Occiput relatively sharply angled at mid-height .....***L. gregburtoni*** **sp. n.**
9aa Occiput evenly rounded..... ***L. colleenhitchcockae*** **sp. n.**



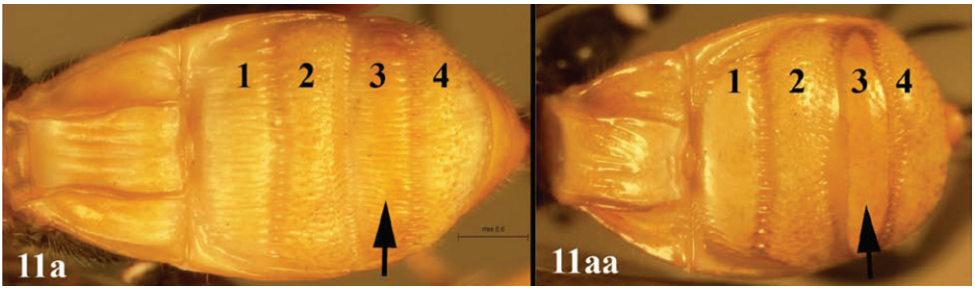
10a Gena acute posterolaterally; 10b. median syntergite 2+3 not heavily sculptured ..... ***L. jessicadimauroae*** **sp. n.**

10aa Gena rounded or obtuse posteroventrally; 10bb. median syntergite 2+3 heavily sculptured ..... ***L. macadamiae*** **(Briceño and Sharkey)**



11a Third lobe of median syntergite 2+3 entirely striate ..... ***L. jessiehillae*** **sp. n.**

11aa Third lobe of median syntergite 2+3 smooth, at least posteriorly..... ..... ***L. mingfangi*** **sp. n.**



Species treatments

Lytopylus bradzlotnicki **Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_bradzlotnicki
Figs 3, 4

Description. Body length 4.1 – 4.5 mm. Ovipositor length 3.9 – 4.2 mm. Gena rounded or with an obtuse angle posterolaterally. Longitudinal groove on interanten-

nal prominence absent. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola not rounded anteriorly. Notauli well-impressed, with crenulae extending well along its length. Posterior margin of syntergum 2+3 straight. Median syntergite 2 + 3 weakly longitudinally rugose in anterior half to two-thirds, smooth posteriorly. Forewing clear except base slightly infuscate. Color as in Figs 3, 4. Color variation: Pale color of mesonotum may be more extensive or completely absent. Pale color of pronotum may be much reduced but always extensive on meso- and metapleuron. Pale color of hind femur varies from almost completely pale to almost completely melanic.

Molecular data. BOLD process ID/ Janzen parasitoid voucher/GenBank accession:
ASHYC4707-10/DHJPAR0037962/JN034688;
ASHYD1561-09/DHJPAR0036370/JN034687;
ASHYC4706-10/DHJPAR0037961/JN034686-

Distribution. Guanacaste Province and Alajuela Province, Costa Rica. Click here for a distribution map.

Biology. All three rearings are from an unidentified Tortricidae of the same species feeding on rain forest *Psidium guajava* (Myrtaceae). Since this food plant is widely introduced into ACG pastures, it is assumed that the "natural" food plant of this caterpillar is some other plant and therefore the *Lytopylus* may be there as well. This tortricid lightly silks two overlapping leaves together and lives in a silk and fecal pellet tangle between them, while skeletonizing the leaf. Therefore, the wasp likely accesses the caterpillar by ovipositing through the leaf. This wasp and *L. rebeccashapleyae* are the only *Lytopylus* reared from more than 5,000 ACG tortricid rearings of dry forest and rain forest caterpillars. *Austroearinus* (Agathidinae) also has been reared in very low numbers from other species of tortricids than those that are *Lytopylus* hosts.

Etymology. *Lytopylus bradzlotnicki* is named in honor of Brad Zlotnick of San Diego, California, who has enthusiastically supported the conservation of the ACG rain forest occupied by this parasitoid wasp.

Material examined. Holotype: ♀, H6409 (DHJPAR0037961) Costa Rica: Guanacaste: Area de Conservación Guanacaste: Sector Pitilla: Estacion Pitilla: 7.ii.2010, 10.9893N/85.4258W, 675m [AEI].

Paratypes [AEI, HIC, INBio]: Costa Rica: Alajuela: Area de Conservación Guanacaste: Sector Rincon Rainforest: Estacion Caribe: 26.v.2009, 10.9018N/85.2749W, 415m: ♀, H7078 (DHJPAR0036370). Sector Pitilla: Estacion Pitilla: 7.ii.2010, 10.989N/85.425W, 675m: ♀, H7071 (DHJPAR0037962). San Carlos: P.N. Arenal: Colada: 1.ii-iii.2000, 10.635N/84.47W, 600m: ♀ H7081, ♀ H7070, ♀ H7073, ♀ H7072, ♀ H7069.

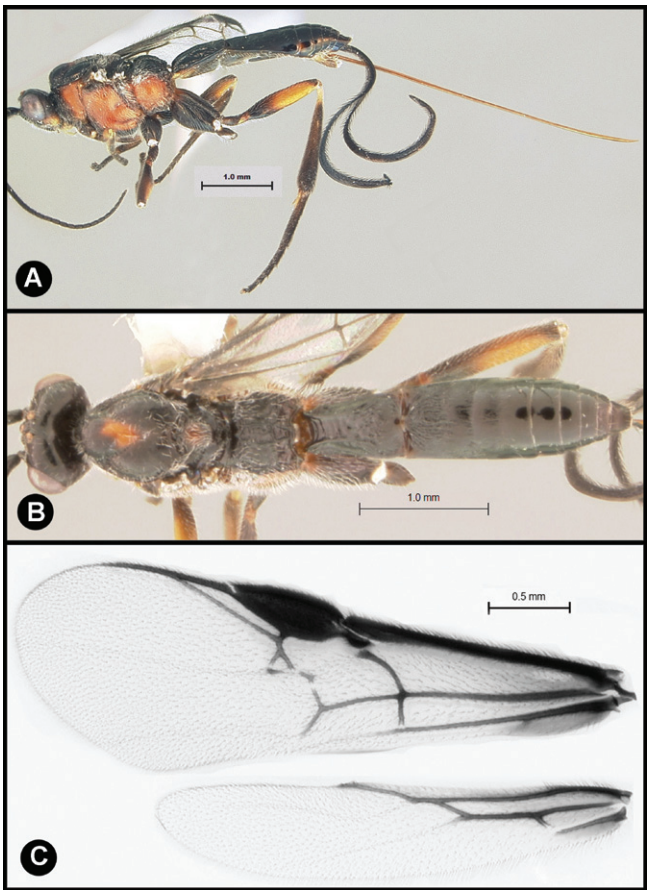


Figure 3. *Lytopylus bradzlotnicki* sp. n. Holotype **a** lateral habitus **b** dorsal habitus **c** wings.

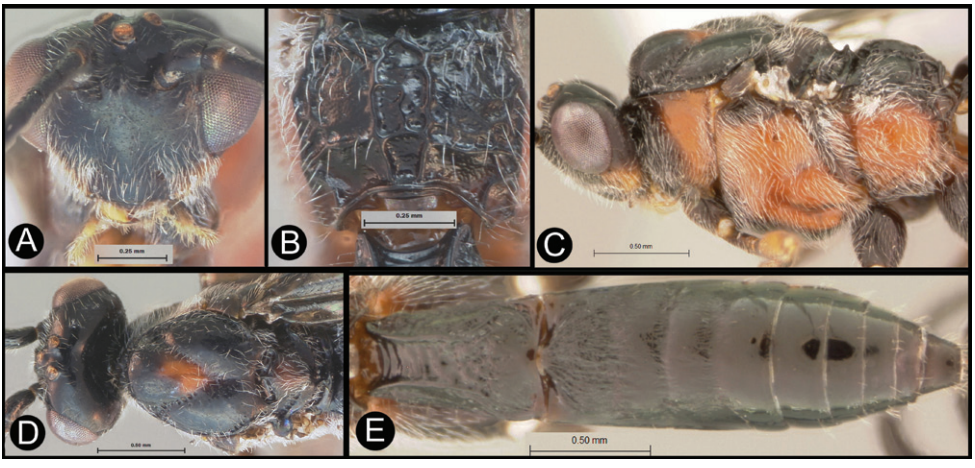


Figure 4. *Lytopylus bradzlotnicki* sp. n. Holotype **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

***Lytopylus colleenhitchcockae* Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_colleenhitchcockae
Figs 5, 6

Description. Body length 5.2 mm. Gena acute posterolaterally, or rounded or with an obtuse angle posterolaterally. Longitudinal groove on interantennal prominence present. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola not rounded anteriorly. Notauli well-impressed, with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior margin of syntergum 2+3 straight. Median syntergite 2 + 3 longitudinally striate except extreme apex smooth. Forewing mostly or entirely infuscate. Color as in Figs 5, 6.

Molecular data. BOLD process ID/Janzen parasitoid voucher/GenBank accession: ASHYF042-09/DHJPAR0028280/JN034689.

Distribution. Guanacaste Province, Costa Rica. Click here for a distribution map.

Biology. The single rearing is from *Antaeotricha* biolep46 (Elachistidae, Stenomatinae) feeding on rain forest *Inga chocoensis* (Fabaceae). It is the only *Lytopylus* reared from *Inga*-eating caterpillars in ACG. The caterpillar lightly webs two overlapping leaves as described for the elachistid hosts of *Lytopylus robpringlei*. The flimsy white wasp cocoon (Fig. 7) is spun between the same two leaves and the wasp eclosed 10 days after spinning.

The inventory has reared 101 wild-caught Elachistidae from *Inga chocoensis* and this is the sole agathidine wasp obtained. The score for all 1,846 rearings of Elachistidae from all species of *Inga* during 33 years is this single *Lytopylus* plus five *Austroearinus* spp. (to be treated elsewhere).

Etymology. Named in honor of Colleen Hitchcock of Boston, Massachusetts, who has enthusiastically supported the conservation of the ACG forest occupied by this parasitoid wasp.

Material examined. Holotype: ♂, H6836 (DHJPAR0028280) Costa Rica: Guanacaste: Area de Conservación Guanacaste: Sector Pitilla: Ingas: 11.0031N/ 85.4204W, 580m, 2.x.2007 [AEI].

***Lytopylus flavicalcar* (Enderlein) comb. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_flavicalcar
Figs 8, 9

Metriosoma flavicalcar Enderlein 1920

Description. Body length 8.2 – 9.5 mm. Ovipositor length 9.0 – 10.5 mm. Gena rounded or with an obtuse angle posterolaterally. Longitudinal groove on interantennal prominence absent. Protuberances on occiput absent. Propodeum mostly smooth, lacking areolae. Notauli absent, or indicated by a weak smooth medio-posterior de-

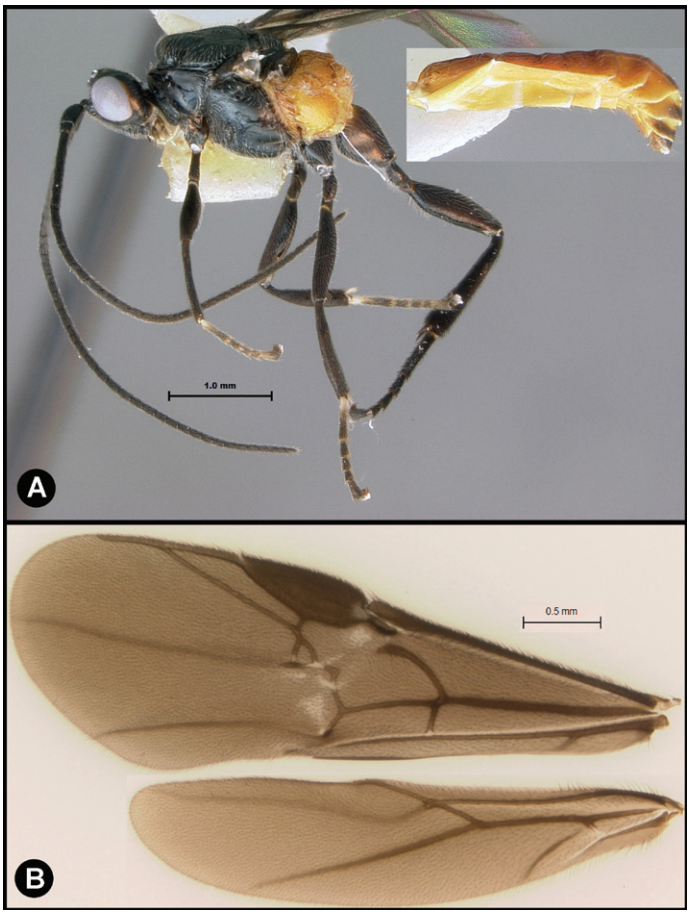


Figure 5. *Lytopylus colleenhitchcockae* sp. n. Holotype **a** lateral habitus **b** wings.

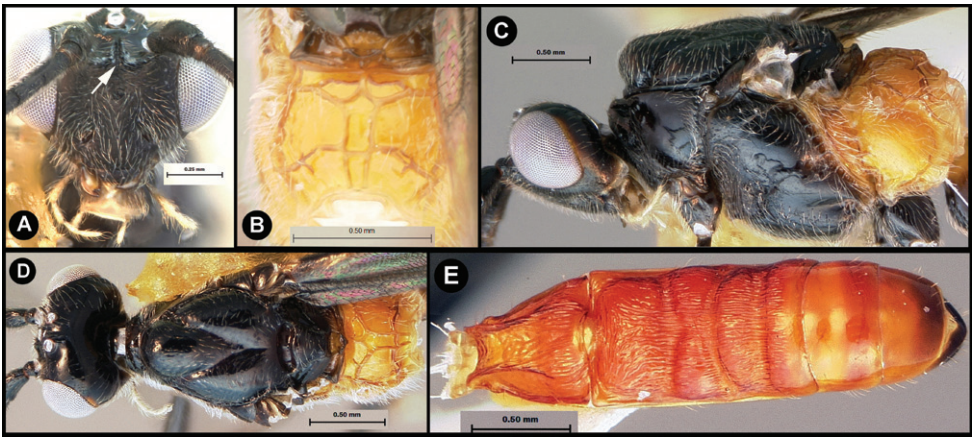


Figure 6. *Lytopylus colleenhitchcockae* sp. n. Holotype **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

Figure 7. *Lytopylus colleenhitchcockae* cocoon.

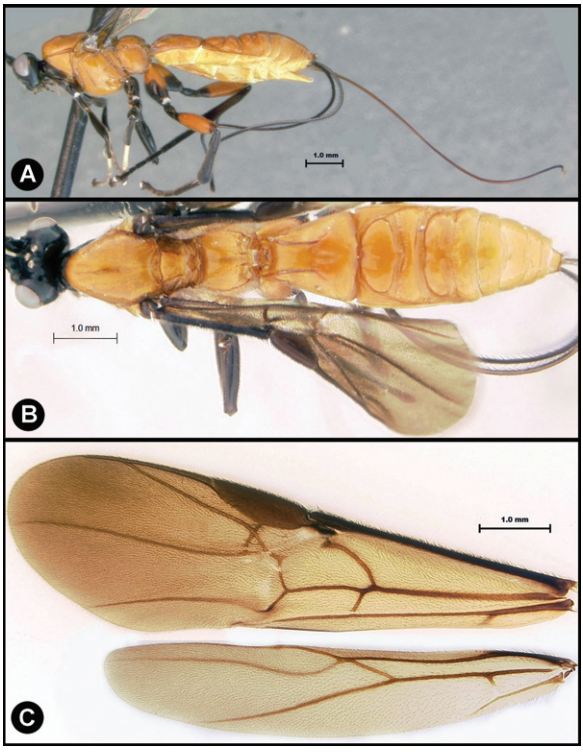


Figure 8. *Lytopylus flavicalcar* (Enderlein) **a** lateral habitus **b** dorsal habitus **c** wings.

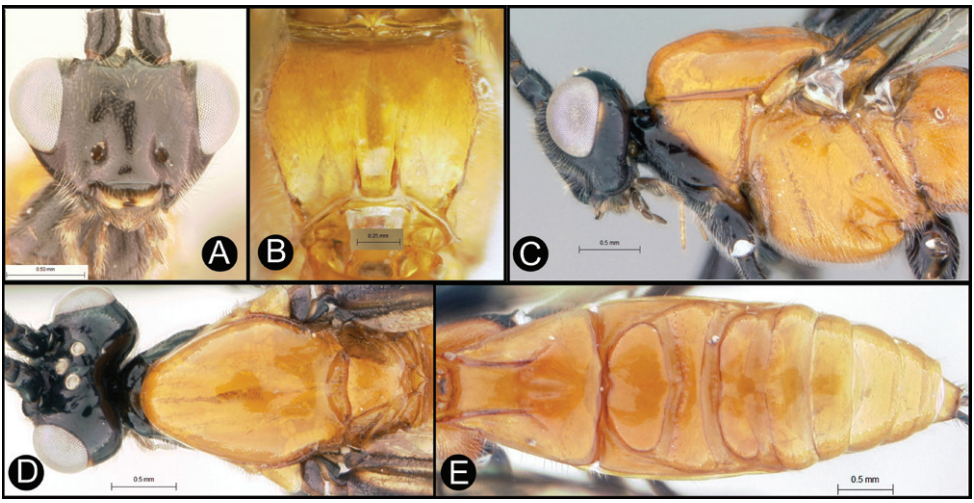


Figure 9. *Lytopylus flavicalcar* (Enderlein) **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

pression. Posterior margin of syntergum 2+3 straight. Median syntergite 2 + 3 smooth, lacking microsculpture. Forewing mostly or entirely infuscate. Color as in Figs 8, 9. Color variation: I have only included specimens here that are colored almost exactly as is the holotype. There are many other specimens from Costa Rica (INBio) that seem structurally to be very similar but differ primarily in that the hind femur is completely melanic. These may or may not be conspecific.

Distribution. Puntarenas and Alajuela provinces, Costa Rica. Click here for a distribution map.

Biology. Unknown.

Material examined. Holotype: ♀, Colombia, Fusagasuga (about 30 km. S. of Bogota), E. Pehlke S. (collector), Museum of the Institute of Zoology, Polish Academy of Science**.**

Non-type material: [HIC, InBio]: Costa Rica: Puntarenas: Buenos Aires: Estacion Altamira: Sendero Los Gigantes: 10.469N/84.339W, 1450m, 15.vii.-16.viii.2000.♀ H6407, ♀ H6465. Alajuela: Upala: Albergue Heliconias: Sendero Mirador, 10.891N/85.015W, 1000m, 20–31.viii.2000: ♀ H7082

Lytopylus gregburtoni **Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_gregburtoni
Figs 10, 11

Description. Body length 6.4 – 7.9 mm. Ovipositor length 3.7 – 5.5 mm. Gena acute posterolaterally, or rounded or with an obtuse angle posterolaterally. Longitudinal groove on interantennal prominence present. Protuberances on occiput present.

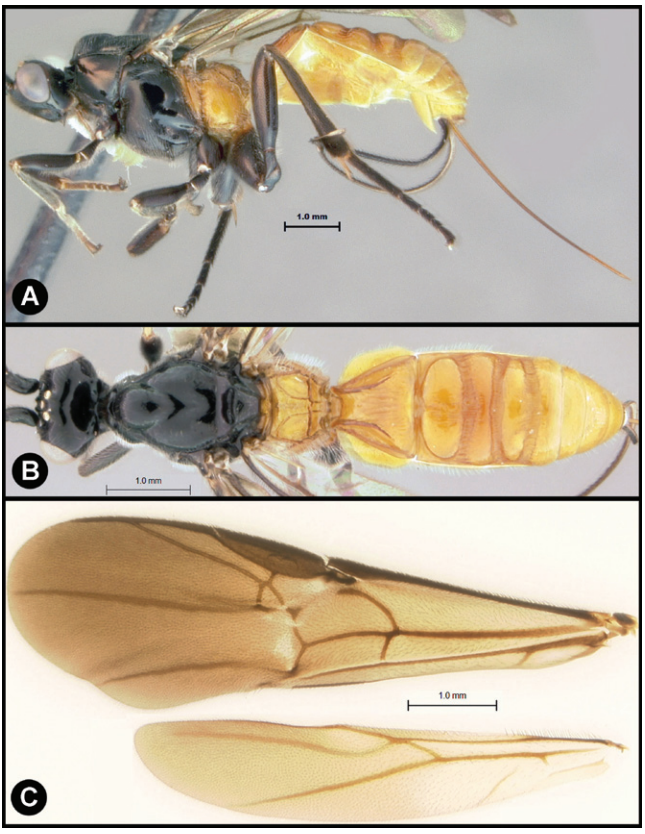


Figure 10. *Lytopylus gregburtoni* sp. n. **a** lateral habitus **b** dorsal habitus **c** wings.

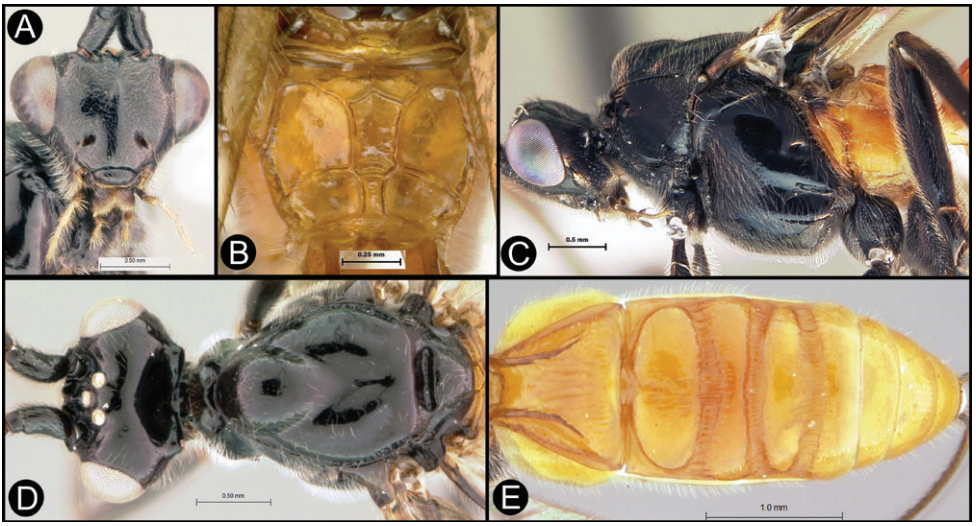


Figure 11. *Lytopylus gregburtoni* sp. n. **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

Propodeum with carinae forming areolae, median areola not rounded anteriorly. Notauli well-impressed, smooth without crenulae, or with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior margin of syntergum 2+3 straight. Median syntergite 2 + 3 mostly smooth with longitudinal striae in the three transverse depressions and sometimes striate anteromedially anterad first transverse depression. Forewing mostly or entirely infuscate. Color as in Figs 10, 11. Color variation: This species is very consistent in color across all 18 specimens examined.

Distribution. Puntarenas Province and Alajuela Province, Costa Rica. Click here for a distribution map.

Biology. The single rearing is from *Desmia* Solis19 (Crambidae, Spilomelinae) feeding on *Psychotria panamensis* (Rubiaceae) in ACG rain forest. The caterpillar makes a large sloppy leaf roll and lives within it, among leaf fragments and fecal pellets. The wasp spins its cocoon inside the leaf roll. This caterpillar has been reared 150+ times from a diverse array of Rubiaceae in the rain forest understory, and this is the only Agathidinae to appear (but it is accompanied by a diverse array of tachinids, ichneumonids and other braconids). *Desmia,* as a generic concept, has been reared 4,000+ times by the inventory, and yielded 51 Agathidinae; all but this one are in the genus *Alabagrus*.

Etymology. Named in honor of Greg Burton of Mountain View, California, who has enthusiastically supported the conservation of the ACG forest occupied by this parasitoid wasp.

Material Examined. Holotype: ♀H6408 (DHJPAR0036705) Costa Rica: Alajuela: Area de Conservación Guanacaste: Sector Rincon Rain Forest: Camino Albergue Oscar: 27.viii.2009, 10.8774N/85.3236W, 560m [AEI].

Paratypes [AEI, HIC, INBio]: Costa Rica: Alajuela: Area de Conservación Guanacaste: Sector Cacao: Cerro Pedregal: 10.928N/85.475W, 1080m: ♀: 4–11.vii.2009: H2408, H2407; H2490 30.v.-6.vi.2009; H4131 13–20.vi.2009; H2493 23–30.v.2009. Puntarenas: Las Tablas: 30.viii.-5.ix.1995, 8.955N/83.12W, 1530m:♀: H6795, H7034, H7032, H7067, H7068, H7066, H7031. Embalse: 17.vi.-13.viii.1996, 1300m: ♀: H6421, H7037. Finca Marcos Morales: 5.vii.-25.viii.1995, 1200m: ♀: H7039, H7033, H6414.

Lytopylus jessicadimauroae **Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_jessicadimauroae
Figs 12, 13

Description. Body length 6.0 – 6.3 mm. Ovipositor length 5.2 – 5.4 mm. Gena acute posterolaterally. Longitudinal groove on interantennal prominence absent. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola not rounded anteriorly. Notauli well-impressed, smooth without crenulae, or with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior

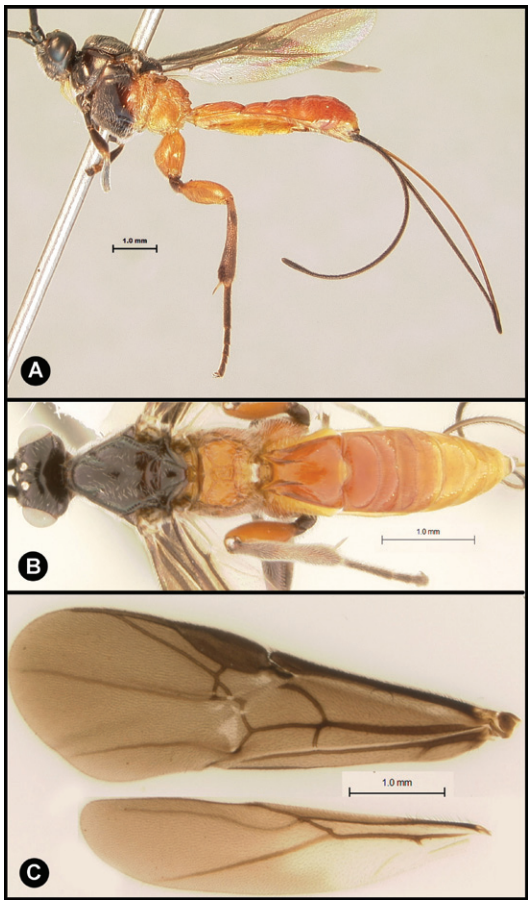


Figure 12. *Lytopylus jessicadimauroae* sp. n. Holotype **a** lateral habitus **b** dorsal habitus **c** wings.

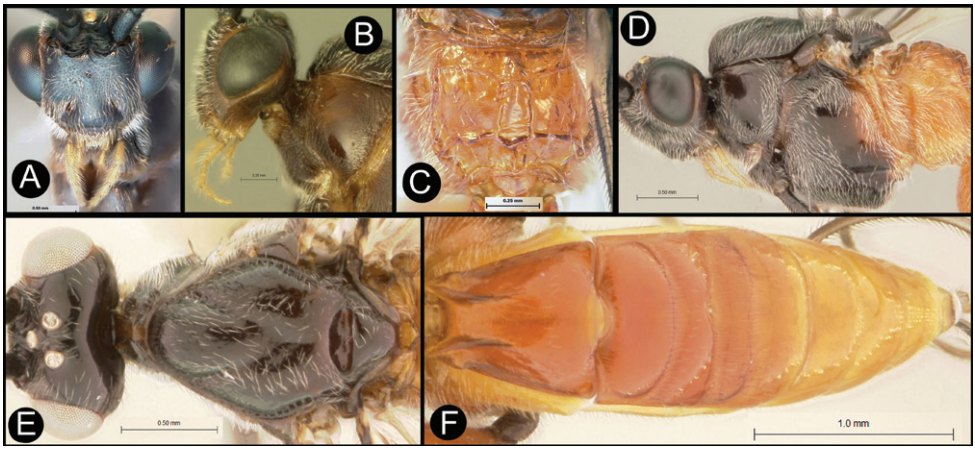


Figure 13. *Lytopylus jessicadimauroae* sp. n. Holotype **a** anterior head **b** lateral head **c** dorsal propodeum **d** lateral head and mesosoma **e** dorsal head and mesosoma **f** dorsal metasoma.

margin of syntergum 2+3 straight. Median syntergite 2 + 3 mostly smooth with longitudinal striae in the transverse grooves, and striae over much of the third lobe. Forewing mostly or entirely infuscate. Color as in Figs 12, 13. Color variation: The three paratypes differ in having more pale coloration on the thorax than does the holotype, although none is completely pale.

Distribution. Guanacaste Province, Costa Rica. Click here for a distribution map.

Biology. All four rearings are from elachJanzen01 Janzen241, a common leaf-rolling Elachistidae (Stenomatinae) that attacks only *Casearia arguta* (Salicaceae - formerly, Flacourtiaceae) in ACG dry forest. The host caterpillar very distinctively rolls the leaf from the tip to the base instead of from side to side. The tubular cavity in the roll is full of silk and fecal pellets. The wasp cocoon is spun inside the leaf roll. While this caterpillar is abundant, the caterpillars from only about 50 leaf rolls were reared to obtain these four wasps. No other parasitoids were encountered in these caterpillars. This is the only "deep dry forest" *Lytopylus* encountered by the inventory, as all the others are from rain forest or from the interface between dry forest and rain forest.

Etymology. Named in honor of Jessica Dimauro of Toronto, Ontario, Canada, who has enthusiastically supported the conservation of the ACG forest occupied by this parasitoid wasp.

Material examined. Holotype: ♀ H6611 (DHJPAR0015415) Costa Rica: Guanacaste: Area de Conservación Guanacaste: Sector Santa Rosa, Area Administrativa 11.viii.1999, 10.8376N/85.6187W, 295m [AEI].

Paratypes [AEI]: Costa Rica: Guanacaste: Area de Conservación Guanacaste: Sector Santa Rosa: Area Administrativa:,10.8376N/85.6187W, 295m: H7076, sex unknown, metasoma largely destroyed by dermestids (DHJPAR0015504) 14.vii.1980. ♀ H6616 (DHJPAR0015505) 12.vii.1980. Bosque San Emilio: 22.x.1987, 10.8438N/85.6138W, 300m. ♂ H7074 (DHJPAR0015506).

***Lytopylus jessiehillae* Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_jessiehillae
Figs 14, 15

Description. Body length 7.0 – 8.3 mm. Ovipositor length 7.2 – 7.7 mm. Gena rounded or with an obtuse angle posterolaterally. Longitudinal groove on interantennal prominence absent. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola rounded anteriorly. Notauli well-impressed, smooth without crenulae, or with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior margin of syntergum 2+3 convex, covering most of terminal terga. Median syntergite 2 + 3 longitudinally striate except apical transverse lobe rugose. Forewing mostly or entirely infuscate. Color as in Figs 14, 15. Color variation: Most commonly the mesosoma varies from completely black, to black except for the propodeum and mesothorax which are yellow or orange in whole or in part.

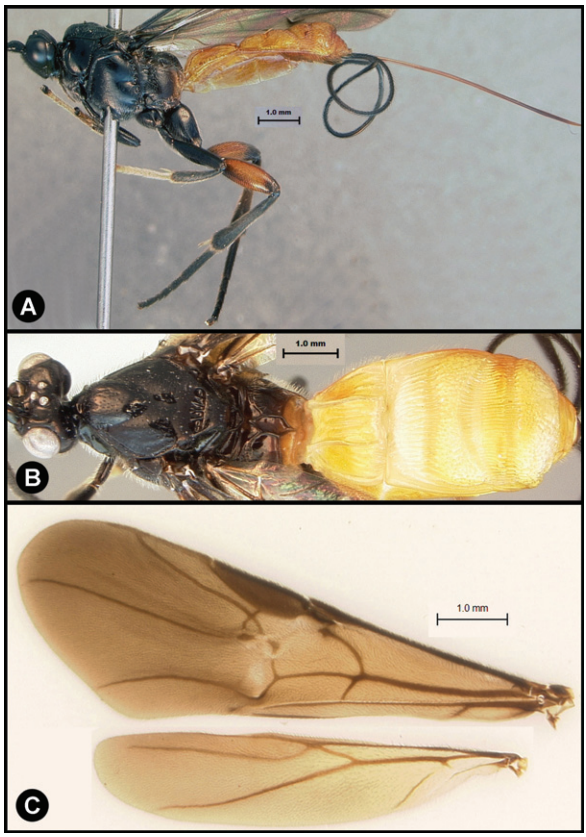


Figure 14. *Lytopylus jessiehillae* sp. n. **a** lateral habitus **b** dorsal habitus **c** wings.

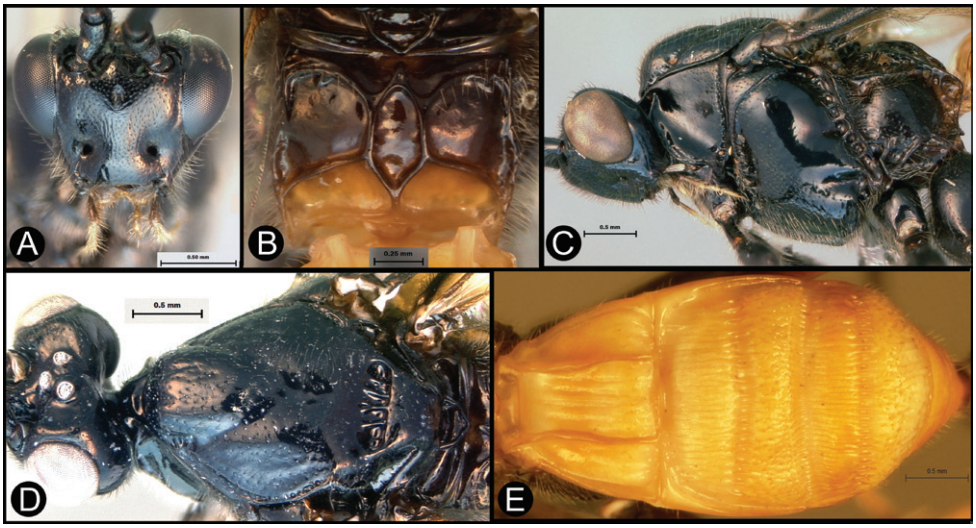


Figure 15. *Lytopylus jessiehillae* sp. n. **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

Rarely, two specimens, the mesosoma is almost entirely pale. The hind femur varies from entirely melanic to mostly pale. Pale parts of the body vary from yellow to orange.

Molecular data. BOLD process ID/Janzen parasitoid voucher/GenBank accession:
ASAG139-07/DHJPAR0015453/JN034705
ASHYE376-08/DHJPAR0028139/JN034704
ASAG138-07/DHJPAR0015452/JN034704
ASHYF079-09/DHJPAR0028317/JN034702
ASHYE1603-09/DHJPAR0036692/JN034701
ASHYE1631-09/DHJPAR0036720/JN34700
ASHYF080-09/DHJPAR0028318/JN034699
ASHYF019-09/DHJPAR0028257/JN034698
ASHYF078-09/DHJPAR0028316/JN034697
ASHYF017-09/DHJPAR0028255/JN034696
ASHYF018-09/DHJPAR0028256/JN034695
ASHYF081-09/DHJPAR0028319/JN034694
ASHYF068-09/DHJPAR0028306/JN034693

Distribution. Guanacaste Province and Heredia Province, Costa Rica. Click here for a distribution map.

Biology. This wasp is the only species of *Lytopylus* found to date using *Dysodia* (Thyrididae) as its host caterpillar (22 wasp rearings from 3,500+ rearings of about 20 *Dysodia* species). These wasp rearings are almost entirely from three species of rain forest *Dysodia* (89 *Dysodia* Janzen12 feeding exclusively on *Hieronyma oblonga*; 1,241 *Dysodia* Janzen06 feeding on many plant families; 182 *Dysodia* Janzen35 feeding on Annonaceae) in dry forest and dry-rain forest intergrades. Additionally, a single *L. jessiehillae* has been reared from *Collinsa ferreiceps* (Thyrididae) feeding on the rain forest tree *Sloanea faginea* (Elaeocarpaceae; 73 rearings); the adult of this moth is very similar in body size and wing shape to *Zeuzerodes caenosa* (and very different from *Dysodia*) but the caterpillar is very similar to that of *Dysodia* in body size and leaf roll type. Furthermore, it is the only agathidine reared from the 73 rearings of *Collinsa* on *Sloanea*, and I (DHJ) feel that it is very likely to be an "abnormal" host record.

Only one other agathidine has been reared from the 3,500+ rearings of *Dysodia*, a single specimen of *Amputoearinus niger* from the rain forest *Heisteria concinna* (Olacaceae) being fed on by *Dysodia* Janzen06. *Dysodia* in ACG is, however, also used by at least 7 species of Tachinidae and Microgastrinae braconids.

Dysodia caterpillars construct a close-fitting conical-tubular shelter by cutting a lengthy curved slit in the food plant leaf and rolling that partly detached segment up around its base. The caterpillar then eats the inner parts of the leaf roll. The ovipositing wasp must then penetrate 1–3 layers of leaf and the caterpillar can only move forward and backward to escape. The caterpillar remains in one leaf roll for many days, pushing or ejecting fecal pellets out the "front door". The distinctive leaf rolls are easily recognized by the researcher, and presumably by a searching wasp as well, but many are empty because the caterpillar has moved on or been taken by a predator. The prepupal caterpillar (Fig. 16) spins a tough silk cocoon between two overlapping leaves

(or in the leaf roll). At this time the wasp larva feeds heavily and within 2–3 days has consumed the caterpillar innards and ruptures the caterpillar cuticle to emerge into the pupal chamber and spin a tough white cocoon with the caterpillar head capsule and remaining pelt scrunched onto one end (Fig. 17).

Etymology. Named in honor of Jessie Hill of Hawaii, who has enthusiastically supported the conservation and biodiversity inventory of the ACG forest occupied by this parasitoid wasp.

Material examined. Holotype: ♀, H7093 (DHJPAR0028316 – this is a short sequence) Costa Rica: Guanacaste: Area de Conservación Guanacaste: Sector Pitilla: Loaiciga, 7.ix.2008, 11.019N/85.4134W, 445m [AEI].

Paratypes [AEI, HIC, INBio]: Costa Rica: Guanacaste: Area de Conservación Guanacaste:Sector Pitilla: Loaiciga, 11.019N/85.4134W, 445m: ♀ H7090 (DHJPAR0028305) 7.ix.2008, ♀ H7091 (DHJPAR0028257) 5.ix.2008, ♀ H7098 (DHJPAR0028319) 4.ix.2008, ♀ H7063 (DHJPAR0028306) 4.ix.2008, ♀ H7083 (DHJPAR0028309) 9.iv.2008. ♂ H7085 (DHJPAR0028313) 6.ix.2008, ♂ H7096 (DHJPAR0028255) 4.ix.2008, ♂ H7089 (DHJPAR0028256) 28.viii.2008. Sendero Cuestona, 10.9945N/85.4146W, 640m: ♀ H8398 (DHJPAR0015455) 9.iv.2004, ♂ H8399 (DHJPAR0015454) 7.iv.2004. Sector Cacao: Sendero Toma Agua, 10.928N/85.4668W, 1140m: ♀ 4.iv.2001: H7088 (DHJPAR0015453), ♀ H7086 (DHJPAR0015452), ♂ H8396 (DHJPAR0015451). Sector Del Oro: Guacimos, 11.014N/85.4749W, 380m: ♂ H7087 (DHJPAR0036692) 3.viii.2009. Sector Mundo Nuevo: Vado Ocotea, 10.7638N/85.3784W, 565m: ♀ H7095 (DHJPAR0028139)

Figure 16. *Lytopylus jessiehillae* prepupal host caterpillar.

Figure 17. *Lytopylus jessiehillae* cocoon.

30.vii.2008. Vado Zanja Tapada, 10.7648N/85.3845W, 550m: ♀ H7094 (DHJPAR0040216) 4.vii.2010, ♀ H7099 (DHJPAR0040224) 3.vii.2010. Porton Rivas, 10.7586N/85.3727W, 570m: ♀ H6410 (DHJPAR0028318) 9.vii.2008, ♂ H7092 (DHJPAR0028317) 6.vii.2008. Punta Plancha, 10.7416N/85.4273W, 420m: ♀ H7097 (DHJPAR0040226) 1.vii.2010. Area de Conservación Guanacaste: Sector Rincon Rain Forest: Camino Albergue Oscar, 10.8774N/85.3236W, 560m: ♀ H7084 (DHJPAR0036720) 1.ix.2009.

Costa Rica: Heredia: Est. Biol. La Selva, 10.433N/84.017W, 150m: ♀ H8397 vii.1993.

Lytopylus macadamiae **(Briceño and Sharkey) comb. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_macadamiae
Fig. 18, 19

Bassus macadamiae Briceño and Sharkey 2000.

Description. Body length 4.4 – 6.8 mm. Ovipositor length 4.7 – 7.1. Gena rounded or with an obtuse angle posterolaterally. Longitudinal groove on interantennal prominence absent. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola not rounded anteriorly. Notauli well-impressed, smooth without

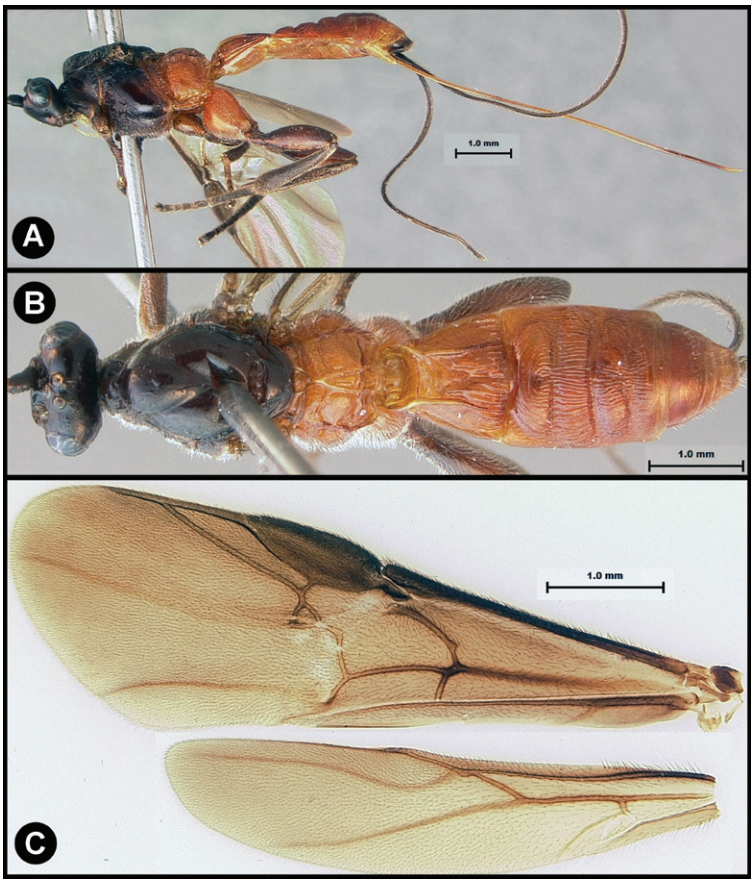


Figure 18. *Lytopylus macadamiae* (Briceno and Sharkey) **a** lateral habitus **b** dorsal habitus **c** wings.

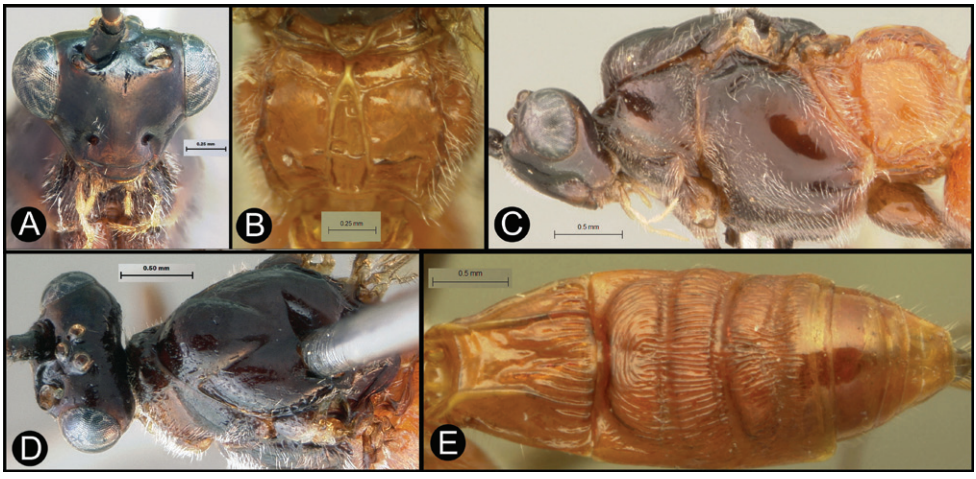


Figure 19. *Lytopylus macadamiae* (Briceno and Sharkey) **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

crenulae, or with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior margin of syntergum 2+3 straight. Median syntergite 2 + 3 longitudinally striate except extreme apex and medial transverse groove smooth. Forewing mostly or entirely infuscate. Color as in Figs 18, 19. Color variation: There is very little variation in color.

Distribution. Known from Venezuela and Costa Rica. For a distribution map, click here.

Biology. Reared from *Ecdytolopha aurantiana* and *Ecedytolopha tortricornis* (Tortricidae), both on *Macadamia integrifolia* (see Briceño and Sharkey, 2000).

Material examined. See Briceño and Sharkey, 2000.

***Lytopylus mingfangi* Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_mingfangi
Figs 20, 21

Description. Body length 6.5 – 6.9 mm. Ovipositor length 5.3 – 5.6 mm. Gena rounded or with an obtuse angle posterolaterally. Longitudinal groove on interantennal prominence absent. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola rounded anteriorly. Notauli well-impressed, smooth without crenulae, or with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior margin of syntergum 2+3 convex, covering most of terminal terga. Median syntergite 2 + 3 striate between lobes, first lobe usually smooth but varies from smooth to weakly rugose; second lobe varies from smooth to weakly rugose to striate; third lobe always smooth medially; fourth lobe varies from weakly striate to weakly rugose to smooth. Forewing mostly or entirely infuscate. Color as in Figs 20, 21. Color variation: Quite consistent in color. The propodeum may be pale posteriorly. The pale color of the abdomen is almost always yellow but it is orange in a few specimens.

Molecular data. BOLD process ID/Janzen parasitoid voucher/GenBank accession:
ASBC962-07/DHJPAR0021150/JN034721
ASHYC4672-10/DHJPAR0037927/JN034720
ASHYM043-08/DHJPAR0023291/JN034719
ASAG218-07/DHJPAR0015532/JN034718
ASHYD1531-09/DHJPAR0036340/JN034717
ASHYF030-09/DHJPAR0028268/JN034716
ASHYD1533-09/DHJPAR0036342/JN034715
ASHYD1534-09/DHJPAR0036343/JN034714
ASHYE1634-09/DHJPAR0036723/JN034713
ASHYE268-08/DHJPAR0028031/JN034712
ASHYD2379-10/DHJPAR0038806/JN034711
ASBC979-07/DHJPAR0021167/JN034721

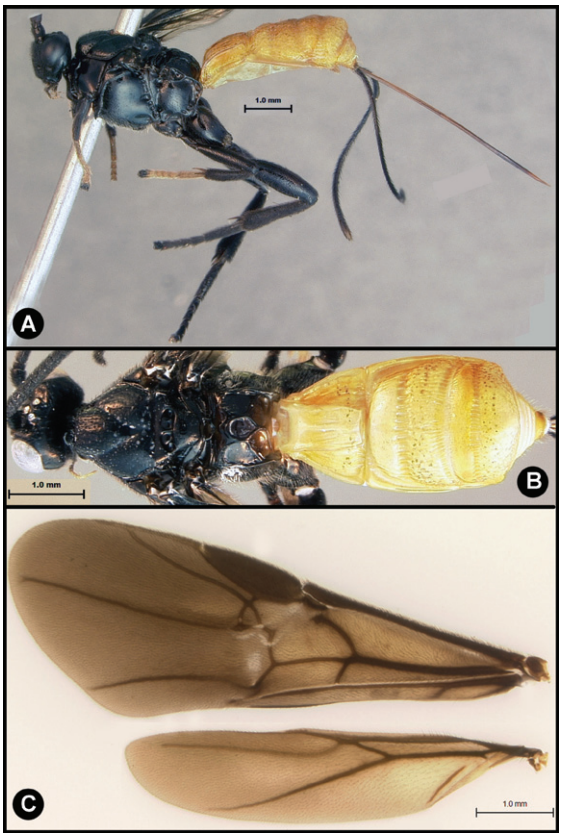


Figure 20. *Lytopylus mingfangi* sp. n. **a** lateral habitus **b** dorsal habitus **c** wings.

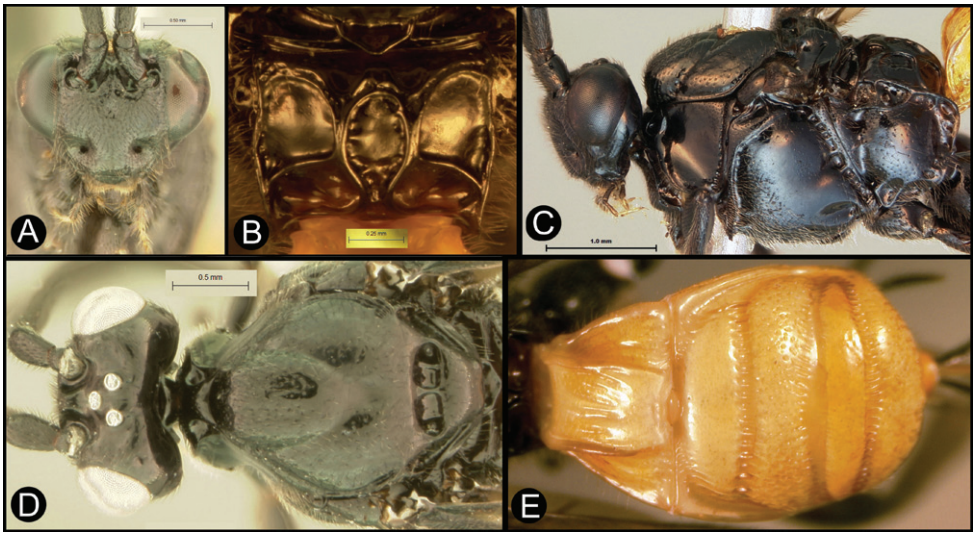


Figure 21. *Lytopylus mingfangi* sp. n. **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

ASHYC4673-10/DHJPAR0037928/JN034709
ASHYC4672-10/DHJPAR0037927/JN034720

Distribution. Alajuela Province, Costa Rica. Click here for a distribution map.

Biology. This wasp is the only species of *Lytopylus* found to date using *Zeuzerodes caenosa* (Thyrididae) as its host caterpillar (26 wasp rearings from 193 rearings of wild caught *Zeuzerodes caenosa* caterpillars), and apparently uses only this caterpillar. These parasitoid rearings are from the small rain forest trees *Mortoniodendron costaricense* (Tiliaceae, n =16) and *Quararibea funebris* (Bombacaceae, n = 10). Although the DNA barcode cluster contains significant divergence (max K2P 4.98%, average 1.216%), there is no morphological or ecological indication that these host-tree records suggest a wasp species complex, but rather, that the wasp finds *Zeuzerodes caenosa* wherever it is.

Zeuzerodes caenosa caterpillars construct a leaf roll shelter as described for *Dysodia*, but it is more sloppy and loose-fitting to the caterpillar, seemingly with more room to move around in (and perhaps in which to flee from a wasp ovipositor). The wasp cocoon is spun inside the caterpillar prepupal chamber (Fig. 22) but usually kills the prepupal caterpillar before it has had the occasion to spin a full (and very tough) cocoon.

In ACG rain forest, *Zeuzerodes caenosa* is used only by *Lytopylus mingfangi*, with the exception of a single unidentified tachinid fly parasitoid record.

Of all 5,700+ rearings of ACG Thyrididae caterpillars, only these two *Lytopylus* species appear to be regular users of the thryridid caterpillar fauna. The single rearing of *Austroearinus niger* and of *Therophilus* Sharkey01 from Thyrididae suggest that these

Figure 22. *Lytopylus mingfangi* cocoon.

two species of wasps normally use other species of host caterpillars, leaving *L. mingfangi* and *L. jessiehillae* as the two agathidine parasitoids of the ACG thyridids known to date.

Etymology. Named in honor of Ming Fang of Hawaii and China, who has enthusiastically supported the conservation of the ACG forest occupied by this parasitoid wasp.

Material examined. Holotype: ♀, H8016 (DHJPAR0040338), Costa Rica: Guanacaste: Area de Conservación Guanacaste: Sector San Cristobal: Tajo Angeles, 7.viii.2010, 10.86472N/85.4153W, 540m [AEI].

Paratypes [AEI, HIC, INBio]: Costa Rica: Guanacaste and Alajuela: Area de Conservación Guanacaste: Sector San Cristobal: Rio Blanco Abajo, 10.90037N/85.3725W, 500m: ♀H7055 (DHJPAR0021150) 18.vii.2007. ♂ H7062 (DHJPAR0021167) 5.viii.2007. San Gabriel, 10.87766N/85.3934W, 645m: ♀ H6416 (DHJPAR0023291) 9.vii.2007. ♀ H7059 (DHJPAR0028031) 3.vii.2008. ♀ H7058 (DHJPAR0037927) 10.xi.2009. ♂ H7057 (DHJPAR0038806) 11.iii.2010. ♂ H7061 (DHJPAR0037928) 12.xi.2009. Sendero Carmona, 10.87621N/85.3863W, 670m: ♀ H7060 (DHJPAR0028268) 28.viii.2008. Sendero Colegio, 10.89296N/85.3788. 520m: ♀ H7064 (DHJPAR0015532) 31.x.2005. Sendero Corredor, 10.87868N/85.3896W, 620m.♀ H7054 (DHJPAR0036723) 22.viii.2009. Tajo Angeles, 10.86472N/85.4153W, 540m: ♀ H6626 (DHJPAR0036342) 8.viii.2009. ♀ H7961 (DHJPAR0041593) 25.x.2010. ♀ H7052 (DHJPAR0036344) 9.viii.2009. ♀ H7905 (DHJPAR0041599) 13.viii.2010. ♀ H8014 (DHJPAR0040346) 4.viii.2010. ♀ H7065 (DHJPAR0036340) 7.viii.2009. ♂ H7051 (DHJPAR0038907) 28.viii.2010. H7053 (DHJPAR0036343) 7.viii.2009. H7955 (DHJPAR0041595) 11.x.2010. ♂ H7952 (DHJPAR0041590) 25.x.2010. Sector Rincon Rain Forest: Sendero Albergue Crater, 10.84866N/85.3281W, 980m: ♀ H7056 (DHJPAR0037916) 6.xi.2009.

Lytopylus rebeccashapleyae **Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_rebeccashapleyae
Figs 23, 24

Description. Body length 4.2 – 4.9 mm. Ovipositor length 4.2 – 4.5 mm. Gena acute posterolaterally. Longitudinal groove on interantennal prominence absent. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola rounded anteriorly, or with carinae forming areolae, median areola not rounded anteriorly. Notauli well-impressed, smooth without crenulae, or with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior margin of syntergum 2+3 straight. Median syntergite 2 + 3 mostly smooth except for weak striae anteromedially. Forewing clear except base slightly infuscate. Color as in Figs 23, 24. Color variation: Body color is consistent across the five specimens examined.

Molecular data. BOLD process ID/Janzen parasitoid voucher/GenBank accession:
ASHYB1809-10/DHJPAR0039521/JN034725
ASHYB1810-10/DHJPAR0039522/JN034724

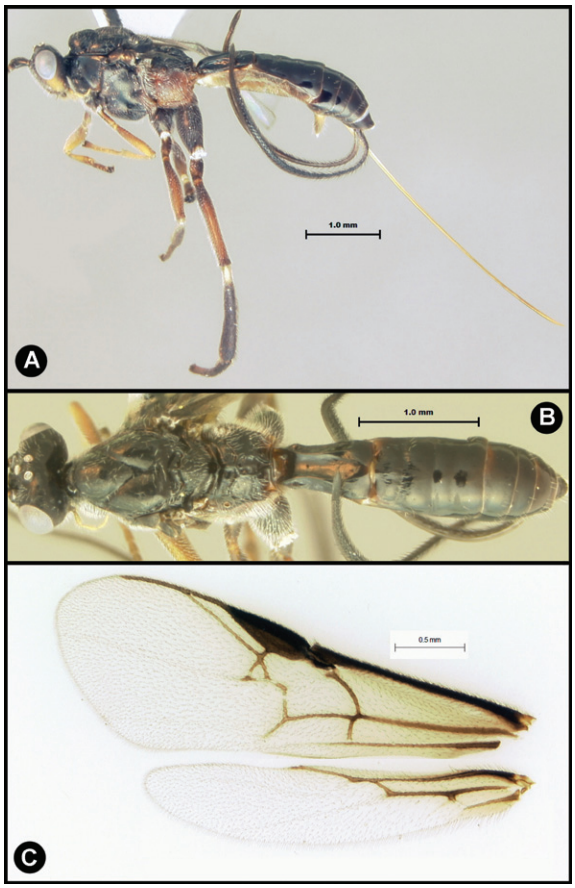


Figure 23. *Lytopylus rebeccashapleyae* sp. n. **a** lateral habitus **b** dorsal habitus **c** wings.

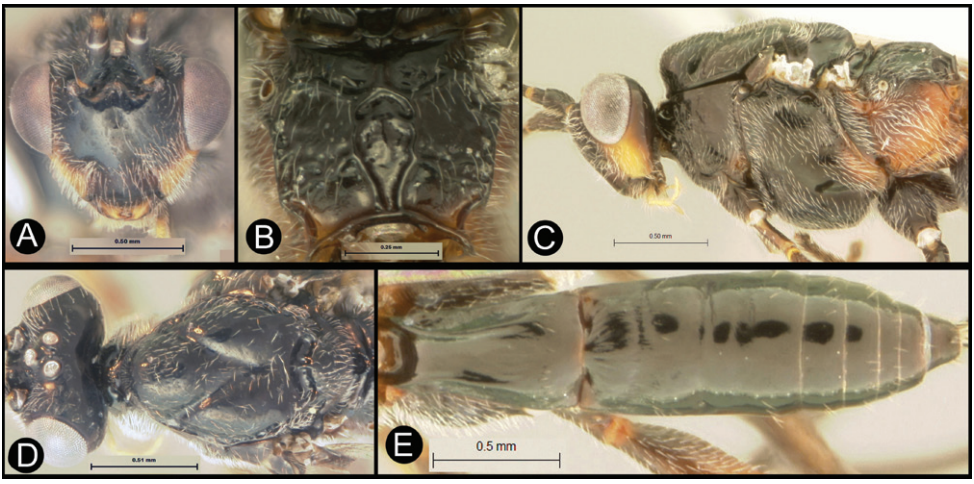


Figure 24. *Lytopylus rebeccashapleyae* sp. n. **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

ASHYB1794-10/DHJPAR0039506/JN034723
ASHYB1813-10/DHJPAR0039525/JN024722

Distribution. Alajuela Province and Puntarenas Province, Costa Rica. Click here for a distribution map.

Biology. All five rearings are from *Episimus* Brown002 (Tortricidae, Olethreutinae), a relatively common solitary leaf webber feeding on the shrubs *Vismia baccifera* and *Vismia billbergiana* (Clusiaceae) that occur throughout disturbed ACG rain forest sites (150+ caterpillar rearings). However, all five wasp rearings are from a batch of *Episimus* Brown002 larvae collected in late April and early May in just one intermediate elevation site on the very wet Caribbean slopes of Volcan Rincon de la Vieja in Sector Rincon Rain Forest.

Etymology. *Lytopylus rebeccashapleyae* is named in honor of Rebecca Shapley of Mountain View, California, who has enthusiastically supported the conservation of the ACG forest occupied by this parasitoid wasp.

Material examined. Holotype: ♀, H8047 (DHJPAR0039525) Costa Rica: Alajuela: Area de Conservación Guanacaste: Sector Rincon Rain Forest: Sendero al Crater: 19.v.2010, 10.8488N/85.3281W, 980m. [AEI].

Paratypes [AEI, HIC, INBio]: Costa Rica: Alajuela: Area de Conservación Guanacaste: Sector Rincon Rain Forest: Camino Albergue Oscar: 10.8774N/85.3236W, 560m: 17.v.2010: ♀ H8020 (DHJPAR0039521), ♀ H7959 (DHJPAR0039506); ♀ H7960 (DHJPAR0039507) 14.v.2010. ♀ H8032 (DHJPAR0039522) 8.v.2010.

***Lytopylus robpringlei* Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_robpringlei
Figs 25, 26

Description. Body length 7.5 mm sole female (5.8 – 7.2 males). Ovipositor length 5.8 mm. Gena rounded or with an obtuse angle posterolaterally. Longitudinal groove on interantennal prominence present. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola not rounded anteriorly. Notauli well-impressed, smooth without crenulae, or with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior margin of syntergum 2+3 straight. Median syntergite 2 + 3 varying from entirely striate except for smooth apex to smooth with longitudinal striae restricted to the transverse grooves. Forewing mostly or entirely infuscate. Color as in Figs 25, 26. Color variation: Mesoscutal lobes slightly melanic in one male specimen otherwise color consistent across the four examined specimens.

Molecular data. BOLD process ID/Janzen parasitoid voucher/GenBank accession:
ASHYB1814-10/DHJPAR0039526/JN034728
ASHYE1114-09/DHJPAR0035292/JN034727

Distribution. Alajuela Province, Costa Rica. Click here for a distribution map.

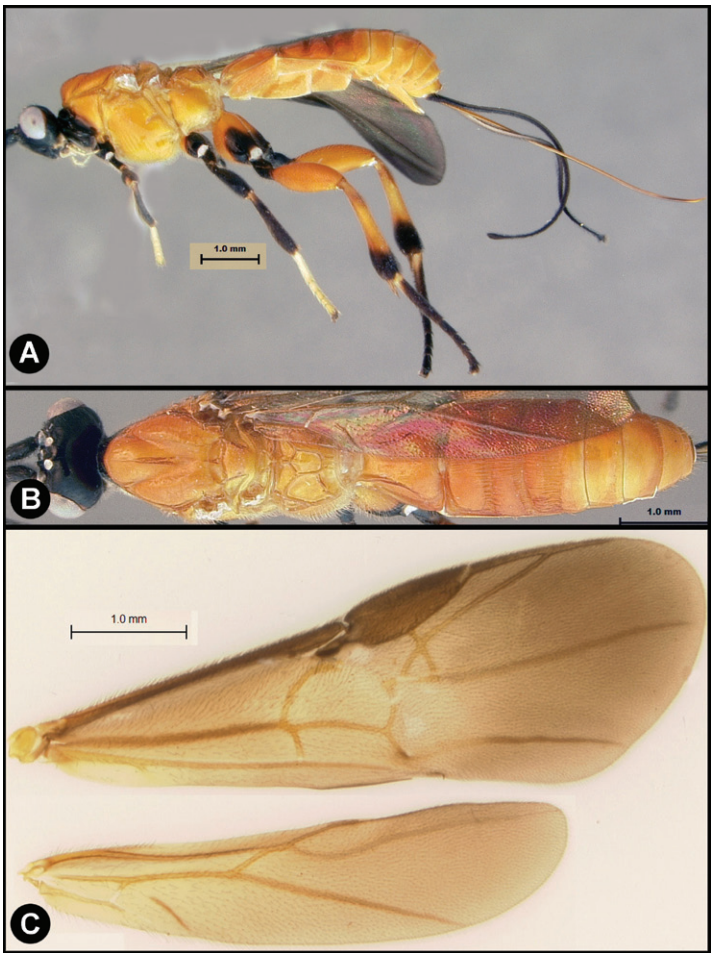


Figure 25. *Lytopylus robpringlei* sp. n. Holotype **a** lateral habitus **b** dorsal habitus **c** wings.

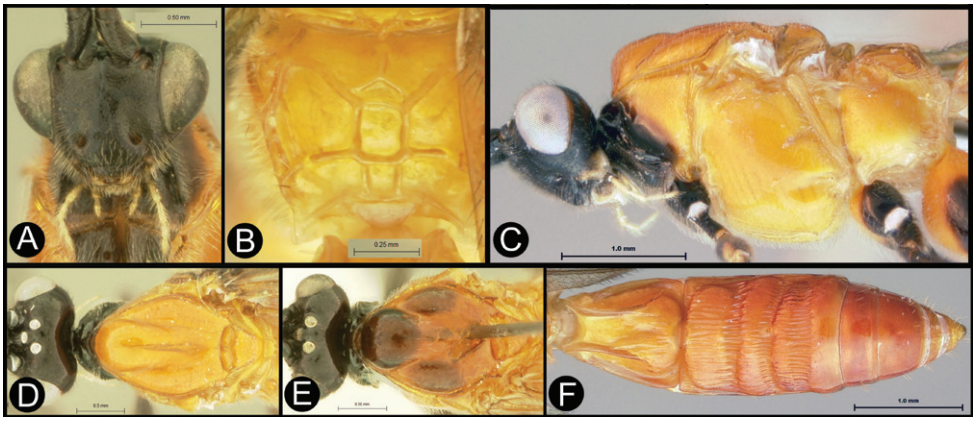


Figure 26. *Lytopylus robpringlei* sp. n. Holotype **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal head and mesosoma variation **f** dorsal metasoma.

Biology. All four rearings are from Elachistidae (Stenomatinae) leaf tiers feeding on rain forest Sapotaceae: 3 from *Chlamydastis rhomaeopa* on *Chrysophyllum brenesii*, and 1 elachJanzen01 Janzen35 from *Pouteria* 17499. These leaf tiers construct a somewhat tubular channel of silk and a few fecal pellets between two overlapping leaves that are quite tightly silked together, and then surface skeletonize the leaf and feed at the leaf edges. The ovipositing wasp would need to penetrate through the leaf from above or below, skewering the caterpillar in the process. There is no externally visible indication that there is a wasp egg or larva inside the wild-collected caterpillar. At about the time the caterpillar is prepupal (which tends to be at least 5–10 days after the caterpillar is brought in from the wild), the wasp larva feeds strongly enough to immobilize the caterpillar, and 1–2 days later emerges through the body wall to spin a white cocoon in the caterpillar pupal chamber that is a space between the two leaves silked together and in a loosely defined tubular nest of silk and fecal pellets. The cranium and pelt fragments of the caterpillar are bunched together at one end of the wasp cocoon. The pupal period of the wasp is 12–20 days.

The elachistid host caterpillars feeding on Sapotaceae are parasitized by a variety of tachinid flies, ichneumonid wasps and microgastrine braconid wasps, but (at least with this small number of rearing records) appear not to be also attacked by other agathidine wasps.

Etymology. *Lytopylus robpringlei* is named in honor of Rob Pringle of Princeton, New Jersey, who has enthusiastically supported the conservation of the ACG forest occupied by this parasitoid wasp.

Material examined. Holotype: ♀, H8019 (DHJPAR0039526) Costa Rica: Alajuela: Area de Conservación Guanacaste: Sector San Cristobal: Tajo Angeles: 11.vi.2010, 10.865N/85.415W, 540m [AEI].

Paratypes [AEI, HIC, INBio]: Costa Rica: Alajuela: Area de Conservación Guanacaste: Sector San Cristobal: Tajo Angeles, 10.8647N/85.4153W, 540m: ♂ H7814 (DHJPAR0041557) 8.i.2011. ♂ H6635 (DHJPAR0035292) 14.v.2009. Rio Blanco Abajo, 10.9003N/85.3725W, 500m: ♂ H6435 (DHJPAR0015456) 14.iv.2003.

Lytopylus sandraberriosae **Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_sandraberriosae
Figs 27, 28

Description. Body length 8.9 mm (sole female) 7.9 – 8.2 (2 males). Ovipositor length 8.9 mm. Gena rounded or with an obtuse angle posterolaterally. Longitudinal groove on interantennal prominence absent. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola rounded anteriorly, or with carinae forming areolae, median areola not rounded anteriorly. Notauli well-impressed, smooth without crenulae, or with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior margin of syntergum 2+3 straight. Median syntergite 2 + 3 mostly weakly rugose with fine transverse striae apically. Forewing banded yellow

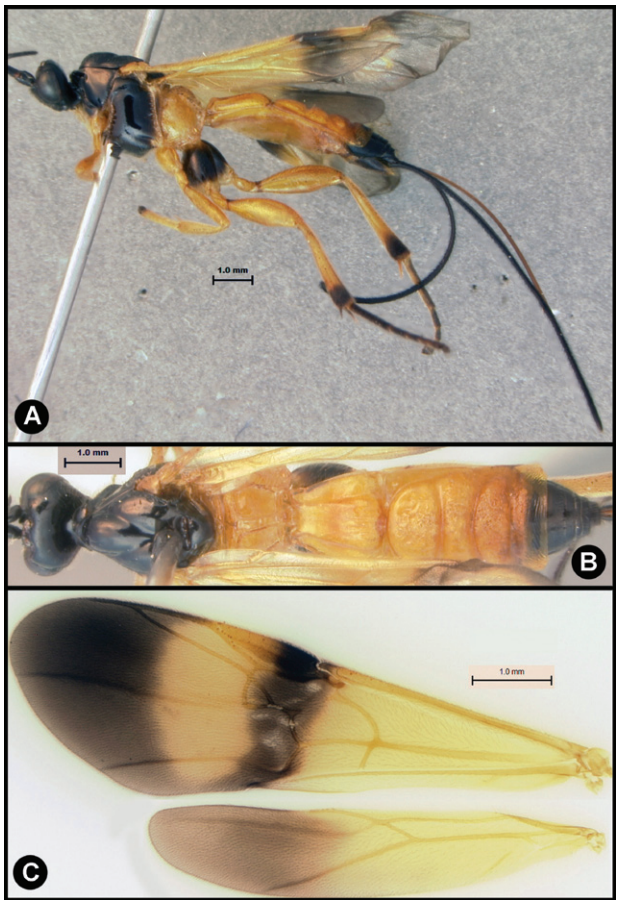


Figure 27. *Lytopylus sandraberriosae* sp. n. Holotype **a** lateral habitus **b** dorsal habitus **c** wings.

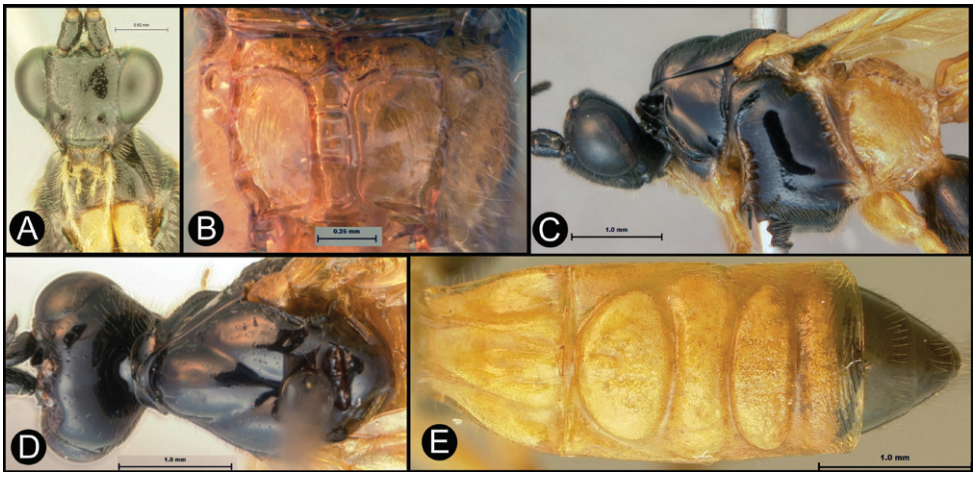


Figure 28. *Lytopylus sandraberriosae* sp. n. Holotype **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

and infuscate. Color as in Figs 27, 28. Color variation: There is little color variation across the three specimens examined.

Molecular data. BOLD process ID/ Janzen parasitoid voucher/GenBank accession: ASBC960-07/DHJPAR0021148/JN034729.

Distribution. Guanacaste province, Costa Rica. Click here for a distribution map.

Biology. All three rearings are from Pyralidae (Epipaschiinae) gregarious leaf webbers (*Deuterollyta oediperalis*) that live in conspicuous groups of 2–50 sib larvae moving freely through the silk and leaf mass in the crowns of rain forest understory Lauraceae (in this case, *Nectandra hihua* and an unidentified species of Lauraceae). Oviposition into one of the unrestrained caterpillars in the silk and leaf tangle will be a quite different challenge from oviposition into a single larva in its nest between two silked-together leaves (as is the case with other *Lytopylus*). Only DHJPAR0021148 has successfully barcoded, so the grouping of these three individuals as one species is based solely on their morphology. Their host records give credence to this grouping.

The wasp cocoon is spun in the caterpillar's prepupal chamber on the leaf surface (Fig. 29). The inventory has reared 5,422 epipaschiine pyralids from various food plants in ACG rain forest and dry forest (about half in the Lauraceae) during 33 years, to yield these three *Lytopylus* specimens (plus one *Alabagrus* and two *Austroearinus*).

L. sandraberriosae is a strange agathidine morphologically, biologically, and in COI composition. When we included another outgroup, a species of *Alabagrus*, in parsimony and NJ analyses (not shown), *L. sandraberriosae* did not nest with the other *Lytopylus*. Rather, *Braunsia* was positioned as the sister to the remaining *Lytopylus*. The species could well represent a new genus, but more molecular data is needed to confirm this suspicion.

Figure 29. *Lytopylus sandraberriosae* cocoon.

Etymology. Named in honor of Sandra Berrios Torres of Atlanta, Georgia, who has enthusiastically supported the conservation of the ACG forest occupied by this parasitoid wasp.

Material examined. Holotype: ♀, H6432 (DHJPAR0040220) Costa Rica: Alajuela: Area de Conservación Guanacaste: Sector Rincon Rain Forest: Conguera, 2.vii.2010, 10.9159N/85.2663W, 420m [AEI].

Paratypes [AEI, HIC, INBio]: Costa Rica: Guanacaste: Area de Conservación Guanacaste: Sector Rincon Rain Forest: Conguera, 10.9159N/85.2663W, 420m: ♂ H6428 (DHJPAR0040219) 4.vii.2010. Camino Rio Francia, 10.9042N/85.2865W, 410m: ♂ H6628 (DHJPAR0021148) 7.vii.2007.

***Lytopylus vaughntani* Sharkey sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Lytopylus_vaughntani
Figs 30, 31

Description. Body length 3.9 – 4.8 mm. Ovipositor length 3.1 – 3.8 mm. Gena acute posterolaterally, or rounded or with an obtuse angle posterolaterally. Longitudinal groove on interantennal prominence present. Protuberances on occiput absent. Propodeum with carinae forming areolae, median areola not rounded anteriorly. Notauli well-impressed, smooth without crenulae, or with one or two crenulae restricted to extreme anterior apex along border of mesoscutum. Posterior margin of syntergum 2+3 straight. Median syntergite 2 + 3 mostly smooth with longitudinal striae restricted to the transverse grooves, rarely the third lobe is partially striate. Forewing mostly or entirely infuscate. Color as in Figs 30, 31. Color variation: Color is quite consistent across the six specimens examined. Some specimens are slightly paler than that shown in figures 30 and 31 especially on the metasoma.

Molecular data. BOLD process ID/ Janzen parasitoid voucher/GenBank accession: ASHYB1349-09/DHJPAR0030608/JN034730.

Distribution. Heredia and Alajuela provinces, Costa Rica. Click here for a distribution map.

Biology. The single rearing is from an unidentified elachistid (Elachistidae, Stenomatinae) leaf roller/webber on the rain forest herbaceous composite *Fleischmannia pycnocephala* (Asteraceae). While 52 rearing records from this plant have yielded a diverse array of Crambidae, Thyrididae, Tortricidae and Elachistidae parasitized by a diverse array of ichneumonids, tachinids and microgastrine braconids, this is the only Agathidinae encountered to date.

Etymology. Named in honor of Vaughn Tan of Cambridge, Massachusetts, who has enthusiastically supported the conservation of the ACG forest occupied by this parasitoid wasp.

Material examined. Holotype: ♀H6614 (DHJPAR0030608) Costa Rica: Alajuela: Area de Conservación Guanacaste: Sector San Cristobal: Puente Palma: 13.ii.2009, 10.916N/85.379W, 460m [AEI].

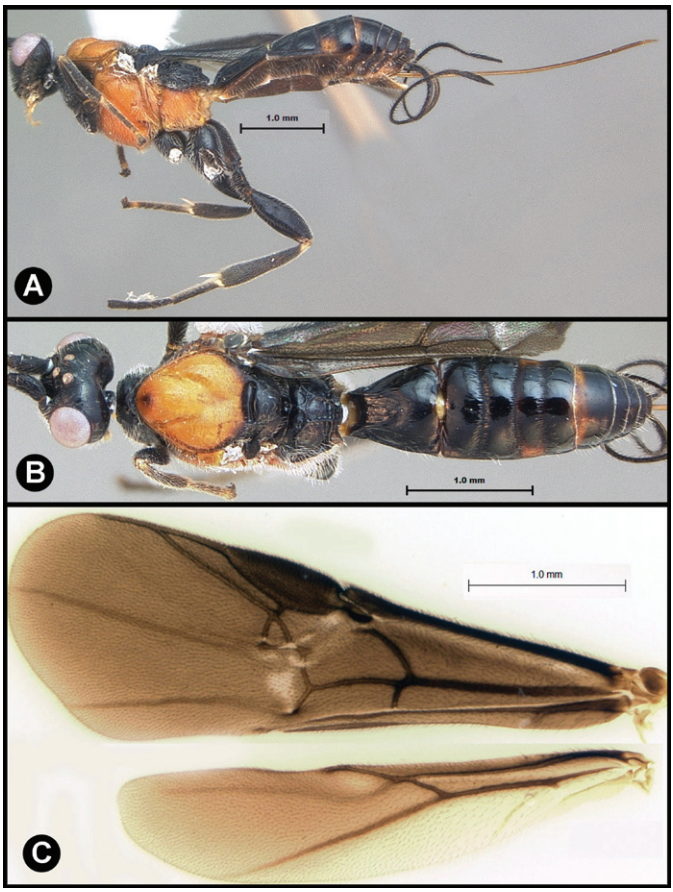


Figure 30. *Lytopylus vaughntani* sp. n. Holotype **a** lateral habitus **b** dorsal habitus **c** wings.

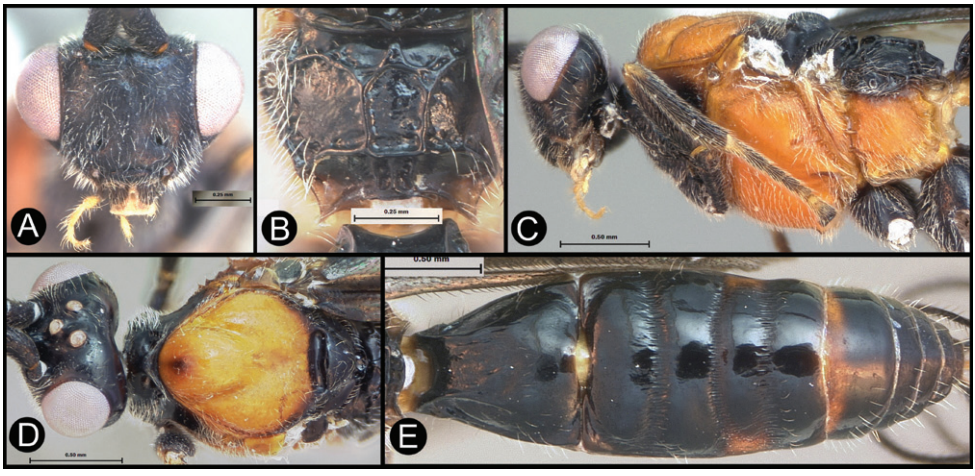


Figure 31. *Lytopylus vaughntani* sp. n. Holotype **a** anterior head **b** dorsal propodeum **c** lateral head and mesosoma **d** dorsal head and mesosoma **e** dorsal metasoma.

Paratypes [AEI, HIC, INBio]: Costa Rica: Heredia: Est. Bio. La Selva: 10.433N/84.017W, 150m: ♀H7080 vii.1998, ♂H7079 xii.1999. Sector Cocori: Limon: 1.1995, 10.365N/83.734W, 100m: ♀: H6467, H7075, ♂H7077.

Acknowledgments

This study is dedicated to Alex Rasnitsyn on the occasion of his 75th birthday. Dr. Rasnitsyn has had, and continues to have, a profound influence on our understanding of hymenopteran phylogeny and evolutionary history and he has been generous in sharing his knowledge with the first author (MJS). We emphatically and gratefully acknowledge the support of the ACG parataxonomist team in finding and rearing these caterpillars and their parasites, and Area de Conservacion Guanacaste for preserving the forest in which they live, and the Guanacaste Dry Forest Conservation Fund for funding portions of the research. This study was also supported by NSF DEB 0515699 to DHJ and by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to MAS. Laboratory analyses on sequences generated since 2009 were funded by the Government of Canada through Genome Canada and the Ontario Genomics Institute (2008-0GI-ICI-03).

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Appendix I

DELTA data matrix, images, and other files to the dichotomous key for *Lytopylus* (Hymenoptera: Braconidae: Agathidinae) of Costa Rica. (doi: 10.3897/zookeys.130.1569.app1)

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Citation: Sharkey MJ, Clutts S, Tucker EM, Janzen D, Hallwachs W, Dapkey T, Smith MA (2011) *Lytopylus* Förster (Hymenoptera: Braconidae: Agathidinae) species from Costa Rica, with an emphasis on specimens reared from caterpillars in Area de Conservación Guanacaste. ZooKeys 130: 397–419. doi: 10.3897/zookeys.130.1569.app1

Appendix II

DELTA data matrix, images, and other files to species descriptions for *Lytopylus* (Hymenoptera: Braconidae: Agathidinae) of Costa Rica. (doi: 10.3897/zookeys.130.1569.app2)

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Citation: Sharkey MJ, Clutts S, Tucker EM, Janzen D, Hallwachs W, Dapkey T, Smith MA (2011) *Lytopylus* Förster (Hymenoptera: Braconidae: Agathidinae) species from Costa Rica, with an emphasis on specimens reared from caterpillars in Area de Conservación Guanacaste. ZooKeys 130: 397–419. doi: 10.3897/zookeys.130.1569.app2

Appendix III

Interactive key, in IntKey format, to *Lytopylus* (Hymenoptera: Braconidae: Agathidinae) of Costa Rica. (doi: 10.3897/zookeys.130.1569.app3)

Note: To run the identification key, you will need Windows 95/NT or a later version. You also need to download Intkey software and reboot your computer, if it is not already installed. The software package, Intkey, can be downloaded from

http://delta-intkey.com/www/programs.htm. Once Intkey is installed you need only click on the .ink file (below) and the key will open. Click on any character on the left to begin.

More details on how to use Intkey efficiently are found at http://florabase.calm.wa.gov.au/help/keys/intkey_tutorial.pdf.

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ZooKeys 130: 421–453 (2011)
doi: 10.3897/zookeys.130.1453
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RESEARCH ARTICLE

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New and revised maimetshid wasps from Cretaceous ambers (Hymenoptera, Maimetshidae)

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Abstract

New material of the wasp family Maimetshidae (Apocrita) is presented from four Cretaceous amber deposits – the Neocomian of Lebanon, the Early Albian of Spain, the latest Albian/earliest Cenomanian of France, and the Campanian of Canada. The new record from Canadian Cretaceous amber extends the temporal and paleogeographical range of the family. New material from France is assignable to *Guyotemaimetsha enigmatica* Perrichot et al. including the first females for the species, while a series of males and females from Spain are described and figured as *Iberomaimetsha* Ortega-Blanco, Perrichot, and Engel **gen. n.**, with the two new species *Iberomaimetsha rasnitsyni* Ortega-Blanco, Perrichot, and Engel **sp. n.** and *I. nihtmara* Ortega-Blanco, Delclòs, and Engel **sp. n.**; a single female from Lebanon is described and figured as *Ahiromaimetsha najlae* Perrichot, Azar, Nel, and Engel **gen. et sp. n.**, and a single male from Canada is described and figured as *Ahstemiam cellula* McKellar and Engel **gen. et sp. n.** The taxa are compared with other maimetshids, a key to genera and species is given, and brief comments made on the family.

Keywords

Hymenoptera, Maimetshidae, France, Lebanon, Spain, Canada, Neocomian, Albian, Campanian, Mesozoic, taxonomy

Dedication

We lovingly dedicate this humble contribution to the discoverer of the Maimetshidae, our friend and colleague, Prof. Alexandr P. Rasnitsyn, on the occasion of his 75th birthday. It is greatly hoped that Alex, as the great docent of hymenopterological paleontology, will look upon our work with favor and pride, knowing that his rich body of inquiry has inspired every aspect of our own probes into the history of this fascinating order.

Introduction

The family Maimetshidae was established as an extinct lineage of apocritan wasps based on a single incomplete female and male preserved in Santonian Taimyr amber (Rasnitsyn 1975). A single genus and species, *Maimetsha arctica* Rasnitsyn, was recognized and considered to be intermediate between Megalyridae and Ceraphronoidea, linking these otherwise disparate groups (Rasnitsyn 1975, 2002).

More than a quarter century later, Perrichot et al. (2004a) described a second genus and species which shared considerable similarities with *Maimetsha* Rasnitsyn and *Cretogonalys* Rasnitsyn, a genus originally attributed to Trigonalyidae but subsequently recognized as a possible maimetshid (Rasnitsyn and Brothers 2009). Given the uncertainties of the time, *Guyotemaimetsha* Perrichot et al. was considered as family *incertae sedis* (Perrichot et al. 2004a). Later, Perrichot (2009) reported new specimens of *Guyotemaimetsha* as well as undescribed material from Spanish amber, all of which appeared to suggest closer affinities with Trigonalyidae [This name often appears as Trigonalidae, given that Cresson (1887) first used this spelling. However, ICZN (1999: Art. 29.3)

dictates that the name is to be based on the correct stem by deleting the case ending of the genitive singular, in the present case giving "Trigonalyd–", thus the name would be automatically corrected to Trigonalydidae, with the same author and date, except that (Art. 29.3.1.1) notes that the unelided form, Trigonalyidae, is to be retained since the elided form (Trigonalydidae) is not in prevailing usage. Accordingly, Trigonalidae is a *nomen imperfectum*, which is *recte* Trigonalyidae Cresson, 1887].

Maimetshidae are presently known only from the Cretaceous and largely as inclusions in amber, similar in this respect to the families Radiophronidae (Ortega-Blanco et al. 2010), Stigmaphronidae (Rasnitsyn 1975, 1991; Engel and Grimaldi 2009; Ortega-Blanco et al. in press; McKellar and Engel in press), Alavarommatidae (Ortega-Blanco et al. 2011a), Gallorommatidae (Gibson et al. 2007; Ortega-Blanco et al. 2011a), and Serphitidae (Kozlov and Rasnitsyn 1979; McKellar and Engel 2011; Ortega-Blanco et al. 2011b; Engel et al. 2011). Rasnitsyn and Brothers (2009) described various maimetshids from Late Cretaceous compressions, and, as mentioned before, *Cretogonalys* is possibly also of this family, as could be the species of *Turgonalus* Rasnitsyn (Rasnitsyn 1990; Rasnitsyn et al. 1998).

The classification of Maimetshidae has been controversial, with various alternative interpretations of their putative relationships. For example, many authors have recognized them as an extinct, isolated family of Ceraphronoidea s.l. (Rasnitsyn 1975, 1977, 1988; Ronquist et al. 1999; Rasnitsyn and Brothers 2009; Perrichot 2009; Ortega-Blanco et al. 2010), while Shaw (1988, 1990) considered them as a basal clade within the Megalyridae. Vilhelmsen et al. (2010a) provided the first critical phylogenetic evaluation for the group, recognizing Maimetshidae as sister to Trigonalyidae, uniting these two by at least asymmetrical mandibles (not observed in all maimetshids) and the tarsal plantulae in females. Maimetshidae differ from Trigonalyidae, however, at least by the ovipositor exserted (instead of concealed in Trigonalyidae: *vide* Oeser 1962) and the absence of antennal tyloids (these are present in all trigonalyids except the primitive genus *Orthogonalys* Schulz: *vide* Carmean and Kimsey 1998). While the relationship between Maimetshidae and Trigonalyidae now seems well corroborated, the classification of these within an expanded Ceraphronoidea (or Stephanoidea *sensu* Rasnitsyn and Brothers 2009 = Stephanidae, Megalyridae, Trigonalyidae, Maimetshidae, Ceraphronidae, Megaspilidae, Stigmaphronidae, and Radiophronidae) is not well supported, and the phylogenetic placement of Ceraphronoidea s.str. (= Ceraphronidae, Megaspilidae, Stigmaphronidae, and Radiophronidae) is debatable, although many higher-level analyses do recover them as part of the Evaniomorpha (Sharkey 2007; Davis et al. 2010; Vilhelmsen et al. 2010b; Rasnitsyn and Zhang 2010) rather than Proctotrupomorpha (Ronquist et al. 1999; Sharkey and Roy 2002). Most recently Heraty et al. (2011) failed to recover a monophyletic Evaniomorpha, although ceraphronoids did not group with Proctotrupomorpha, but their analysis also had Orussidae nested within a paraphyletic evaniomorph grade which is certainly controversial.

Herein we provide a systematic overview of new material of maimetshids in Cretaceous amber, including the descriptions of three new genera and four new species.

Material and methods

The species discussed herein were recovered from four different Cretaceous deposits, two in southwestern Europe (France and Spain), one in western Asia (Lebanon), and the last from northcentral North America (Canada). Details of each are briefly summarized below and more thorough discussions on their stratigraphy, paleoecology, and paleoenvironment can be found in Perrichot et al. (2010), Peñalver and Delclòs (2010), Azar et al. (2010), and McKellar and Wolfe (2010), respectively. Morphological terminology generally follows that used elsewhere in the Hymenoptera (e.g., Goulet and Huber 1993), and for consistency the wing terminology as applied in Perrichot et al. (2004a). Acronyms for the institutions with collections studied herein are as follows: MNHN, Muséum National d'Histoire Naturelle, Paris, France; IGR, Géosciences Rennes, Université Rennes 1, Rennes, France; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain; and CNC-CAS, Canadian National Collection of Insects and Arthropods, Ottawa, Canada.

Photomicrographic images of specimens preserved in transparent amber were prepared using digital cameras attached to stereomicroscopes or to an Infinity K-2 long-distance microscopic lens. Fossils preserved in opaque amber were first detected using propagation phase contrast X-ray synchrotron microradiography, then three-dimensionally imaged using microtomography (PPC-SRμCT), a non-invasive method which allows incomparable possibilities for the visualization of both external and internal structures of amber fossils (Soriano et al. 2010; Perreau and Tafforeau 2011). Imaging was performed on beamline ID 19 of the European Synchrotron Radiation Facility (ESRF) in Grenoble using local tomography protocol (Tafforeau et al. 2006; Lak et al. 2008). The microtomographic scan of specimen IGR.ARC-370.7 was performed using a monochromatic beam at 30 keV with an isotropic voxel size of 5.06 μm and 990 mm of propagation distance. The tomography was obtained using a 180 degree continuous scan with 1500 projections and 0.5s of exposure time. The scan of specimen IGR.ARC-378.2 was performed at 25 keV with an isotropic voxel size of 1.67 μm, 50 mm of propagation distance, and 0.12s of exposure time. After the scan, data were reconstructed using a filtered back-projection algorithm adapted for local tomography applications (PyHST software, ESRF) and adapted ring artifacts correction protocols. Specimen IGR.ARC-370.7 was segmented in 3D using region growing techniques with VGStudioMax (Volume Graphics, Heidelberg, Germany). All of the synchrotron microtomographic data (original stacks of slices, segmentations, animations, pictures, and 3D-volume models) are available at the paleontological online database of the ESRF (http://paleo.esrf.eu), and 3D models in ABS plastic are deposited with the amber piece in Rennes University and at the ESRF.

French amber. Since the description of *G. enigmatica* by Perrichot et al. (2004a) based on two males, eight new conspecific specimens have been found, including two females previously unknown, five males, and one specimen of uncertain gender. Three

further individuals assignable to Maimetshidae may also belong to this species but are too incompletely preserved for accurate attribution.

Six out of the eight new specimens were found in amber from the same outcrop as the type series, i.e., the Font-de-Benon Quarry near the village of Archingeay, in Charente-Maritime, southwestern France. The amber pieces were collected within the lowermost of two amber-bearing strata, e.g., the level A1sl-A *sensu* Batten et al. (2010) = A1sl1 *sensu* Néraudeau et al. (2002). The dating of this level remains problematic, it contains some palynomorphs (dinoflagellate cysts) suggesting a latest Albian age (Dejax and Masure 2005), while recently discovered megaspores are more indicative of the Early Cenomanian (Batten et al. 2010). Two other specimens were collected in a single piece of amber from the same stratigraphic level in the Cadeuil Quarry, about 30 km from Archingeay (see "Arc 1" and "Cdl 1" in Perrichot et al. 2010: figs 1–2).

Similar to the type series, four amber pieces were reworked using a scalpel as a microsaw and the five fossils, separated this way from their syninclusions, were embedded in Canada Balsam between cover slips following the method detailed in Perrichot et al. (2004b). The specimens were assigned collection numbers IGR.ARC-1, IGR.ARC-309.11, IGR.ARC-378.1, IGR.CDL-2.5, and IGR.CDL.2.33. The three other fossils (collection numbers IGR.ARC-370.7, IGR.ARC.378.2, and IGR.ARC-393.4) are preserved in pieces of fully opaque amber and were imaged using PPC-SRμCT as detailed above.

Spanish amber. The material originates from Peñacerrada I, in Moraza, Burgos Province, Basque-Cantabrian Basin, Spain (Peñalver and Delclòs 2010). Each fossil is preserved in a thin polished piece of amber, which has been embedded in a clear, synthetic block of epoxy resin according to the method of Corral et al. (1999) except for MCNA-9373, which is not embedded in epoxy. Specimen MCNA-9928, type specimen for one of the new species described herein, is well-preserved and almost complete. Specimen MCNA-13049, holotype for the second species from Spanish amber, is missing the apical parts of the metasoma, of the right antenna, and most legs. Other specimens are incomplete and fossilized in rather opaque amber, partly covered by small bubbles or foggy material, so that some parts are hidden or poorly visible.

Lebanese amber. The material originates from an outcrop near Maknouniyyeh Village, Caza (Department) of Jezzine, in southern Lebanon, which corresponds to an ancient field that was used for lignite mining during the French governance of Lebanon and World Wars I and II. The amber is found with lignite in grey lenses of clay corresponding to channels intercalated between fluvial sand deposition of Neocomian age. The precise dating of this sandstone remains problematic and could be anywhere between the Hauterivian and Early Aptian (Azar et al. 2010). The amber is dark orange to red, brittle, with a lot of carbonized vegetal inclusions. This may indicate that the resin was produced in response to a forest fire. The specimen considered herein is exquisitely preserved, missing only the apical portions of the mid and hind legs. It was fossilized in a piece of amber together with a beetle, an evaniid wasp, a roach, and a rhagionid fly, but each inclusion was separated from the others and embedded in

Canada balsam between glass coverslips. The specimen is provisionally deposited in the Department of Entomology of the MNHN.

Canadian amber. The material was collected from the Taber Coal Zone within the uppermost Foremost Formation, at the Grassy Lake locality in southern Alberta, Canada (McKellar and Wolfe 2010). The specimen was prepared in a similar fashion to the Spanish material described above. The male holotype is nearly complete but is surrounded by a relatively thick layer of dark orange amber with multiple internal fractures; this renders observation difficult. Photographs were taken using glycerin and a cover slip. The type specimen exhibits minor taphonomic distortion, and is missing both metatarsi and much of the forewing apices.

Systematic paleontology

Order Hymenoptera Linnaeus, 1758

Family Maimetshidae Rasnitsyn, 1975

http://species-id.net/wiki/Maimetshidae

Maimetshidae Rasnitsyn, 1975: 73. Type genus: *Maimetsha* Rasnitsyn, 1975. Rasnitsyn 1988: 124; Ronquist et al. 1999: 33; Rasnitsyn and Brothers 2009: 192; Perrichot 2009: 2; Ortega-Blanco et al. 2010: 266; Vilhelmsen et al. 2010a: 674.
Dinapsinae [Megalyridae], *partim*: Shaw 1988: 107.
Dinapsini [Megalyridae], *partim*: Shaw 1990: 578.

Diagnosis. Modified from Rasnitsyn and Brothers (2009): Head hypognathous, without ocular carina, without subantennal groove accommodating antennal base; vertex with or without longitudinal median sulcus; antenna filiform, with scape short to moderate, never elongate, flagellomeres variable in number (14–19), most often 16, without apparent sexual dimorphism; mandibles often asymmetrical, with 3–4 teeth. Pronotum short medially; mesoscutum with notauli and median sulcus; axillae meeting anterior to mesoscutellum or separated by scutoscutellar sulcus; propodeum areolate. Forewing with costal space moderate to wide; C and pterostigma present; basal sections of Rs and M subequal in length, not continuously aligned (i.e., not forming smooth basal vein); cell [$2R_1$] (i.e., marginal cell) closed, wide (not triangular), moderately short to moderately long; cells [1Rs] and/or [2Rs] closed; cell [1M] closed, small, distant from [1Rs]; cell [2M] open or delimited by spectral or nebulous 2m-cu; 1cu-a antefurcal. Hind wing with no posterobasal lobe; 4–5 distal hamuli; basal cell [R] closed; free apex of Rs present, short to long; free apices of M and Cu short or absent, that of A absent. Legs with trochantelli; tibial spur formula 1-2-2; tarsi pentamerous; tarsal plantulae present in some females; pretarsal claws with preapical tooth. Metasoma rather short, compact, not much sculptured, attached low on propodeum, first segment longest [articulatory ring referred to by Rasnitsyn and Brothers (2009) is not

evident and apparently an incorrect interpretation], apical sternum of female elongate, nearly reaching metasomal apex; ovipositor external but not very long, sheaths at most as long as metasoma, not fitting tightly to ovipositor (often preserved detached).

Included genera. *Andyrossia* Rasnitsyn and Jarzembowski, 2000 (Wealden, England, Barremian; a replacement name for *Arossia* Rasnitsyn and Jarzembowski *in* Rasnitsyn et al. 1998); *Ahiromaimetsha* Perrichot, Azar, Nel, and Engel gen n. (Lebanese amber, Neocomian); *Iberomaimetsha* Ortega-Blanco, Perrichot, and Engel gen. n. (Spanish amber, Lower Albian); *Guyotemaimetsha* Perrichot et al., 2004a (French amber, latest Albian/earliest Cenomanian); *Afrapia* Rasnitsyn and Brothers, 2009 (Orapa Mine, Botswana, Turonian); *Afromaimetsha* Rasnitsyn and Brothers, 2009 (Orapa Mine, Botswana, Turonian); *Maimetshorapia* Rasnitsyn and Brothers, 2009 (Orapa Mine, Botswana, Turonian); *Maimetsha* Rasnitsyn, 1975 (Taimyr amber, Santonian); and *Ahstemiam* McKellar and Engel gen. n. (Canadian amber, Campanian). Table 1 summarizes the species diversity of the family.

Genus *Guyotemaimetsha* Perrichot, Nel & Néraudeau, 2004a

http://species-id.net/wiki/Guyotemaimetsha

Guyotemaimetsha Perrichot, Nel & Néraudeau, 2004a: 159 [*Incertae sedis* in Ceraphronoidea *sensu* Rasnitsyn 2002]. Type species: *Guyotemaimetsha enigmatica* Perrichot, Nel & Néraudeau, 2004a. Rasnitsyn and Brothers 2009: 192 [in Maimetshidae]; Ortega-Blanco et al. 2010: 266; Vilhelmsen et al. 2010a: 661.

Revised diagnosis. *Male*: total body length (excluding mandibles and parameres) 1.7 to 2.9 mm; compound eyes oval and bulging, large, 0.66× height of head; vertex without longitudinal medial line; fine occipital carina present; mandibles asymmetrical, right with four teeth and left with three teeth; scape flattened laterally, short, its maximal width 0.9× its length; pedicel nearly as broad as long, 0.75× length of scape; 14 flagellar articles cylindrical in shape and progressively shortening and slightly narrowing; maxillary palpus apparently with five palpomeres; labial palpus apparently with three palpomeres, all short; forewing with pterostigma moderately long, shorter than [2R1]; r-rs originating within apical one-third of pterostigmal length; 2R present as long stub, about half length of 1R; [1M] small, nearly rhombic, with first abscissa of Rs+M one-half length of second abscissa (2Rs+M), so that apical corner (junction of Rs+M and 1m-cu crossvein) positioned anterior to pterostigma; [1Rs] triangular, with Rs and 1rs-m crossvein both fade to become nebulous posteriorly; cross-veins 2rs-m and 2m-cu at most spectral, generally absent; hind wing with cells [R] and [Cu] enclosed by nebulous veins, with free apex of Cu.

Female: very similar to male but larger, total body length (excluding mandibles and ovipositor) 3.7 to 4.1 mm; pedicel more elongate, 0.75× as broad as long, 0.85× length of scape; legs with tarsal plantulae; ovipositor apparently simple, not serrate or toothed.

Table 1. Known records for Maimetshidae s.l. (A = amber inclusion; C = compression fossil).

Taxon	Stage	Geography	Sex
Family Maimetshidae Rasnitsyn, 1975			
Genus *Andyrossia* Rasnitsyn & Jarzembowski, 2000			
A. joyceae (Rasnitsyn & Jarzembowski, 1998)	Barremian (C)	England	?
Genus *Ahiromaimetsha* Perrichot, Azar, Nel & Engel, **gen. n.**			
A. najlae Perrichot, Azar, Nel & Engel, **sp. n.**	Neocomian (A)	Lebanon	♀
Genus *Iberomaimetsha* Ortega-Blanco, Perrichot & Engel, **gen. n.**			
I. nihtmara Ortega-Blanco, Delclòs & Engel, **sp. n.**	Albian (A)	Spain	♀♂
I. rasnitsyni Ortega-Blanco, Perrichot & Engel, **sp. n.**	Albian (A)	Spain	♀♂
Genus *Guyotemaimetsha* Perrichot et al., 2004			
G. enigmatica Perrichot et al., 2004	Albian/Cenomanian (A)	France	♀♂
Genus *Afrapia* Rasnitsyn & Brothers, 2009			
A. globularis Rasnitsyn & Brothers, 2009	Turonian (C)	Botswana	♀
A. variicornis Rasnitsyn & Brothers, 2009	Turonian (C)	Botswana	♀♂
Genus *Afromaimetsha* Rasnitsyn & Brothers, 2009			
A. robusta Rasnitsyn & Brothers, 2009	Turonian (C)	Botswana	♀
Genus *Maimetshorapia* Rasnitsyn & Brothers, 2009			
M. africana Rasnitsyn & Brothers, 2009	Turonian (C)	Botswana	♀
Genus *Ahstemiam* McKellar & Engel, **gen. n.**			
A. cellula McKellar & Engel, **sp. n.**	Campanian (A)	Canada	♂
Genus *Maimetsha* Rasnitsyn, 1975			
M. arctica Rasnitsyn, 1975	Santonian (A)	Siberia	♀*
Incertae sedis (but possibly maimetshids, *sensu* Rasnitsyn & Brothers 2009)			
Genus *Cretogonalys* Rasnitsyn, 1977**			
C. taimyricus Rasnitsyn, 1977	Cenomanian (C)	Siberia	?
Genus *Turgonalus* Rasnitsyn, 1990			
T. cooperi Rasnitsyn & Jarzembowski, 1998	Barremian (C)	England	?
T. minor Rasnitsyn, 1990	Neocomian (C)	Siberia	?

* Unfortunately, the holotype of *M. arctica* was destroyed. Should new material eventually be discovered a neotype will be necessary in order to stabilize the application of the name for the species, genus, and even family.

** *Cretogonalys* is the type genus of the family-group name Cretogonalinae Rasnitsyn, 1977 (*nomen imperfectum*; *recte* Cretogonalyinae Rasnitsyn, 1977), which, if the genus is definitively placed in Maimetshidae, would make the former family-group name a junior synonym of the latter family.

Comments. *Guyotemaimetsha* is most similar to *Maimetsha* in the absence of cell [2Rs]. It differs in cell [1Rs] being anteriorly petiolate instead of sessile, the hind wing with a free apex of Cu, the absence of a medial line on the vertex, and the presence of tarsal plantulae in females.

***Guyotemaimetsha enigmatica* Perrichot, Nel & Néraudeau, 2004a**
http://species-id.net/wiki/Guyotemaimetsha_enigmatica
Figs 1–4

Guyotemaimetsha enigmatica Perrichot, Nel & Néraudeau, 2004a: 159, figs. 1A-B, 2 [♂].

Type material. Holotype MNHN.F.A30174 (♂); paratype MNHN.F.A30175 (♂); in amber collection of the Museum National d'Histoire Naturelle, Paris, France.

Other material examined. Specimens IGR.ARC-1 (♀, missing anterior part of the head and with cuticle somewhat altered by taphonomy), IGR.ARC-309.11 (sex unknown, missing apices of right forewing and metasoma), IGR.ARC-370.7 (= scan ESRF-A-018g, reconstructed, ♀, in opaque amber), IGR.ARC-378.1 (♂, missing head, most metasoma and apices of all legs), IGR.ARC-378.2 (scan ERSF A-401-378, not reconstructed; ♂), IGR.ARC-393.4 (= radiograph ESRF-A-053d, not reconstructed; ♂), IGR.CDL-2.5 (♂, with forewing fragment in IGR.CDL-2.16, missing apical flagellomeres of left antenna; ex collection Arnaud), IGR.CDL-2.33 (♂, missing left antenna and apices of right antenna, right forewing, and all legs; ex collection Arnaud). All specimens deposited in the amber collection of the Department of Geosciences of the University Rennes I, France.

Indeterminate specimens. IGR.ARC-171 (♂, missing head, anterodorsal part of metasoma, and forelegs); IGR.ARC-191 (♂?, missing part of the head and mostly obscured, preserved in very dark amber); IGR.ARC-275 (♀, missing parts of mesosoma, left legs, and with metasoma mostly obscured by a bacterial film). These specimens agree in most respects with the definition of *G. enigmatica* but little is preserved and attribution to this species cannot be asserted. All specimens deposited in the amber collection of the Department of Geosciences of the University Rennes I, France.

Type locality. Font-de-Benon quarry, 1 km east of Archingeay, Charente-Maritime, France.

Stratigraphic horizon. Lithological subunit A1sl-A, Uppermost Albian–Lowermost Cenomanian, middle Cretaceous.

Diagnosis. As for the genus (see above).

Redescription. *Male*: Integument reddish-brown in color, with dense, minute punctures and fine, decumbent pubescence. Head transverse, with length approximately 0.8x width; ocelli separated from each other by one ocellar diameter; antennae inserted between compound eyes, closer to each other than to compound eye margin or posterior clypeal margin; scape globular in lateral view, laterally compressed in frontal view, with faintly concave apex; pedicel with sides convex; flagellum with dense coat of short, inclined setae, with first article longest, twice length of pedicel; penultimate article as broad as long; apical article with rounded apex; clypeus transverse, about twice as broad as long, with anterior margin rounded and posterior margin straight; mandibles large, with outer margin convex, overlapping apically when closed; right mandible with basal tooth large, second and third teeth equally smaller, apical tooth

Figure 1. Photomicrographs of male of *Guyotemaimetsha enigmatica* Perrichot et al., 2004a (IGR.CDL-2.5) **A** Left lateral habitus **B** Right lateral habitus.

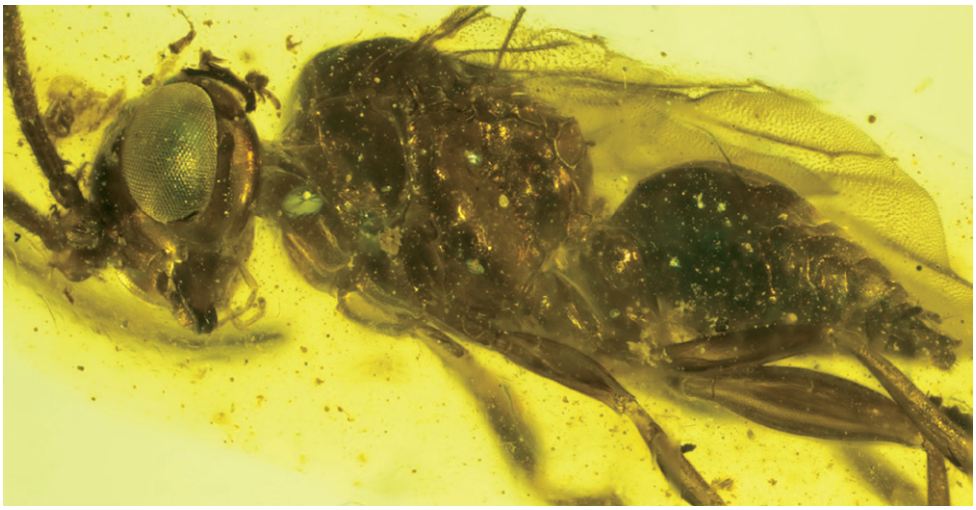

Figure 2. Photomicrograph detail of male of *Guyotemaimetsha enigmatica* Perrichot et al., 2004a (IGR. CDL-2.5).

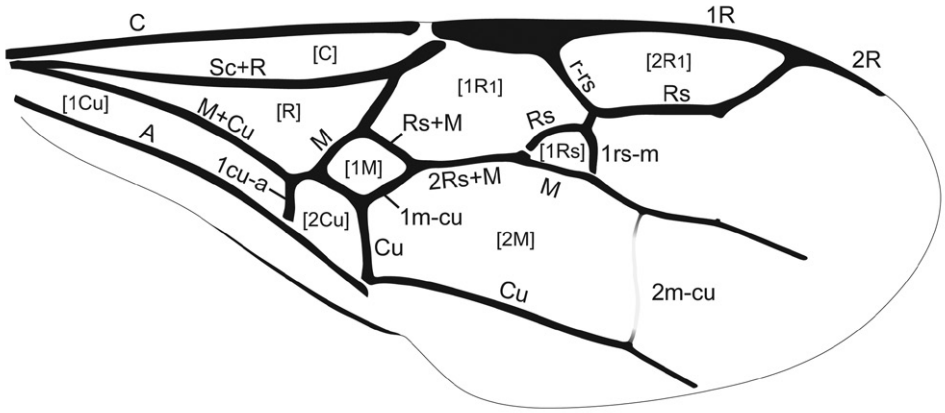

Figure 3. Forewing venation of *Guyotemaimetsha enigmatica* Perrichot et al., 2004a (paratype MNHN-A30175), annotated with vein and cell nomenclature employed herein.

largest; left mandible with basal tooth large, median tooth smallest, apical tooth largest. Mesosoma compact, 0.7x as high as long; pronotum in dorsal view reduced to a short neck; mesoscutum broader than long, about 0.4x mesosomal length, abruptely truncate anteriorly to form a flat vertical surface, bordered by a transverse carina at anterolateral corners, with low dorsal convexity; median mesoscutal sulcus crenulate, notauli deeply impressed, slightly diverging anteriorly; mesoscutellum with low dorsal convexity, small triangular axillae separated anteriorly by large foveate groove; propodeum areolate, gradually sloping to pronounced posterior lip; meso- and metapleuron with anterior margin foveolate. Forewing hyaline, with costal cell distinctly enlarged

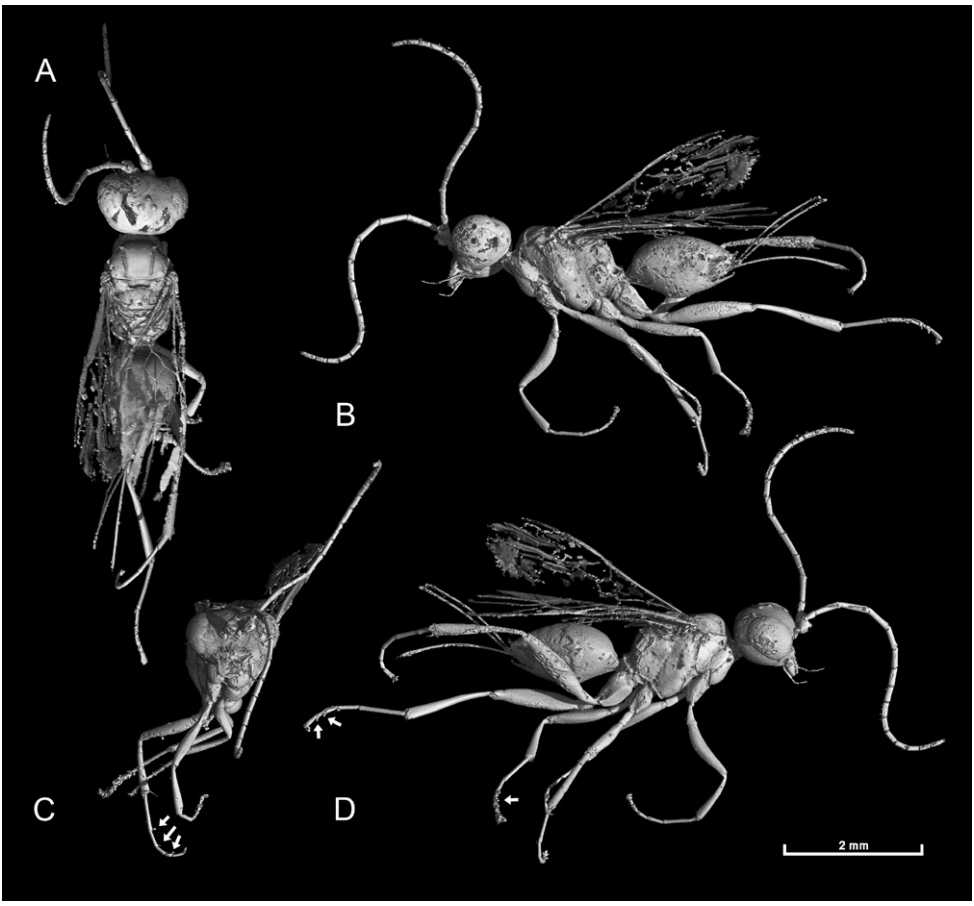

Figure 4. 3D virtual extraction of female of *Guyotemaimetsha enigmatica* Perrichot et al., 2004a (IGR. ARC-370.7, scan ESRF-A-018g), using PPC-SRμCT (voxel size 5.06 μm, propagation distance 990 mm, 30 keV) **A** Dorsal habitus **B** Left lateral habitus **C** Facial aspect **D** Right lateral habitus. The arrows indicate tarsal plantulae.

around midlength; Rs junction with Sc+R forming an acute angle; cell [1M] with vein M slightly arched, roughly aligned with Rs, vein Cu shortest, M and Rs+M subequal in length; cells [1M] and [1Rs] well distant from each other, separated by long vein 2Rs+M; 2Cu significantly longer than 1Cu and 1m-cu; M and Cu nebulous at apex, reaching wing margin; 2A fading to nebulous vein posterior of [2Cu]. Hind wing with Sc+R, R, M+Cu, Cu, and A tubular, other veins nebulous; Sc+R and R more heavily sclerotized than M+Cu, Cu, and A; Cu fading to nebulous vein apically; free apex of Rs and Cu short. Metacoxa approximately 1.4x length of pro-and mesocoxae, all with broad bases and distinct apical constriction, in lateral view inserted posteroventrally on mesosoma; metafemur distinctly enlarged around midlength; all tibiae approximately subequal to femora in length, with basitarsus length slightly less than combined length of all subsequent tarsomeres. Metasoma compact, as long as mesosoma; parameres

trapezoidal, narrowed toward apex, with outer surface slightly convex, with short erect setae around apex; cerci small, spatulate, inserted just anterior to parameres.

Female: Very similar to male but with pedicel cylindrical and each leg with a small plantar lobe (or tarsal plantula) on ventral apex of tarsomeres I–IV; ovipositor approximately as long as metasomal length, apex acute. Integument sculpturing and pubescence not visible, altered on specimen IGR.ARC.1 and not reconstructed in microtomographic scan of specimen IGR.ARC-370.7.

Iberomaimetsha Ortega-Blanco, Perrichot & Engel, gen. n.

http://species-id.net/wiki/Iberomaimetsha

Type species. *Iberomaimetsha rasnitsyni* Ortega-Blanco, Perrichot & Engel, sp. n.

Diagnosis. Antennae with 16 articles; pedicel straight; notauli parallel; forewing costal cell thinner than pterostigma width; prestigma incrassate, wider than base of R, and about the length of 1Rs (distinctly separated from pterostigma); pterostigma longer than distance from base of Rs to base of 2r-rs; cell [$2R_1$] short, about 2.4x longer than wide; cells [1Rs] and [2Rs] present but with 2rs-m slightly sclerotized; extremely light nebulous 2m-cu (only visible playing with light incidence angle); protibial spur biseriate apically.

Etymology. The new genus-group name is a combination of Iberia, referring to the Iberian Peninsula, and *Maimetsha*, type genus of the family. The name is feminine.

Comments. *Iberomaimetsha* is well distinguished from *Maimetsha* and *Guyotemaimetsha* in the simultaneous presence of cells [1Rs] and [2Rs] (rm cells *sensu* Rasnitsyn and Brothers 2009); it differs from *Afromaimetsha* by its parallel notauli (instead of diverging anteriorly); the prestigma is incrassate, clearly wider than basalmost R, not as in *Afrapia*; the origin of Rs in *Iberomaimetsha* is well separated from pterostigma, not as close as in *Maimetshorapia*; the pedicel is straight and not "comma-shaped" as in *Ahstemiam* (see below); *Andyrossia* was described from just a forewing but *Iberomaimetsha* differs clearly in several details, such as the length of cell [$2R_1$] (around 2.4 times longer than wide versus 3.6 in *Andyrossia*), and the width of cell [C] (narrower than pterostigmal width in *Iberomaimetsha* versus wider in *Andyrossia*).

Iberomaimetsha rasnitsyni Ortega-Blanco, Perrichot & Engel, sp. n.

urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Iberomaimetsha_rasnitsyni
Figs 5–7

Type material. Holotype MCNA 9928 (♀); paratype MCNA 8765 (♂). All specimens deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain.

Type locality. Peñacerrada I, Moraza, Burgos Province, Basque-Cantabrian Basin, Spain.

Figure 5. Photomicrograph of holotype female of *Iberomaimetsha rasnitsyni* Ortega-Blanco, Perrichot, and Engel gen. et sp. n. (MCNA 9928).

Stratigraphic horizon. Escucha Formation, Lower Albian, Lower Cretaceous.

Diagnosis. Mandibles moderately large, each with three teeth, with almost straight margins and teeth (when mandibles opened, teeth facing forward, not curved inward); all flagellomeres of similar length (gradual slight reduction of length); protibial distal margin without comb of stiff setae; tarsal plantulae present on female; cell [1M] about as large as cell [2Cu], both almost square or rhomboidal; 2Rs+M much shorter than 1m-cu and shorter than cell [1Rs]; apicalmost sector of Cu arising at midlength of cell [2Cu]; metasoma elongate, about as long as remainder of body; female ovipositor with apex of second valvula 4-toothed.

Description. *Female* (holotype): Body length 2.8 mm. Head rounded in anterior view, length 0.4 mm, width 0.85 mm; compound eyes not especially bulging, oval, large, well separated by 0.43 mm dorsally; basal part of palps not visible but maxillary palps with at least five palpomeres; labial palps with at least three palpomeres; slight, triangular, supra-antennal elevation above torulus, intertorular area flattened; toruli closer to each other than to inner margin of compound eyes; antennae 2.4 mm in length, inserted on frons below midpoint of compound eyes; scape and pedicel short and globular, flagellomeres cylindrical; lengths of antennomeres as follows (all in mm): scape 0.15, pedicel 0.10, flagellomeres 0.22, 0.20,

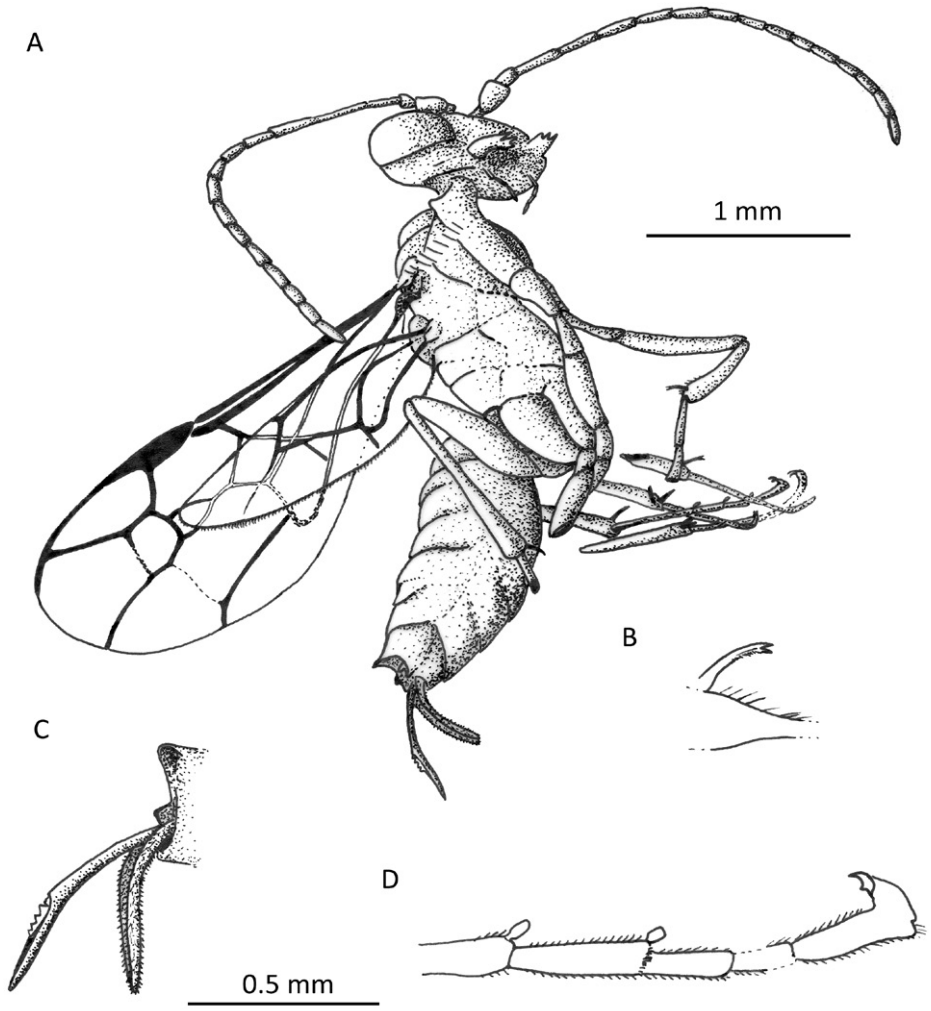

Figure 6. *Iberomaimetsha rasnitsyni* Ortega-Blanco, Perrichot, and Engel gen. et sp. n. (MCNA 9928) **A** Habitus diagram of holotype female **B** Detail of tibial spur **C** Detail of metasomal apex **D** Detail of metatarsus showing tarsal plantulae.

0.20, 0.20, 0.18, 0.15, 0.14, 0.14, 0.12, 0.12, 0.12, 0.12, 0.12, 0.15; malar space short, 0.15 mm in length. Mesosoma only laterally visible, 1.15 mm in length; pronotum 0.20 mm in length; mesoscutum 0.35 mm in length; mesoscutellum strongly convex, 0.30 mm in length; propodeum slightly rugose, 0.30 mm in length. Only left mid and hind legs are complete, but foreleg can be reconstructed by mixing right and left parts; no visible division of metatrochantellus; tarsi pentamerous, tarsomeres I–IV each with apicoventral plantar lobe (well visible on left metatarsus: Figs 5, 6D); pretarsal claws with small preapical tooth; leg measure-

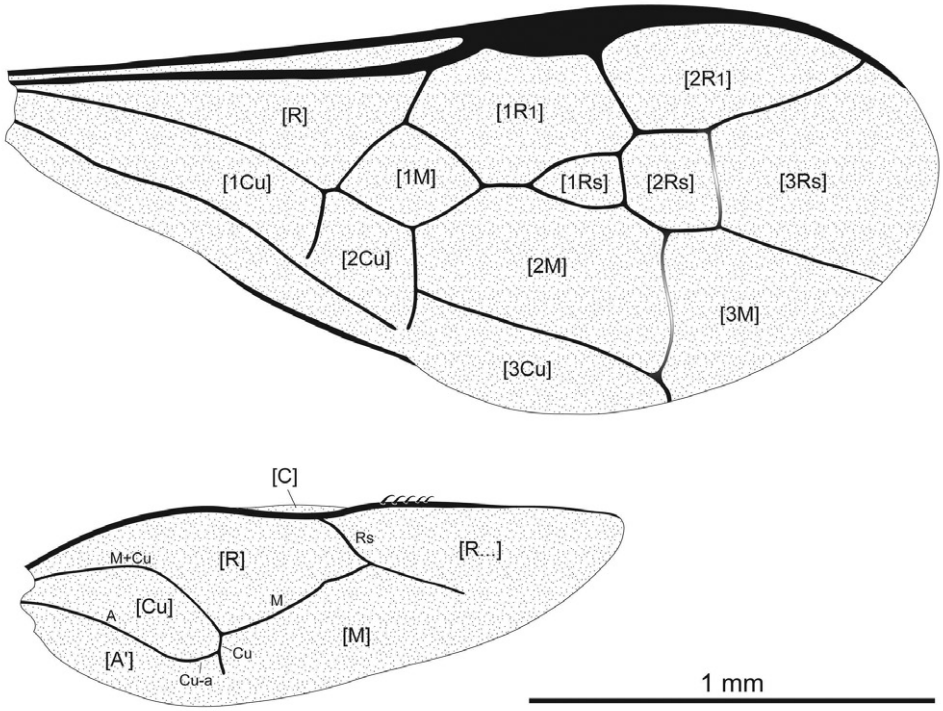

Figure 7. Wing venation of *Iberomaimetsha rasnitsyni* Ortega-Blanco, Perrichot, and Engel gen. et sp. n. (MCNA 9928), annotated with cell nomenclature employed herein.

ments (all in mm): profemur (with protrochantellus) 0.85, protibia 0.50, protarsomeres I–V 0.30/0.15/0.12/?/?; mesofemur 0.75, mesotibia 0.72, mesotarsomeres 0.32/0.15/0.10/0.07/0.12; metafemur 0.95, metatibia 0.90, metatarsomeres 0.38/0.15/0.10/0.08/0.14. Forewing hyaline, length 2.4 mm, maximum width 0.95 mm, densely covered by microtrichia; all veins tubular except for nebulous crossveins 2rs-m and 2m-cu, thus only cells [2Rs] and [2M] pseudo-opened apically (Fig. 7A); 1rs-m not aligned with r-rs; 2m-cu curved at each distal end; veins M and Cu reaching wing margin, with distal end of Cu strongly bent posteriorly; cell [$1R_1$] longer than both cells [1Rs] + [2Rs]; cell [1Rs] about half the surface of cells [1M] and [2Rs]; vein r-rs emerging at two-thirds from base of pterostigma; cell [$2R_1$] short, with vein Rs slightly anteriorly bent distad 2rs-m. Hind wing hyaline and densely covered by microtrichia, length 1.65 mm, maximum width 0.45 mm; five strong hamuli present on costal vein in distal half of wing (Fig. 7B); distal sections of veins Rs and Cu reaching nebulous wing margin; vein A lost beyond cu-a. Metasoma pedunculate, elongate and globoid, length 1.3 mm, greatest height 0.5 mm; sterna hard, convex; no apparent metasomal armature on sternum II or III; cerci very short; ovipositor moderately exserted, first valvula 0.65 mm long (as preserved), second valvula 0.35 mm long, apically with four dorsal teeth, with sheaths covered by very short, sparse setae (Figs. 4, 5A, 5C).

Male: Very similar to female except in following minor differences: Body length 3.63 mm; tarsi without plantar lobes; metasoma slightly longer than mesosoma.

Etymology. The specific epithet is a patronym honoring Prof. Alexandr P. Rasnitsyn for his numerous important contributions to the study of Hymenoptera and his generous friendship with the authors.

***Iberomaimetsha nihtmara* Ortega-Blanco, Delclòs & Engel, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Iberomaimetsha_nihtmara
Figs 8–10

Type material. Holotype MCNA 13049 (?); paratypes MCNA 8758(♀?), MCNA 8790 (♂), MCNA 9373 (?), MCNA 9918 (♀), and MCNA 10732 (?). All specimens deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain.

Type locality. Peñacerrada I, Moraza, Burgos Province, Basque-Cantabrian Basin, Spain.

Stratigraphic horizon. Escucha Formation, Lower Cretaceous, Lower Albian.

Diagnosis. Mandibles distinctly large, exserted, asymmetrical, right 4-toothed, left 3-toothed, arched inwards (teeth pointing toward teeth of opposite mandible); basal flagellomeres (from F1 to F3–4) distinctly larger than apical flagellomeres (F1–F4 about 2–1.5× the length of F7–F14); protibial distal margin with a comb of stiff setae; cell [1M] square or rhomboidal, distinctly smaller than [2Cu] which has a short but distinct connection between 1M+Cu and M (then, [2Cu] composed by five aristae); 2Rs+M longer than 1m-cu and longer than cell [1Rs]; apicalmost sector of Cu arising from almost apical posterior margin of [2Cu]; metasoma moderately short, as long as mesosoma.

Description. Body length (from paratypes, as incomplete metasoma in holotype) around 2.55–2.61 mm. Head rounded in anterior view, length 0.41 mm, width 0.68 mm with a short occipital carina and apparently some polygonal dorsal sculpture; compound eyes not bulging, slightly oval, separated dorsally by 0.39 mm; toruli about at same distance to inner margin of compound eyes and each other; antennae 2.54 mm in length, inserted on frons below midpoint of compound eyes; scape and pedicel short and globular, flagellomeres cylindrical; lengths of antennomeres as follows (all in mm): scape 0.12, pedicel 0.09, flagellomeres 0.29, 0.28, 0.27, 0.23, 0.20, 0.18, 0.15, 0.14, 0.12, 0.12, 0.11, 0.11, 0.10, 0.12; malar space short, length approximately 0.11 mm. Mesosoma (dorsal view) 0.95 mm in length; pronotum not distinct dorsally; mesoscutal length 0.27 mm, with parallel notauli and longitudinal medial line, all three present as linear series of grooves more than well-delimited lines (Fig. 9); axillae wide and long, well distinct, separating completely mesoscutellum and mesoscutum; mesoscutellum distinctly convex, length 0.22 mm; propodeum 0.29 mm in length, areolate (seen in paratype MCNA 8790). Legs distinctly elongate; division of trochantellus not

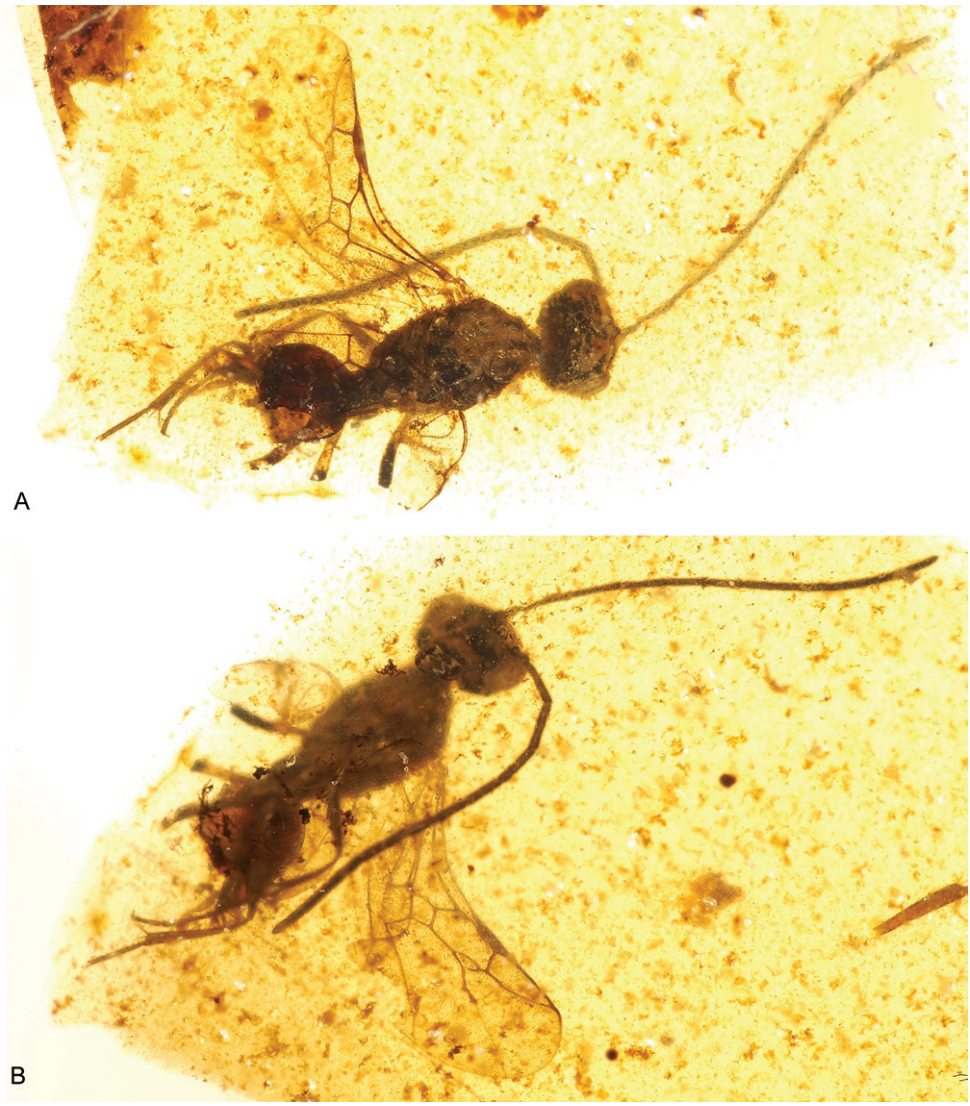

Figure 8. Photomicrographs of holotype of *Iberomaimetsha nihtmara* Ortega-Blanco, Delclòs, and Engel sp. n. (MCNA 13049) **A** Dorsal aspect **B** Ventral aspect.

visible; tarsi with no plantar lobes visible; leg measurements (all in mm): profemur 0.82, protibia 0.46, protarsomeres I–V 0.34/0.15/0.10/0.09/0.10; mid-legs very poorly preserved but apparently with mesofemur 0.68, mesotibia ?, mesotarsomeres 0.24/0.12/0.10/?/?; metafemur 1.0, metatibia 0.83, metatarsomeres 0.46/0.20/0.15/0.09/0.12. Forewing hyaline, length 2.1 mm, maximum width 0.80 mm, densely covered by microtrichia; all veins tubular except for nebulous 2rs-m and 2m-cu, thus, only cells [2Rs] and [2M] pseudo-opened apically (Figs 9, 10); 1rs-m not aligned with r-rs; 2m-cu curved S-like; veins M and Cu reach-

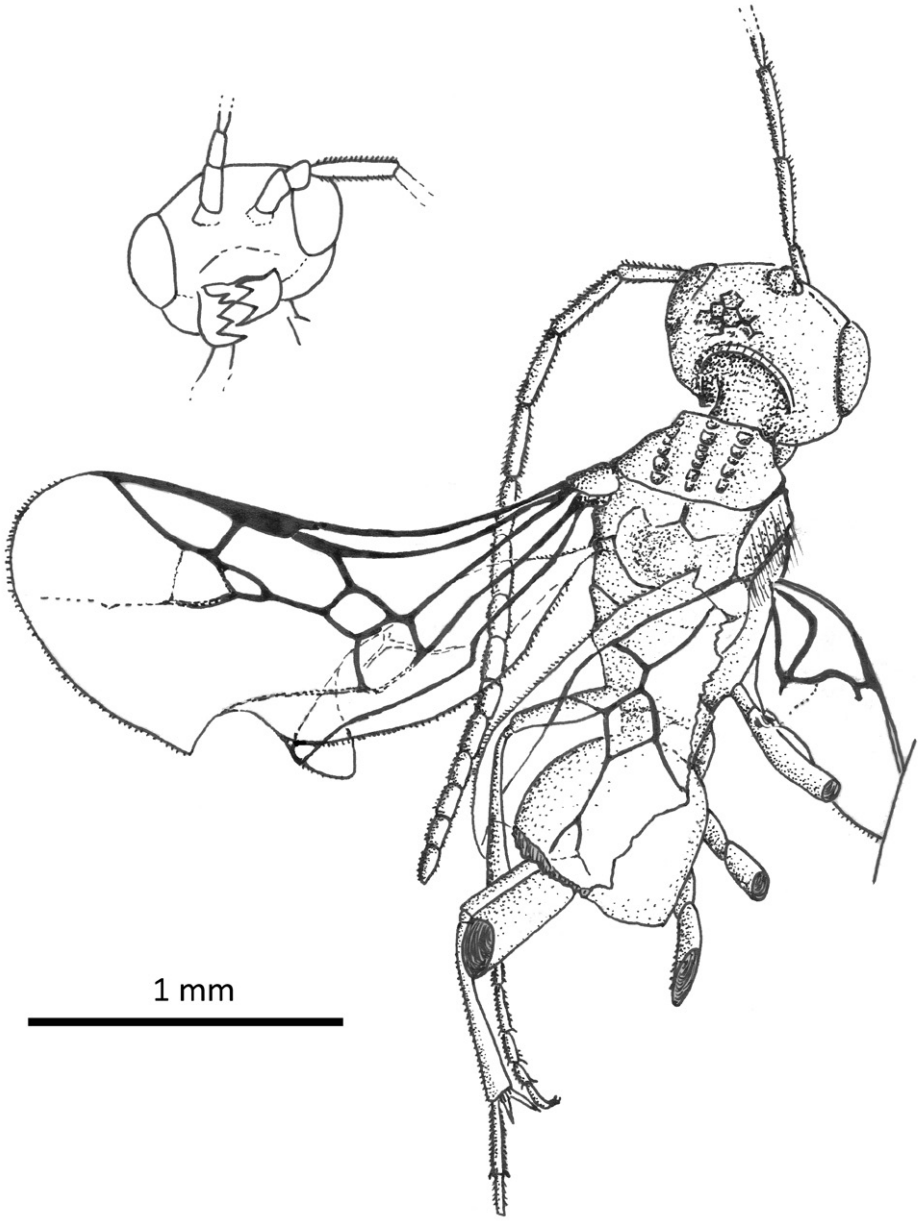

Figure 9. Habitus diagram of holotype of *Iberomaimetsha nihtmara* Ortega-Blanco, Delclòs, and Engel sp. n. (MCNA 13049), with inset of facial aspect.

ing wing margin (although M somewhat nebulous), with apicalmost sector of Cu slightly angled posteriorly; cell [$1R_1$] longer than both cells [1Rs]+[2Rs]; cell [1Rs] almost ¾ the surface of cell [1M] and almost half of [2Rs]; vein r-rs emerging at two-thirds from base of pterostigma; cell [$2R_1$] short, with vein Rs slightly anteri-

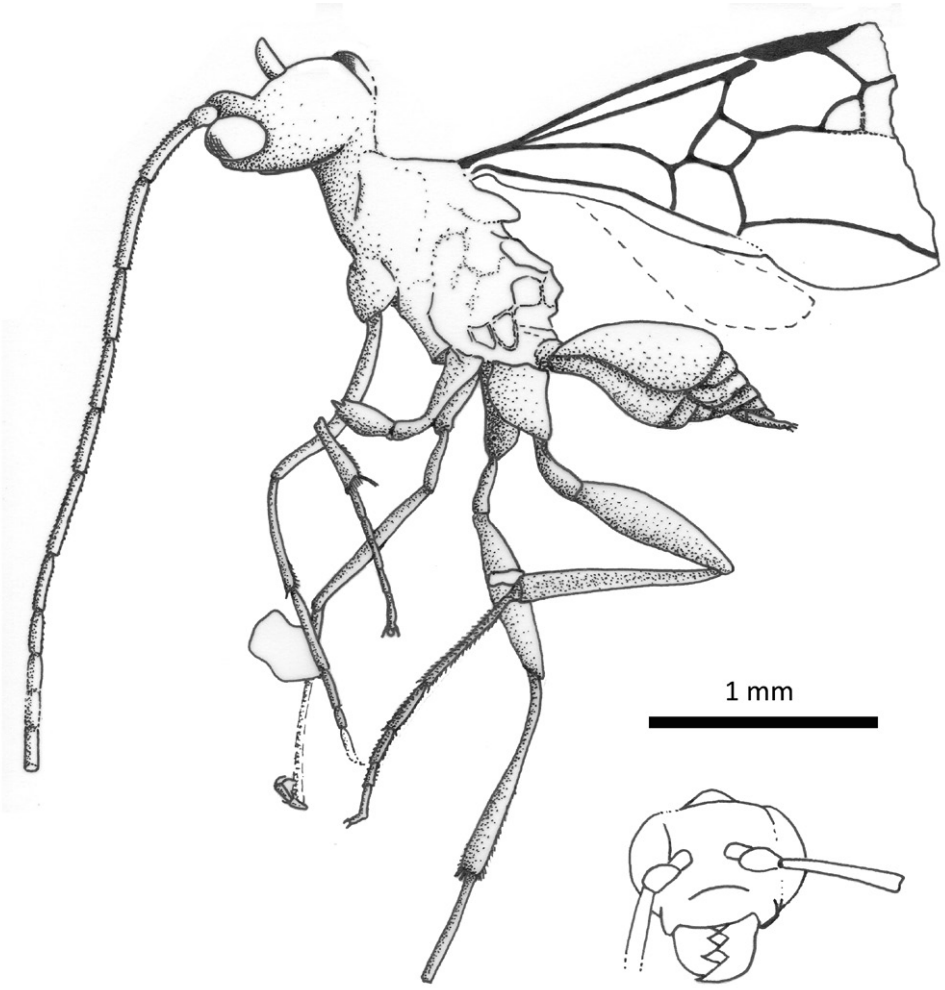

Figure 10. Habitus diagram of male paratype of *Iberomaimetsha nihtmara* Ortega-Blanco, Delclòs, and Engel sp. n. (MCNA 8790), with inset of facial aspect.

orly bent distad 2rs-m. Hind wing difficult to observe, hyaline and densely covered by microtrichia, length approximately 1.22 mm, maximum width approximately 0.41 mm; three strong hamuli present on costal vein in distal half of wing. Metasoma (checked on paratype MCNA 8790) pedunculate, short and slightly flattened, length 0.98 mm, greatest height 0.41 mm; sterna hard, convex; no apparent metasomal armature on sternum II or III.

Male: Parameres spatulate, with apparently three short stiff setae apically (Fig. 10).

Etymology. The specific epithet is a noun in apposition and is the Anglo-Saxon word for nightmare, in reference to the terrifying appearance of the species in frontal view and with its enlarged mandibles.

***Ahiromaimetsha* Perrichot, Azar, Nel & Engel, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Ahiromaimetsha

Type species. *Ahiromaimetsha najlae* Perrichot, Azar, Nel & Engel, sp. n.

Diagnosis. Antennae apparently with 16 articles; pedicel straight; forewing costal cell apically about as wide as pterostigmal width; prestigma not incrassate, not wider than base of R, about as long as 1Rs (distinctly separated from pterostigma); cell [$2R_1$] long, nearly 4x longer than wide; cells [1Rs] and [2Rs] present, former greatly enlarged; 2Rs+M absent owing to confluence of 1m-cu with 2Rs; 1rs-m exceptionally minute (Figs 11, 12D); 2rs-m completely sclerotized; protibial spur bifurcate apically; female tarsi with apicoventral plantar lobes.

Etymology. The new genus-group name is a combination of Ahirom, Phoenician king of Byblos (ca. 1000 BC) whose sarcophagus bears the oldest inscription in the Phoenician alphabet, and *Maimetsha*, type genus of the family. The name is considered to be feminine.

Comments. *Ahiromaimetsha* can be distinguished most easily from other genera by the effective absence of 2Rs+M owing to the confluence of 1m-cu with the second free abscissa of Rs. Like *I. rasnitsyni* and *A. joyceae*, *Ahiromaimetsha najlae* has a large cell [1Rs] but even more so than in the aforementioned species and, unlike *I. rasnitsyni*, the prestigma is not incrassate.

***Ahiromaimetsha najlae* Perrichot, Azar, Nel & Engel, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Ahiromaimetsha_najlae
Figs 11–12

Type material. Holotype MKN-1A (♀), collection Azar, provisionally deposited in the Muséum National d'Histoire Naturelle, Paris, France.

Type locality. Maknouniyyeh, Caza Jezzine, Mouhafazit Loubnan Al-Janoubi (South Lebanon district), Lebanon.

Stratigraphic horizon. Neocomian (Valanginian–Lowermost Aptian), Lower Cretaceous.

Diagnosis. As for the genus (see above).

Description. *Female*: Total body length ca. 5.2 mm. Head nearly rounded in anterior view, length 0.97 mm, width 1.35 mm, finely setose; compound eyes somewhat bulging, oval, large, length 0.78 mm, width 0.62 mm; ocelli positioned on swelling; mandibles strong, asymmetrical, right with four teeth and left with three teeth both with apical tooth largest; maxillary palps well developed, elongate, distinctly longer than mandibles, with six palpomeres; labial palps short, with four palpomeres; antennae partly damaged but complete, with apparently 16 segments

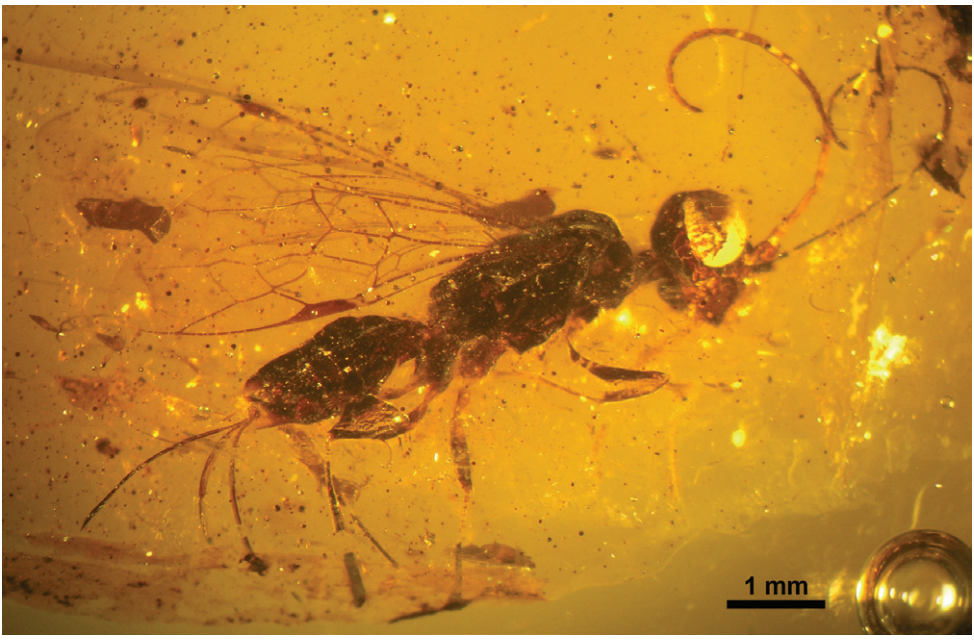

Figure 11. Photomicrograph of holotype female of *Ahiromaimetsha najlae* Perrichot, Azar, Nel, and Engel gen. et sp. n. (MKN-1A).

(some segments have secondary constrictions owing to compression), scape and pedicel short and globulous, flagellomeres cylindrical, length of antennomeres as follows (all in mm): scape 0.3, pedicel 0.16, flagellomeres 0.47, 0.52, 0.45, 0.34, 0.32, 0.32, 0.22, 0.17, 0.17, 0.16, 0.16, 0.14, 0.11, 0.11; antenna with fine setae and sparse sensilla. Mesosomal length 2.21 mm, height 1.09 mm, finely setose but without visible foveae or sculpturing; mesoscutal length 0.71 mm, with strong anterior median depression; mesoscutellum not clearly visible, obscured by wings. Metacoxa with an outer basal extension; metatrochantellus diagonally divided and appearing two-segmented; protibial calcar bifurcate (Fig. 12B), with defined velum and trunk, velum smooth, trunk with spine-like microsculpture, basitarsal comb composed of blunt, flattened pegs; pretarsal claws cleft; leg measurements (all in mm, given for those observable): procoxa 0.21, protrochanter 0.42, profemur 0.82, protibia 0.60, probasitarsus 0.61, second protarsomere 0.16, third protarsomere 0.11, mesocoxa 0.39, mesotrochanter 0.55, mesofemur 0.81, metacoxa 0.48, metatrochanter 0.16, metafemur 1.10. Wings hyaline, forewing length 4.81 mm, width 1.54 mm; hind wing length 3.12 mm, width 1.15 mm; venation as in figure 12D; five distal hamuli on hind wing. Metasomal length 2.11 mm; height 0.81 mm; metasomal sterna well sclerotized, convex; ovipositor long, length 2.16 mm, with clearly visible denticles at apex (Fig. 12C).

Male: Unknown.

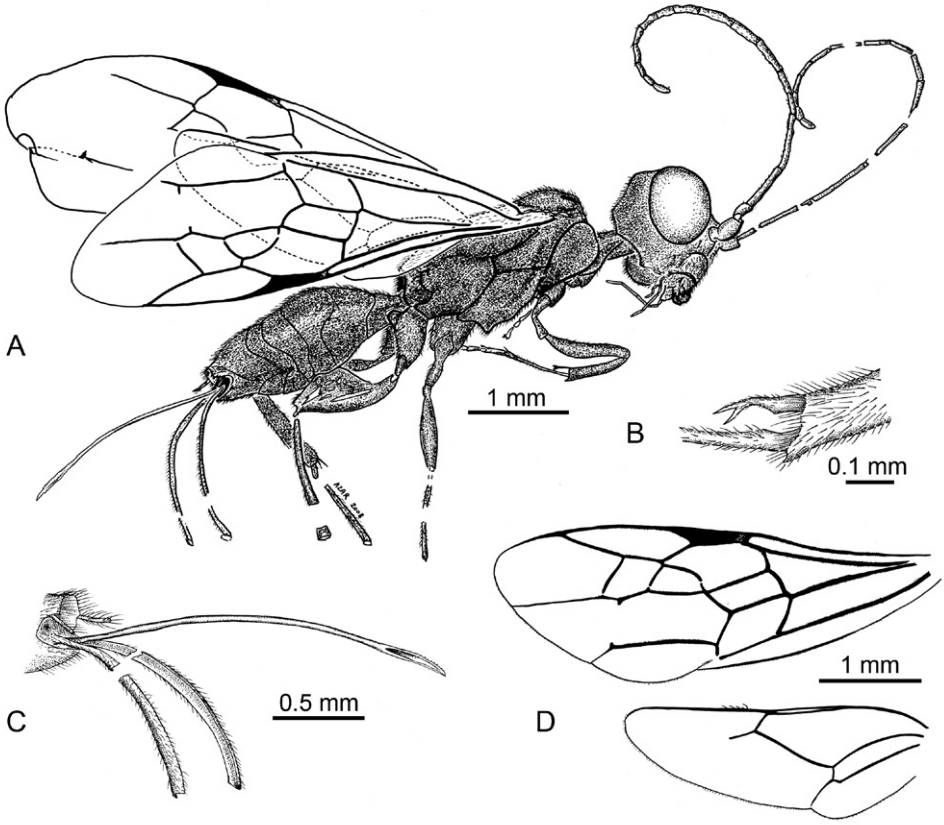

Figure 12. A Habitus diagram of holotype female of *Ahiromaimetsha najlae* Perrichot, Azar, Nel, and Engel gen. et sp. n. (MKN-1A), with inset of **B** fore tibial spine **C** ovipositor **D** forewing and hind wing venation.

Etymology. The specific epithet is a matronym honoring Dr Najla Zeidane-Gèze, wife of the collector of the holotype.

***Ahstemiam* McKellar & Engel, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Ahstemiam

Type species. *Ahstemiam cellula* McKellar & Engel, sp. n.

Diagnosis. Total body length near 1.2 mm; compound eyes globular and protuberant; fine occipital carina present; pedicel 'comma-shaped' in lateral view, 0.54x length of scape and inserted deeply into scape's apex; 14 flagellomeres, cylindrical in shape and progressively shortening; maxillary palpus with at least three palpomeres,

ultimate palpomere with three apical stiff setae, penultimate palpomere with one apical and two mid-body stiff setae; labial palpus apparently with three palpomeres, all short and bearing numerous stiff setae; junction between Sc+R and Rs very close to pterostigma, 2Sc+R shorter than Rs; pterostigma elongate, longer than [$2R_1$], with gradual apical taper; r-rs originating within apical one-third of pterostigmal length; 2R present as small stub; [1M] relatively small, apical corner (junction of Rs+M and 1m-cu crossvein) positioned posterior to pterostigma; [1Rs] triangular, bounded by very thin M posteriorly, 2Rs and 1rs-m forming anterior and apical margins of cell, both fade to become nebulous throughout most of cell's length; first apparent metasomal segment much shorter than cell [$2R_1$].

Etymology. The new genus-group name is the inverse of the type genus, *Maimetsha*, and is considered a meaningless euphonious combination of letters. The name is designated to be feminine in gender.

Comments. *Ahstemiam* is most similar to *Maimetshorapia*. The new genus differs in the presence of a prestigma (abscissa of R between 1Rs and pterostigma) that is only slightly inflated (as opposed to distinctly incrassate) and faded apically, as well as a first apparent metasomal tergum that is much shorter than cell [$2R_1$]. The nebulous veins bordering the posterior edges of cell [1Rs], as well as the small size of the cell itself, are distinct among known members of the family Maimetshidae.

Ahstemiam cellula McKellar & Engel, sp. n.

urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Ahstemiam_cellula
Figs 13–14

Type material. Holotype CNC-CAS 1038 (♂) (Fig 13). Deposited in Canadian National Collection of Insects and Arthropods, Ottawa, Ontario, Canada.

Type locality. Grassy Lake, Alberta, Canada.

Stratigraphic horizon. Uppermost Foremost Formation, Campanian, Upper Cretaceous.

Diagnosis. As for the genus (see above).

Description. *Male* (holotype): Body color apparently dark brown, with paler brown antennae and femora, and yellow legs distal to femora (Fig. 13). Head slightly distorted in type specimen, appearing broad (transverse) and foreshortened (exsagittal), with length 0.57× width; ventral margin of gena with prominent notches, more so adjacent to mandibles; frons deeply impressed, antennal bases inserted in shallow depression between compound eyes (Fig. 13); vertex with sparse, short, inclined setae; scape taphonomically distorted, in lateral view, elongate and narrow basally with pronounced apical flare, and concave apex (Fig. 14); pedicel with row of midlength stiff setae inclined upon ventral margin; apical flagellar article slightly wider than preceding articles, and tapering to bluntly-rounded apex; flagellum with dense coat of short, curled setae in various orientations. Mesoscutum with low dorsal convexity, appar-

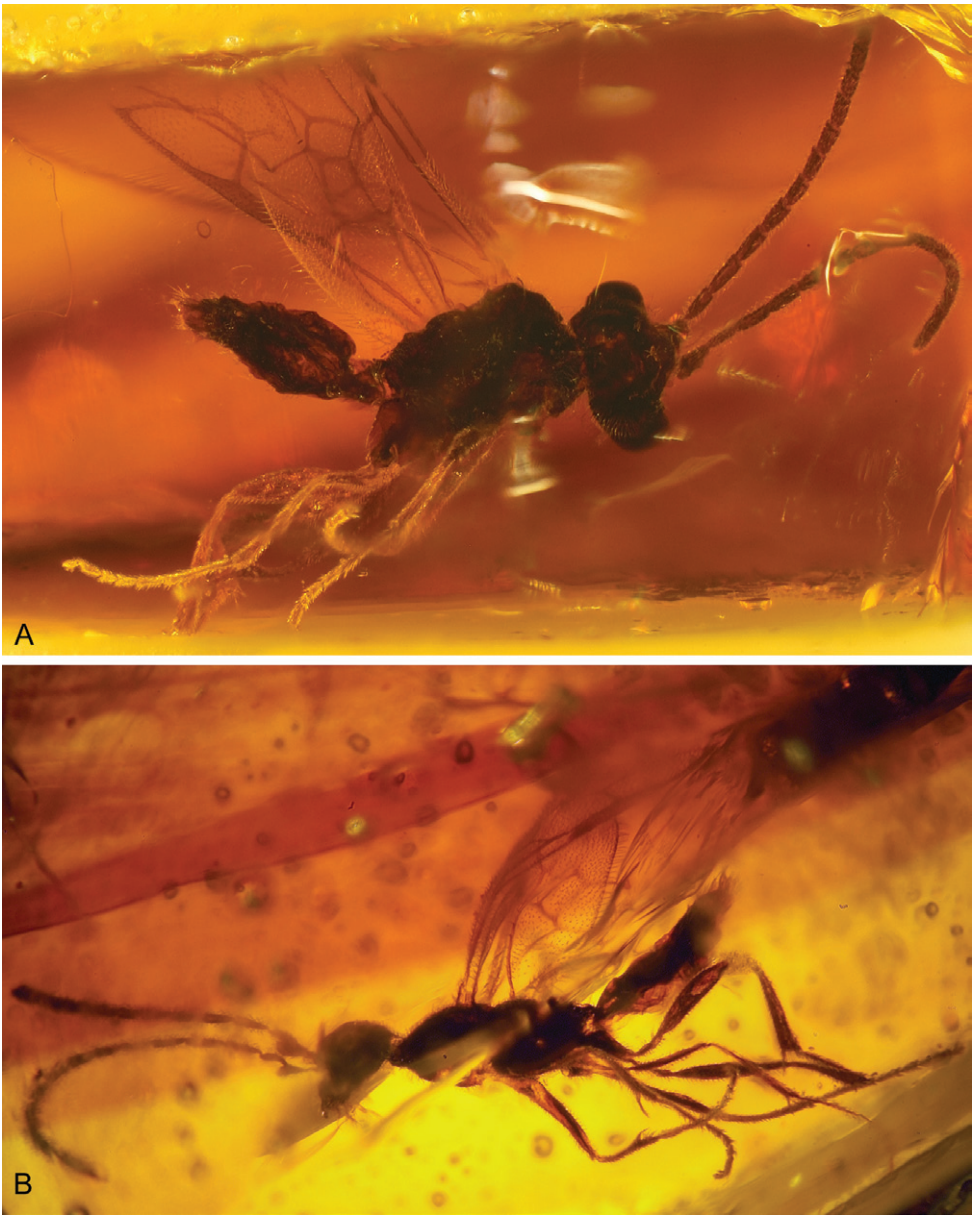

Figure 13. Photomicrographs of holotype male of *Ahstemiam cellula* McKellar and Engel gen. et sp. n. (CNC-CAS 1038) **A** Oblique ventral view **B** Lateral view.

ently near one-half of mesosomal length; mesoscutellum with low dorsal convexity, overhanging metanotum slightly, bearing numerous short, inclined setae; metanotum with prominent ridge along posterior margin which projects posterodorsally over propodeum; propodeum gradually sloping to pronounced posterior lip. Forewing at least 0.96 mm in length and 0.42 mm in width, hyaline with microtrichial vestiture and

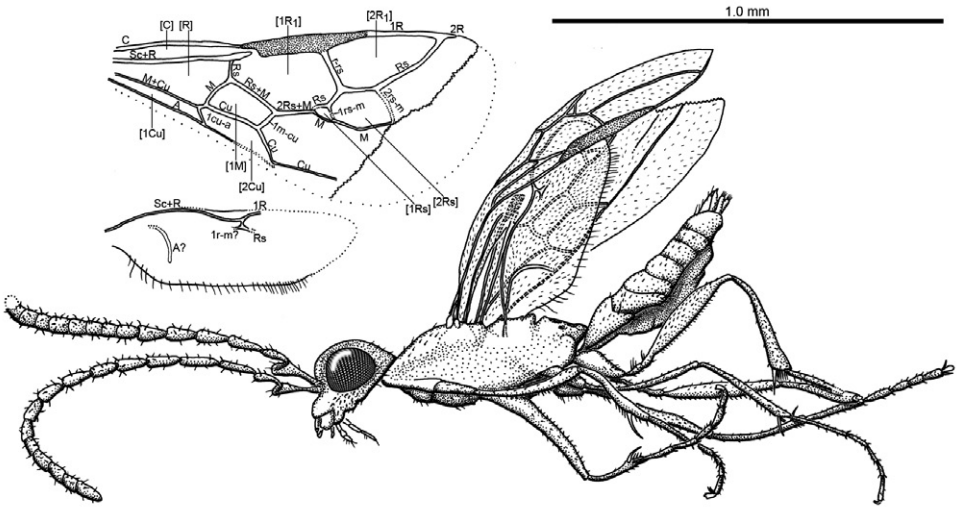

Figure 14. Habitus diagram male of *Ahstemiam cellula* McKellar and Engel gen. et sp. n. (CNC-CAS 1038), with inset of forewing and hind wing venation.

pterostigma pale brown, like tubular veins in wing; Sc+R slightly thicker than other veins, narrowing basally but expanding apical to junction with Rs; fusion of Rs and M angled, veins not parallel to each other; 2rs-m apparently nebulous throughout its course, but preserved in only one wing, which appears taphonomically affected in this region; apex of M not preserved in type specimen; 2Cu significantly longer than 1m-cu; 3Cu appears relatively short, terminating posterior to 1rs-m; 2A fading to nebulous vein at midlength of cell [2Cu]. Hind wings poorly visible; apparent length near 0.64 mm; only anterior veins partly visible; broad, open costal cell apparent near apex of Sc+R; R appears to curve anteriorly and rapidly fade along anterior margin of wing; 2Rs and putative 1rs-m both fade distally, and are removed from 1R by relatively long 1Rs; faint curved vein within posterior portion of wing base assumed to represent A; marginal setae visible along posterior margin of wing are fine, elongate and relatively sparse, with greater density in apical positions. Legs with pervasive coat of short, stiff setae densely inclined upon most surfaces; pro- and mesocoxae with elongate setae inclined upon ventral surface; profemur with two rows of short, stiff setae suberect upon ventral surface, protibia bearing row of at least three stout spines approximately one-half of calcar's length on posterior surface; calcar gently curved and robust (as wide as probasitarsus), deeply inserted into protibial apex, extending only slightly beyond apex; fine setae inclined upon both sides of calcar, and matching longitudinal comb of erect spicules on basal half of probasitarsus; probasitarsus length slightly less than all subsequent tarsomeres combined, with approximately four irregularly distributed spines upon apical half of plantar surface; protarsomeres III and IV much shorter than others, one-half to two-thirds length of protarsomere V; all tarsi with serrate pretarsal claws and large arolium, with two apical spines on all tarsomeres (potentially absent

on protarsomeres, but orientation obscures observation); meso- and metacoxae both approximately 1.5× length of procoxa, with broad bases and apical constriction; mesofemur with two rows of short, stiff setae inclined upon ventral surface; mesotibia with patch of fine, short spines along posterior surface near apex; two mesotibial spurs short and stout, slightly longer than apical width of mesotibia, and bearing minute setae along both margins; metafemur with significant midlength inflation, laterally compressed, with two rows of short, stiff setae suberect along ventral surface; metatibia with moderate apical expansion, bearing two apical spurs slightly longer than metatibial apical width, as well as comb-like row of six spicules each approximately two-thirds of spurs' length; metatarsi not preserved. Metasoma with six apparent terga; terga appear to bear frills of elongate setae along posterior and lateral margins, terga more pilose within posterior of metasoma; parameres spatulate, each with four elongate setae erect on apex.

Female: Unknown.

Etymology. The specific epithet is the Latin diminutive noun in apposition, *cellula* (meaning, "small room") and refers to the very small size of cell [1Rs].

Key to genera and species of Maimetshidae

The following key is modified from that of Rasnitsyn and Brothers (2009).

1 Forewing with three submarginal cells, i.e. cells [1Rs] and [2Rs] both present, [1Rs] sometimes incompletely delimited (Fig. 7); flagellomere number 14–19 (unknown in *Andyrossia* Rasnitsyn and Jarzembowski) **2**

– Forewing with two submarginal cells, i.e. cells [1Rs] and [2Rs] not simultaneously present (Fig. 3); 14 flagellomeres **10**

2(1) Forewing 2Rs+M (second abscissa Rs+M, distal to 1m-cu) shorter than 1m-cu to effectively absent (Figs 7, 12D) **3**

– Forewing 2Rs+M (second abscissa Rs+M, distal to 1m-cu) subequal to or longer than 1m-cu (Figs 9, 10, 14) **5**

3(2) Forewing 1m-cu basad to second free abscissa of Rs such that 2Rs+M present (Fig. 7; Rasnitsyn et al. 1998: fig. 13) **4**

– Forewing 1m-cu effectively confluent with second free abscissa of Rs such that 2Rs+M absent (Figs 11, 12) (Neocomian, Lebanon) ....***Abiromaimetsha najlae*** **Perrichot, Azar, Nel & Engel, gen. et sp. n.**

4(3) Forewing cell [2Rs] not widened anteriorly; prestigma incrassate, about as long as 1Rs; 2m-cu present; pterostigma slightly widening apically (Figs. 5–7) (Albian, Spain) ....***Iberomaimetsha rasnitsyni*** **Ortega-Blanco, Perrichot & Engel, gen. et sp. n.**

– Forewing cell [2Rs] widened anteriorly; prestigma linear, longer than 1Rs; 2m-cu absent; pterostigma linear (Rasnitsyn et al. 1998: fig. 13) (Barremian, England) .....***Andyrossia joyceae*** **(Rasnitsyn and Jarzembowski)**

5(2) Forewing cell [1Rs] not reduced, 1rs-m longer than 3Rs (abscissa of Rs distad 1rs-m; Fig. 10); pedicel, where known, not curved **6**

– Forewing cell [1Rs] greatly reduced, 1rs-m much shorter than 3Rs (abscissa of Rs distad 1rs-m); pedicel arched (Figs 13, 14) (Campanian, Canada) .... ***Abstemiam cellula*** **McKellar & Engel gen. et sp. n.**

6(5) Notauli more-or-less parallel (Fig. 9)..... **7**

– Notauli strongly diverging anteriorly (Rasnitsyn and Brothers 2009: fig. 7b) (Turonian, Botswana) ..... ***Afromaimetsha robusta*** **Rasnitsyn & Brothers**

7(6) Forewing Rs originating well before pterostigma, prestigma about as long as or longer than 1Rs (Figs 9, 10) **8**

– Forewing Rs originating close to pterostigma, prestigma much shorter than 1Rs; prestigma incrassate, swollen apically and broader than basal abscissa Rs (Rasnitsyn and Brothers 2009: fig. 8b) (Turonian, Botswana)..... ..... ***Maimetshorapia africana*** **Rasnitsyn & Brothers**

8(7) Prestigma linear and similar to basal abscissa R (Rasnitsyn and Brothers 2009: figs 1, 2); 2m-cu absent (Genus *Afrapia* Rasnitsyn and Brothers) **9**

– Prestigma incrassate; 2m-cu present, nebulous (Figs 8, 9) (Albian, Spain)..... ..... ***Iberomaimetsha nihtmara*** **Ortega-Blanco, Delclòs & Engel, sp. n.**

9(8) Pterostigma shorter than (about 0.8x) distance between base of Rs and 2r-rs (Rasnitsyn and Brothers 2009: fig. 1b) (Turonian, Botswana)..... ..... ***Afrapia globularis*** **Rasnitsyn & Brothers**

– Pterostigma as long as or longer than distance between base of Rs and 2r-rs (Rasnitsyn and Brothers 2009: fig. 2b) (Turonian, Botswana)..... ..... ***Afrapia variicornis*** **Rasnitsyn & Brothers**

10(1) Forewing cell [1Rs] anteriorly petiolate; hind wing with free apex of Cu; vertex without medial longitudinal line; compound eyes bulging; tarsal plantulae present in females (Figs 1–4) (latest Albian/earliest Cenomanian, France) ..... ***Guyotemaimetsha enigmatica*** **Perrichot et al.**

– Forewing cell [1Rs] anteriorly sessile; hind wing without free apex of Cu; vertex with medial longitudinal line; compound eyes not bulging, almost following head contour; tarsal plantulae absent (Rasnitsyn 1975: fig. 87, pl. IV, figs. 14a, 14b) (Santonian, Siberia) ..... ***Maimetsha arctica*** **Rasnitsyn**

Discussion

The new specimen from Canadian amber extends the temporal range of the family into the Campanian (from the Barremian to the Campanian), as the previous youngest exemplar was *Maimetsha*, from the Santonian amber of Taimyr (Siberia). Our new record also extends the palaeobiogeographic distribution of the family to encompass North America (from south Gondwana to north Laurentia), suggesting an origin during the Early Mesozoic, perhaps sometime in the mid-Jurassic.

Certainly much remains to be undertaken on Maimetshidae, and research into the family is in its infancy. It will be exciting to develop eventually a broad data set meant to examine the interrelationships among the species (indeed, even addressing maimetshid monophyly!) as well along with their relatives among the Trigonalyidae and Megalyridae (along the lines of the study of Vilhelmsen et al. 2010a), and perhaps also among the Ceraphronoidea s.str. In addition, it is not entirely clear that those specimens known only from wing venation are definitively maimetshids, or alternatively, what other fragmentary taxa previously ascribed to Trigonalyidae or elsewhere might more accurately belong in or near Maimetshidae. Once a thorough cladistic analysis has been undertaken for maimetshids, preferably after a greater wealth of diversity and material is discovered and more species analyzed using modern tools such as synchrotron imaging, then the generic classification of the family should be re-evaluated as it presently appears somewhat finely divided.

For now, what started as a singular species discovered and presciently interpreted by Alex Rasnitsyn 36 years ago (Rasnitsyn 1975), has grown rapidly in diversity within the last six years. We can only hope that this trend will continue in the years to come.

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RESEARCH ARTICLE

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A new species of the genus *Disogmus* Förster (Hymenoptera, Proctotrupoidea, Proctotrupidae) from the Eocene Rovno amber

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Abstract

Disogmus rasnitsyni Kolyada & Perkovsky, sp. n. is described from a fossil inclusion of Late Eocene amber (Ukraine). The new species is most similar to *D. basalis* (Thomson, 1857), in particular, in the shape of the tyloids and the general shortening of the segments of antennae, but distinctly differs from it and the other species of the genus by having tyloids on flagellar segments 2–4 compared to 3–6 and 4–7 in other species.

Keywords

Proctotrupidae, *Disogmus*, Late Eocene, Rovno amber, Ukraine

Introduction

The Proctotrupidae is a relatively small, cosmopolitan family of parasitic wasps which prefer regions with temperate and humid climate. They are most diverse in the Holarctic, where they occur predominantly in the forest zone. Proctotrupidae parasitize the larvae of beetles and dipterans or, more rarely, larvae of the lepidopteran family Oecophoridae. In the modern fauna, the family comprises about 320 species classified into 27 genera (Townes 1981; Johnson 1992).

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In the Cenozoic, Proctotrupidae are represented by the extant genera *Fustiserphus* Townes, 1981, *Mischoserphus* Townes, 1981, and *Oxyserphus* Masner, 1961 and are known from the Late Eocene Baltic and Rovno amber (Kolyada and Mostovski 2007). Moreover, from the Florissant locality (USA), currently dated as the uppermost Eocene (Evanoff et al. 2001), in addition to *Mischoserphus* and *Oxyserphus*, the genus *Nothoserphus* Brues, 1940 is known (Kolyada 2009). Unidentified proctotrupids are known from the Middle Eocene deposits in Washington State and in the Middle Eocene Kishenehn Formation in northwestern Montana (USA) as well as in British Columbia, Canada (Okanagan Highlands).

From the Rovno Amber previously there was known only one species of Proctotrupidae: *Oxyserphus obsolescens* (Brues, 1940) (Kolyada and Mostovski 2007). Rovno amber and its arthropod fauna is described in more details by Perkovsky et al. (2007).The present article describes a new species of genus *Disogmus*, which was previously unknown in the palaeontological record.

Material and methods

Material used in this study is deposited in the amber collection of the Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, Kiev (SIZK). Pictures were taken through a Leica M 165 microscope with Leica DFC425 digital camera. To create diffused illumination, a cup of white styrofoam was placed between an object and a light source. The captured images were assembled with Helicon Focus 5.01 software and edited in Helicon Filter 4.7 and Adobe Photoshop CS4.

Systematics

Family PROCTOTRUPIDAE Latreille, 1802
Subfamily PROCTOTRUPINAE Latreille, 1802
Tribe DISOGMINI Kozlov, 1970

Genus *Disogmus* Förster
http://species-id.net/wiki/Disogmus

Disogmus Förster, 1856: 99. Type species: *Proctotrupes areolator* Haliday, designated by Walker (1874), Ashmead (1893). Key to species.

Diagnosis. Front wing 1.8–3.5 mm, long. Body moderately slender. Head clearly transverse, rounded, frons convex. Apical margin of clypeus simple and convex. Mandible moderately stout, with a single point. Cheeks usually with sulcus from eye

to mandible. Occipital carina developed, but not reaching hypostomal sulcus. Male flagellum with noticeable tyloids. Pronotum with strong angular pronotal shoulder that is surmounted by a sharp carina. Epomia present. Scutellar pit without inner longitudinal carinae. Notaulus varying from about 0.5 as long as tegula to quite long and reaching beyond center of mesoscutum. Horizontal mesopleural groove complete and strong. Stigma small, r-rs (vertical part of radius) about 3.0 times as long as wide, radial vein runs from apical 0.3 of stigma. Radial cell long, the side next to costa about 2.8 times as long as depth of stigma. Hind spur is equal to 0.3 of the length of basitarsus or even shorter. Abdomen with stalk about 1.2 times as long as high. Ovipositor sheath 0.7-0.9 times as long as hind tibia, smooth, slender, evenly curved, gradually tapered to a rounded apex, with some erect hairs that are denser near apex.

Distribution. This small genus comprises 5 described species, 3 species of which inhabit the Holarctic and the other 2 species occur only in the Nearctic (Townes 1981, Buhl 1998). Moreover, we have found this genus in Mexico and Taiwan. The specimens of this genus presumably parasitize the larvae of Sciaridae (Sciaroidea, Diptera) (Townes 1981). Sciarids are overrepresented in Rovno amber in comparison with Baltic amber (Perkovsky et al. 2007).

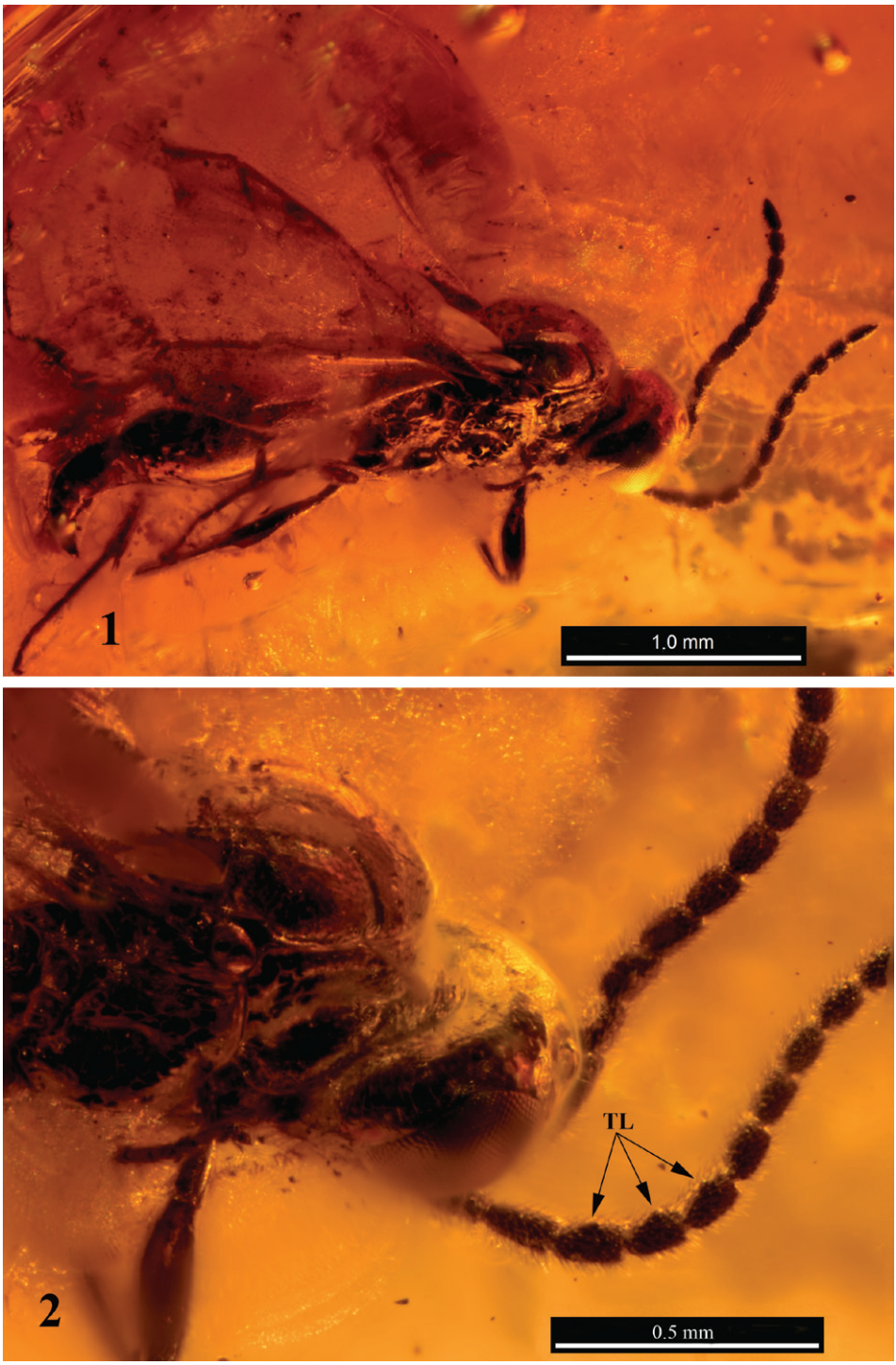
***Disogmus rasnitsyni* Kolyada & Perkovsky, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Disogmus_rasnitsyni
Figs 1–2

Holotype. ♂, SIZK K-3806, Klesov, Rovno amber, Late Eocene. Syninclusions: Diptera (Chironomidae and Tipuloidea), Tipuloidea.

Etymology. Named in honor of the paleoentomologist Prof. Alexander Rasnitsyn.

Description. Length of body 2.5 mm; length of forewing 1.5 mm. Antenna short, length to width ratio of 1, 2 and 9 flagellomeres as 2.5:1.0; 1.7:1.0; 1.3:1.0. Tyloids on flagellar segments 2–4, the tyloids in form of subtriangular slaws that is about 0.3 as long at base as the segments are long (Fig. 2). Side of collar weakly rugulose. Epomia not interrupted. Notaulus quite long, reaching beyond center of mesoscutum. Stigma narrow, r-rs (vertical part of radius) about 3.4 times as long as wide. Radial cell long, side next to costa about 0.8 as long as radius. Mesopleuron below tegula with some fine horizontal wrinkles. Metapleuron rugose, with a small but distinct carina from its upper front part to anterolateral edge of propodeum.

Comparison. Within the genus *Disogmus,* the new species is most similar to *D. basalis (*Thomson, 1857), in particular, by the shape of tyloids and the general shortening of the segments of antennae. The new species distinctly differs from *D. basalis* and the other species of the genus by having tyloids on flagellar segments 2-4 compared to 3–6 and 4-7 that other species have.



Figures 1–2. *Disogmus rasnitsyni*, sp. n., male holotype. **1** body, dorsolateral view **2** tyloids (TL) on flagellar segments.

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RESEARCH ARTICLE

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A new genus of fossil Mymaridae from Cretaceous amber and key to Cretaceous mymarid genera

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Abstract

Myanmymar aresconoides **gen n., sp. n.** is described from one female in Burmese amber, dated as about 100 my. It is similar to *Arescon* on wing features but is unique among Mymaridae in having distinctly segmented palpi. It is the fifth mymarid genus definitely referable to the Cretaceous period. A key to Cretaceous mymarid genera is presented and the features of *Myanmymar* are compared with the other Cretaceous and extant mymarid genera.

Keywords

Carpenteriana, *Enneagmus*, *Macalpinia*, *Myanmymar*, *Triadomerus*, generic key

Introduction

Members of Mymaridae, commonly called fairyflies, are relatively well represented in amber inclusions from the late Cretaceous (70–100 my) to the Miocene (20–40 my), and also in copal (Ross et al. 2010). Yoshimoto (1975) described four genera, *Carpenteriana*, *Macalpinia*, *Protooctonus* and *Triadomerus* in Mymaridae from Cretaceous amber inclusions originating near Medicine Hat, Alberta, and Cedar Lake, Manitoba,

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Canada. Gibson et al. (2007) transferred *Protooctonus* Yoshimoto to Mymarommatidae (Mymarommatoidea) and synonymized it under *Archaeromma* Yoshimoto, 1975. In addition to the mymarids, Yoshimoto (1975) also described three new genera in the family Tetracampidae and one new genus, *Enneagmus,* in the family Trichogrammatidae (Chalcidoidea). Huber (2005) transferred *Enneagmus* to Mymaridae. Though their affinities are uncertain the Cretaceous fossils assigned to Tetracampidae by Yoshimoto (1975) likely do not belong to that family (Gumovsky and Perkovsky 2005; Heraty and Darling 2009). One other family, the Khutelchalcididae (Rasnitsyn et al. 2004), was described from an impression fossil from the earliest Cretaceous or latest Jurrassic period, but Gibson et al. (2007: 106) concluded it does not belong to the Chalcidoidea. Thus, the only extant family of Chalcidoidea definitely extending back to the Cretaceous is the Mymaridae.

The new genus described below is from Burmese amber, which is widely accepted as being at least 100 million years old (Ross et al. 2010), and thus is the oldest known fossil mymarid. The amber was obtained from a mine, first excavated in 2001, in the Hukawng Valley southwest of Maingkhwan in Kachin State (26º20'N, 96º36'E), Burma (Myanmar). This new amber site, known as the Noije Bum 2001 Summit Site, was assigned to the Early Cretaceous, Upper Albian, on the basis of paleontological evidence (Cruickshank and Ko 2003), placing the age at 97–110 mya. Nuclear magnetic resonance spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit site indicate an araucarian (possibly *Agathis*) tree source for the amber (Poinar et al. 2007). No Mymaridae have yet been described from even older amber, from Lebanon, which is dated as at least 121mya.

Methods

The amber specimens were immersed in mineral oil Johnson's baby oil) for photography. Photographs were produced with a high-resolution ProgRes C14+ camera mounted on a Nikon SMZ1500 stereomicroscope. Body measurements of the holotype are in micrometers and are approximate because they were taken from the printed and enlarged digital photographs. One abbreviation is used: fl_x = flagellar segment x.

Taxonomy

***Myanmymar* Huber, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Myanmymar_Huber
Figs 1–3

Derivation of generic name. The genus name is a euphonious combination of letters. The gender is neuter.

Figs 1–3. 1 *Myanmymar aresconoides*, female holotype **1** dorsolateral habitus **2** *M. aresconoides*, antennae and palpus **3** male of uncertain species identity, dorsolateral habitus.

Generic diagnosis. Fore wing narrow, venation extending about two-thirds wing length, marginal vein probably longer than submarginal vein (wing base not clearly visible), and postmarginal vein apparently absent (Fig. 1); antenna with 8-segmented funicle and 2-segmented clava (Fig. 2); palpi (probably maxillary) distinctly 3-segmented (Fig. 2); tarsi 5-segmented and long; metanotum with anterior and posterior margins parallel; petiole ring-like, apparently shorter than wide; and ovipositor sheaths with several setae near apex.

Remarks. Among extant genera the closest in general appearance to *Myanmymar* are some females of *Arescon* Walker. Although very similar in wing shape and venation, *Arescon* females, exemplified by an unidentified extant species from Thailand (Fig. 4), differ from *Myanmymar* in having the funicle 5-segmented, clava 1-segmented, palpi 1-segmented, each ovipositor sheath with only one seta, and tarsi short.

Myanmymar exhibits three plesiomorphic features of Mymaridae: tarsi 5-segemented, female antenna with funicle 8-segmented, and fore wing venation longer than half wing length. Only three extant genera (*Boudiennyia*, *Eustochomorpha*, *Borneomymar*) share all these features; two others (*Gonatocerus*, *Ooctonus)* share the first two features but the venation is less than half the wing length (Huber 2002). *Myanmymar* is unique among described extant Mymaridae, and perhaps also the extinct genera, in having palpi with three distinct segments. The palpi are not visible in known representatives of the other extinct genera so that segmentation cannot be determined, but the fact that the palpi are not visible suggests that they are reduced, as in extant Mymaridae. The latter all have unsegmented palpi, with the single segment terminating in a long apical seta and one or two shorter, preapical setae.

Type species. *Myanmymar aresconoides* Huber, sp. n.

***Myanmymar aresconoides* Huber, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Myanmymar_aresconoides
Figs 1–2

Holotype. Female in amber inclusion in plastic box labeled (inside): "*Myanmymar aresconoides* ♀ Huber Holotype [red label]", deposited in the Poinar amber collection maintained at Oregon State University.

Other material. One male (OSUC) possibly belonging to *Myanmymar* was examined. It is in a triangular amber inclusion in same box as the holotype. It is excluded from type series because it is in poor condition (Fig. 3).

Description. Female. Body length 535. Colour dark brown except antenna mostly, tarsi, ovipositor and wing venation brown and funicle segment 8 and clava lighter in colour (Fig. 1). *Head*. Width 120. Eye moderate in size, apparently with a few setae (Figs 1, 2). Gena wide, distinct. Maxillary palpi clearly 3-segmented (Figs 1, 2).

Figure 4. *Arescon* sp., an extant species from Thailand (lighting from below).

Antenna. Funicle segments 3, 5 and 7 distinctly longer than the remainder, and segments 3 and 5 distinctly the widest. Clava with apical segment slightly longer than basal segment. Measurements (length/width) taken from either left or right antenna: scape -/-, pedicel -/-, $fl_1$15/15, fl_2 28/13, fl_3 30/13, fl_4 38/13, fl_5 38/13, fl_6 28/10, fl_7 28/15, fl_8 25/15, clava (total) 60/18.

Mesosoma. Length 200. Mesoscutum 100, about 1.6 times as long as scutellum (line of demarcation between the two not clear.) Metanotum 23, about ¾ as long as propodeum. Propodeum 30, about 1.2 times as long as metanotum.

Wings. Fore wing narrow, almost parallel-sided (about twice as wide near apex as at narrowest point), the posterior margin with a distinct, rounded lobe at level of base of marginal vein, and longest marginal setae much longer than wing width (Fig. 1). Wing surface without microtrichia, except sparsely in two fairly distinct rows beyond venation. Venation extending well beyond middle of wing. Marginal vein with about 8 setae along its length. Fore wing length/width 406/59, longest marginal setae 112, about 2 times greatest wing width. Hind wing (Fig. 1) narrow and parallel sided, its base not visible but presumably wing membrane not extending to base (as for most Mymaridae). Wing surface without microtrichia. Marginal setae at most about 7 times wing width.

Legs. Tarsi long, probably as long as tibiae (these not clearly visible), and metatarsomere 1 about 1.7 times as long as 2 (Fig. 1). Metatibial spur almost as long as metatarsal segment 3.

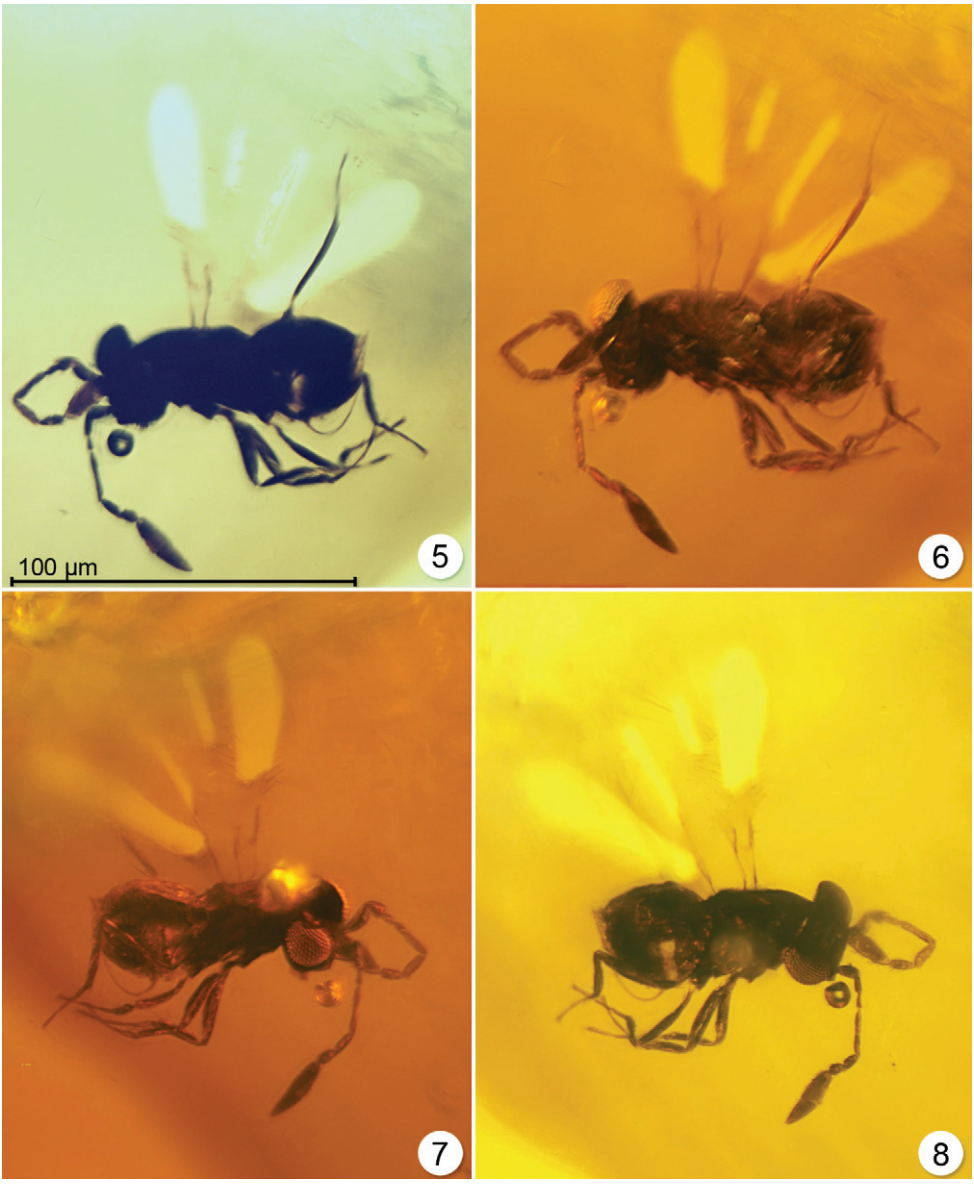
Metasoma. Length 225, longer than mesosoma. Petiole (not clearly visible) somewhat narrower than base of gaster. Gaster with segment 1 the longest (of those clearly demarcated). Ovipositor 218 (effective length); ovipositor sheaths slightly protruding beyond apex of metasoma, with several setae along apical third of exposed part (Fig. 1).

Derivation of species name. After *Arescon*, the genus which *Myanmymar* most resembles based on the fore wing, and –oides, from Greek "eidos" meaning 'resembling' or 'like'. The name is an adjective.

Remarks. The specimen in Fig. 3 appears to be a male based on its antennal structure (probably 11-segmented, the number cannot be determined confidently) and apparent lack of an ovipositor. We tentatively associate this male with the female described as *M. aresconoides*, but it is impossible to be certain that it belongs to the same genus because it is so poorly preserved. Body length 445; head width 148.

Key to genera of Cretaceous Mymaridae. Females.

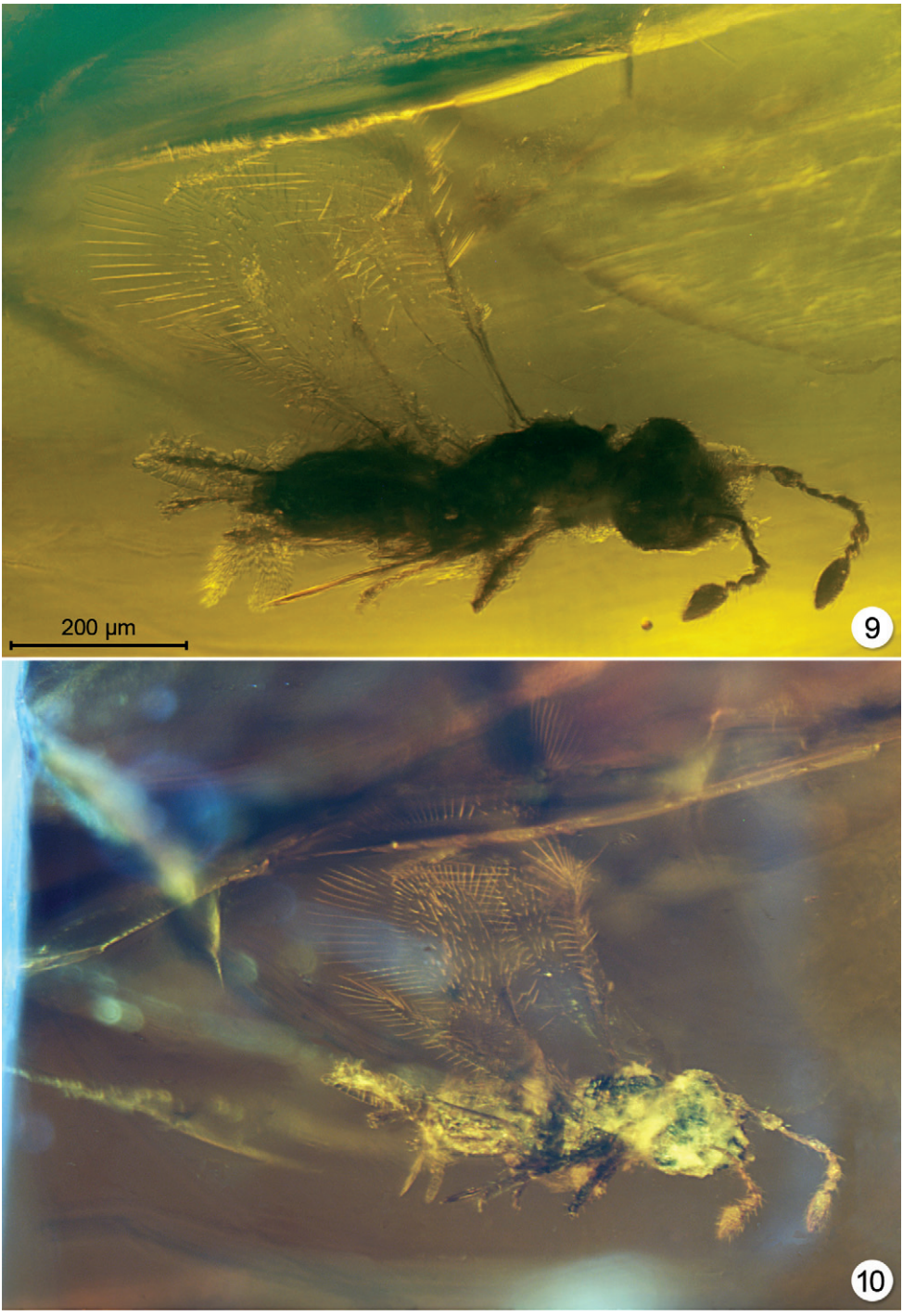
1	Tarsi 3-segmented, funicle 5-segmented (not 4-segmented as stated in Yoshimoto 1975), and clava 3-segmented (Figs 5–8, and figs 22–24 in Yoshimoto 1975)..... ***Enneagmus* Yoshimoto**
–	Tarsi 4- or 5-segmented; funicle 7- or 8-segmented..... **2**
2(1)	Tarsi apparently 4-segmented (Figs 11, 12, and fig. 50A in Yoshimoto 1975) [funicle 8-segmented, clava 3-segmented] ..... ***Macalpinia* Yoshimoto**
–	Tarsi 5-segmented..... **3**
3(2)	Funicle 7-segmented and clava 1-segmented (Figs 9, 10, and figs 18, 19 in Yoshimoto 1975) ..... ***Carpenteriana* Yoshimoto**
–	Funicle 8-segmented and clava 2- or 3-segmented **4**
4(3)	Clava 3-segmented and wings wide, the marginal setae distinctly shorter than maximum wing width (Figs 13–16, and figs 13–17 in Yoshimoto 1975) .... ***Triadomerus* Yoshimoto**
–	Clava 2-segmented and wings narrow, the marginal setae distinctly longer than maximum wing width (Figs 1, 2)..... ***Myanmymar* Huber**



Figures 5–8. *Enneagmus pristinus*, holotype (left and right sides with lighting from below or the side).

Discussion

The late ichneumonid taxonomist Henry Townes once stated "If you don't know what else to do, count". For fossil mymarids his comment might better be worded "If you can't do anything else, count and measure" because often not much else can be done with mymarid amber fossils except to count segments and measure their proportions.



Figures 9–10. *Carpenteriana tumida*, paratype #5331 **9** lighting from below **10** lighting from below and diffused lighting from the side.

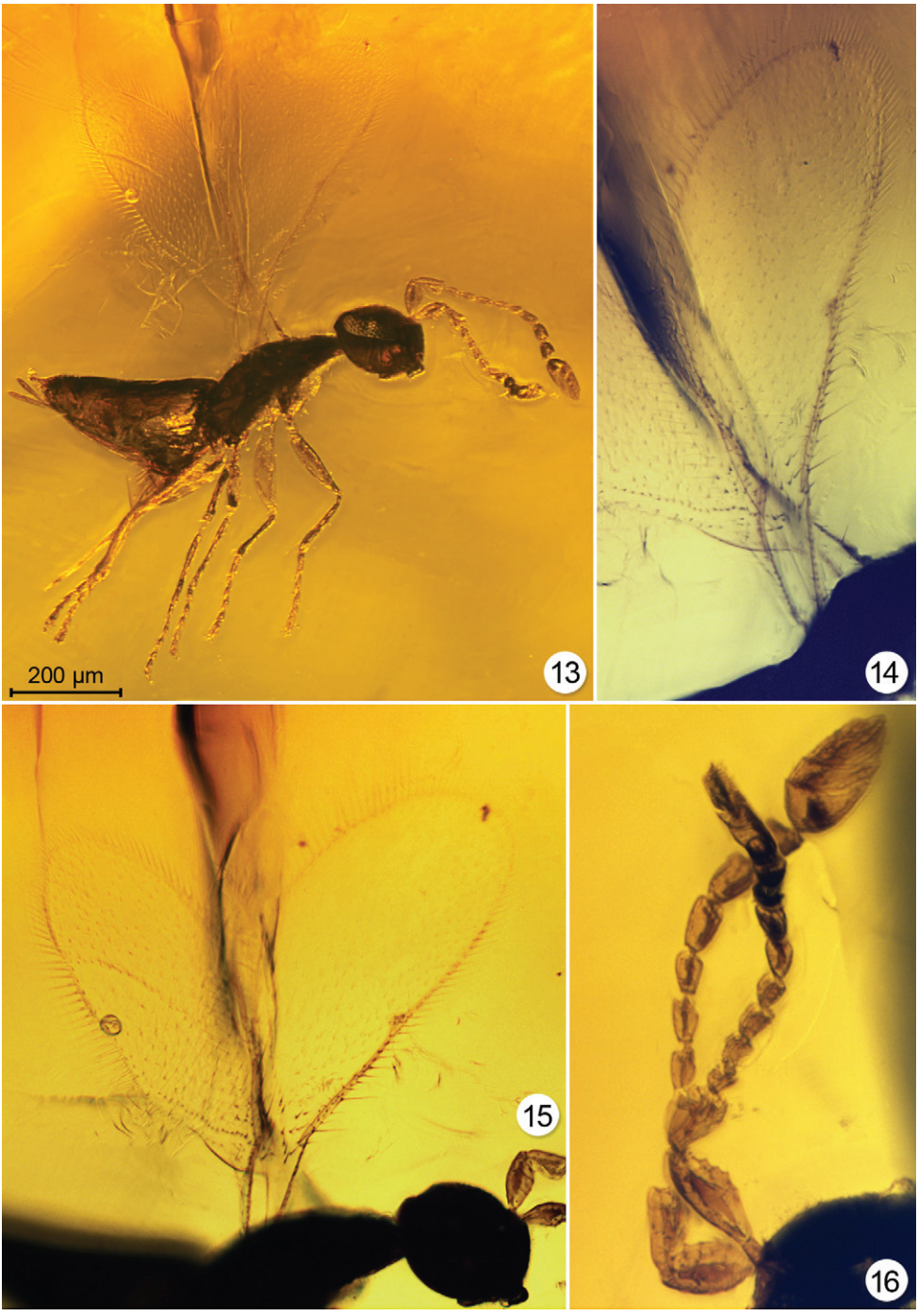
Figures 11–12. *Macalpinia canadensis*, holotype (lighting from below) **11** habitus **12** head and antennae.

So no apology is needed for using almost exclusively the number of antennal and tarsal segments to distinguish genera. Townes' quote actually applies quite well to fairyflies in general because the generic and family level classification of extant Mymaridae historically depended considerably on different combinations of antennal and tarsal segment numbers. Further refinements in defining family-group taxa within Mymaridae based on additional characters, e.g., petiole structure, gave fairly strong support to various proposed subfamilial classifications. At the genus-group level (or tribal level, if

one chooses to recognize tribes) many other features besides segment number are, of course, required to define the taxa properly.

Four reasons are proposed here for the historical dependancy on segment numbers: 1) without good slide preparations, i.e., cleared, dissected and properly oriented (dorsal and lateral) specimens in a suitable permanent mounting medium, most body structures could not easily be examined or interpreted so they were often ignored, 2) meristic characters are unequivocal, so their use in identification keys (or to help define genera) make the keys relatively easy to use, 3) there is a considerable range in antennal and tarsal segment number among mymarid genera – among extant mymarids the number of funicle segments in females varies from 4–8, claval segments vary from 1–3, and tarsal segments of either sex from 3–5 (only one genus with 3) so different combinations can be used to help identify females of various genera; 4) the character is usually invariant within a mymarid genus – all or most of the species of a given genus will have only one combination of segment numbers. The wide range in, at least, number of tarsal segments in Mymaridae has evidently existed since the Cretaceous and is unexpected given that very few Cretaceous amber mymarid specimens have been found. Other families of Chalcidoidea, with few exceptions, are characterized by an invariant number of tarsal segments, either three, four or five. The number of tarsal segments in Mymaridae encompasses the range of all other chalcidoid families together and suggests that mymarids are either much older than the oldest fossils known (so they had lots of time to evolve the differences in segment number) or there was a sudden and rapid diversification just before the Cretaceous.

There is also considerable similarity among the Cretaceous genera. Three of them, but not *Carpenteriana*, have a 2- or 3- segmented clava. Four of them, but not *Enneagmus*, have a 7- or 8-segmented funicle. Only one extant genus, *Eustochomorpha*, also has 8 funicle segments in combination with 2 claval segments. The remaining 100+ extant genera have fewer segments, due to a seemingly independent reduction in number of either claval segments, funicle segments or both. Another similarity is the relatively long marginal vein in Cretaceous mymarids, except apparently in *Enneagmus*. Extant genera with a fore wing venation exceeding half the wing length are found mostly in the Southern Hemisphere, except *Arescon* which is more widespread. *Eustochomorpha* not only has a long marginal vein but also a long and well defined postmarginal vein, as in *Triadomerus*. The similarity of other features between Cretaceous and extant genera is also notable. *Triadomerus* appears to have a distinct, oblique hair line or asetose crease extending from the apex of the marginal vein to the posterior margin of the wing (Figs 13, 15), as in, e.g., *Australomymar*, *Boudiennyia*, and some *Ooctonus*. *Carpenteriana* and *Macalpinia* females have funicle segments that alternate in width (Figs 9, 11, 12) as in many extant species of Mymaridae, particularly some *Gonatocerus* (*Gahanopsis*) (illustrated in Triapitsyn et al. 2010). So although the tendency in evolution of Mymaridae appears to have been towards reductions in flagellar segment number and shortening of fore wing veins, Cretaceous genera do not appear very different from extant genera.



Figures 13–16. *Triadomerus bulbosus*, paratype # 5279 **13** habitus, lighting from the side and below **14** fore wing **15** wings **16** antenna (14–16 with lighting from below).

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This paper is dedicated to Alexander Rasnitsyn, the pre-eminent Hymenoptera paleontologist, on the occasion of his 75th birthday. We thank P. Perkins, Museum of Comparative Zoology, Harvard University, Cambridge, MA, for lending fossils of all but *Macalpinia* (in the Canadian National Collection of Insects, Ottawa, ON) to JH for study. J. Read prepared the illustrations and plates and is thanked for her usual excellent work.

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RESEARCH ARTICLE

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Compression fossil Mymaridae (Hymenoptera) from Kishenehn oil shales, with description of two new genera and review of Tertiary amber genera

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Abstract

Compression fossils of three genera and six species of Mymaridae (Hymenoptera: Chalcidoidea) are described from 46 million year old Kishenehn oil shales in Montana, USA. Two new genera are described: *Eoeustochus* Huber, **gen. n.**, with two included species, *E. kishenehn* Huber (type species) and *E. borchersi* Huber, **sp. n.**, and *Eoanaphes*., **gen. n.**, with *E. stethynioides* Huber, **sp. n.** Three new species of *Gonatocerus* are also described, *G. greenwalti* Huber, **sp. n.** , *G. kootenai* Huber, **sp. n.**, and *G. rasnitsyni* Huber, **sp. n.** Previously described amber fossil genera are discussed and five genera in Baltic amber are tentatively recorded as fossils: *Anagroidea*, *Camptoptera*, *Dorya*, *Eustochus*, and *Mimalaptus*.

Keywords

Mymaridae, Kishenehn Formation, compression fossils, *Eoanaphes, Eoeustochus*, *Gonatocerus*, Baltic amber.

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Introduction

The family Mymaridae (Hymenoptera: Chalcidoidea) is represented by 103 genera and about 1400 nominal extant species in all terrestrial habitats and a few fresh water habitats (Huber 1986, Noyes 2010). Fossil Mymaridae have been described from amber inclusions from various localities, including five extinct genera and species from Cretaceous amber (Yoshimoto 1975, Huber and Poinar 2011) and eight genera (seven still extant, one extinct) from Tertiary amber, mostly from the Samland Peninsula, Kaliningrad district, Russia, and Chiapas, Mexico. Probably because of their small size, no compression fossils of Mymaridae have been discovered until now. Here we describe the first ones, representing three genera and six species. These and the Tertiary amber fossil genera are discussed and compared with extant genera.

Methods

A total of 17 specimens of fossil Mymaridae, all females, were collected in 2009 and 2010 at six sites (e.g. W113°42.173', N48°23.476') along the Middle Fork of the Flathead River in northwestern Montana between Paola and Coal Creeks in accordance with USFS Authorization HUN281. Fossil specimens were collected from the middle sequence of the Coal Creek member of the Kishenehn Formation, which has been estimated to be 46.2 +/- 0.4 myo (Lutetian) by $^{40}Ar/^{39}Ar$ analysis and 43.5 +/- 4.9 myo by fission-track analysis (Constenius 1996). Although the paper/oil shales of the middle sequence are thin (<1 mm to several mm), they were often easily split into even thinner pieces so as to expose unweathered surfaces on which the fossil insects reside.

The compression fossils were immersed in 95% ethanol for examination and photography. For figures 1–10 and 13–18, specimens were photographed using a Zeiss AxioCam MRc5 digital CCD camera mounted on a Zeiss Discovery V20 microscope and Zeiss AxioVision EDF software in Ottawa, ON. Measurements were generated using Zeiss AxioVision software. For figures 11 and 12, specimens were photographed using an Olympus SZX12 microscope, DP-25 camera and DPM imaging software in Washington, DC, and measurements were taken with the DP2-BSW software. All measurements are in micrometers (mm). If a measurement could not be made (e.g., scape length) it is represented by a dash.

Abbreviations used: fl_x = funicle segment x. Measurements were taken as accurately as possible but given that the beginning and end points of a structure were not always clear or were hidden, the measurements may not be accurate. Appendage measurements are the most accurate except the wing bases cannot be clearly determined. Consequently, wing lengths were taken from the visible edge of the mesosoma and therefore they and length/width ratios are slightly smaller than they should be.

Fossils examined are in the following institutions:

AMNH American Museum of Natural History.

IPMGö Institute and Museum für Paläontologie, Georg-August University, Göttingen, Germany.
NMNH National Museum of Natural History, Washington, D.C.
OSU Oregon State University, G. Poinar, Jr. collection, Corvallis, Oregon, USA.
SVT S. V. Triapitsyn private collection, California, USA.
UCRC University of California, Riverside, California, USA.
ZMUC Zoological Museum, University of Copenhagen, Denmark.

The compression fossils are housed in NMNH. Baltic amber fossils were examined from the remaining institutions.

Systematics

***Eoeustochus* Huber, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Eoeustochus
Figs 1–8

Description. Female. Body length 718–1133 (seven specimens in total, only four described and named to species). **Head**. Normal in shape, wider than long and about ¾ as high as wide. Face slightly convex in lateral view; vertex flat and slightly sloping anteriorly, forming a moderately sharp angle with occiput; back of head slightly concave. Eye higher than wide, about 2/3 head height; malar space about 1/3 eye height. **Antenna.** Funicle 6-segmented, with each funicle segment longer than wide; clava 3-segmented with the claval sutures perpendicular to claval length. **Wings**. Fore wing wide, symmetrical, with evenly rounded apex (shape resembling that of the extant genus *Eustochus*); marginal fringe shorter than fore wing width. Venation about 0.4× fore wing length, with long marginal vein and short but distinct stigmal vein. Hind wing narrow; marginal fringe much longer than wing width. **Mesosoma**. Shorter than gaster. Pronotum length at most about half length of mesoscutum. Mesoscutum length subequal to scutellum. Scutellum with frenum apparently entire, not divided longitudinally. Metanotum much shorter than scutellum. **Metasoma**. Constricted at base, probably with short petiole. Gastral terga similar in length. Ovipositor moderately short, probably arising near midpoint of gaster and its apex not or barely exserted beyond gastral apex.

Type species. *Eoeustochus kishenehn* Huber, **sp. n.**

Derivation of generic name. The name is from eo-, Greek for early, and *Eustochus*, an extant genus. The gender is masculine.

Discussion. Two species are described, each from two specimens. Three additional specimens (Kishenehn #30,356, 40,410, and 40,023) belong to *Eoeustochus* but are not included in the type series of either species because they are not in as good a condition.

The relationships of *Eoeustochus* are with *Eustochus*, one extant species of which has a 3-segmented clava in females. Although thirteen extant genera have a definite

3-segmented clava (*Allanagrus*, *Anneckia*, *Idiocentrus*, *Krokella*, *Nesopatasson/Nesomymar*, *Neostethynium, Notomymar*, *Paracmotemnus*, *Parastethynium*, *Polynemoidea*, *Pseudocleruchus*, *Stethynium*), the closest one is *Eustochus*, based on the apparent strong constriction in lateral view between meso- and metasoma (none in *Allanagrus*), transverse sutures between claval segments (sutures oblique in *Stethynium*), shape of fully developed wings (wings almost absent in *Nesopatasson/Nesomymar* and *Notomymar*, and of different shape in *Anneckia, Neostethynium, Parastethynium* and *Pseudocleruchus*) venation shorter than half fore wing length (venation longer in *Krokella* and *Paracmotemnus)*, and ovipositor not distinctly exserted beyond apex of gaster (ovipositor strongly exserted in *Polynemoidea*) or projecting anteriorly under mesosoma (ovipositor strongly projecting anteriorly in *Idiocentrus*).

***Eoeustochus kishenehn* Huber, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Eoeustochus_kishenehn
Figs 1–4

Type material. Holotype female (NMNH), labelled "*Eoeustochus kishenehn* Huber Holotype female #543757".

Paratype female (NMNH), labelled as for holotype but "paratype #543758".

Description. Female. Colour brown, head dark brown, fore wing thinly margined with brown. Holotype (Fig. 1) measurements as follows. Body length 909. Antenna (Fig. 2) with total funicle length 317; scape 95, pedicel 70, fl_1 52, fl_2 63, fl_3 63, fl_4 51, fl_5 47, fl_6 45; clava 180, 0.56× funicle length. Fl_2 and fl_3 the longest segments and fl_6 the shortest (Fig. 2). Mesosoma length 481. Fore wing (Fig. 3) length 912, width 271, length/width 3.36, longest marginal setae 160, venation length 355. Hind wing width 26, longest marginal setae 88. Metasoma length 340. Ovipositor length 290, apparently slightly exserted beyond apex of gaster.

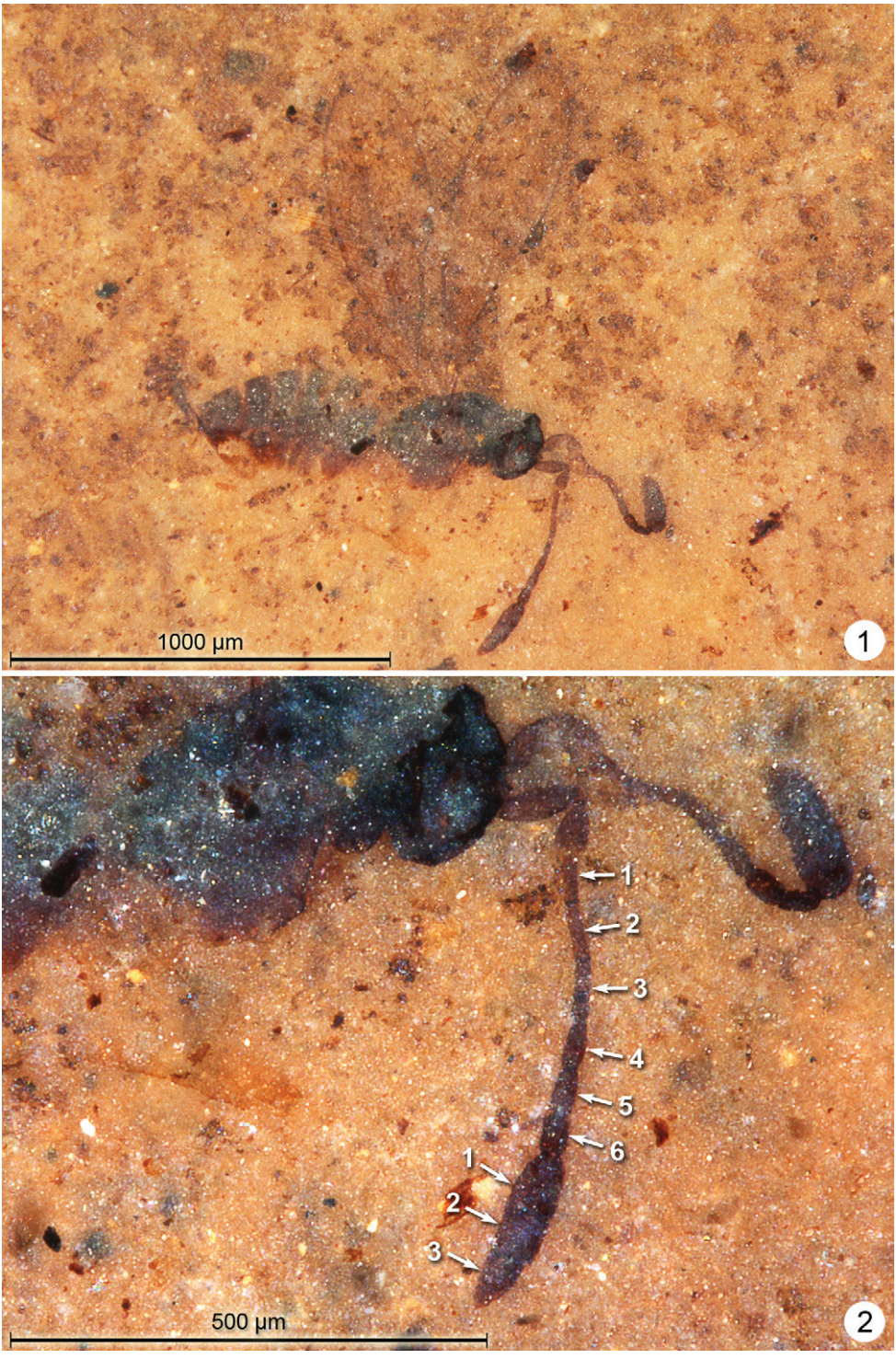
Paratype (Fig. 4) measurements as follows. Body length 966, head width 234, height 132.

Derivation of species name. Named after the Kishenehn Formation shale in which the fossils were found.

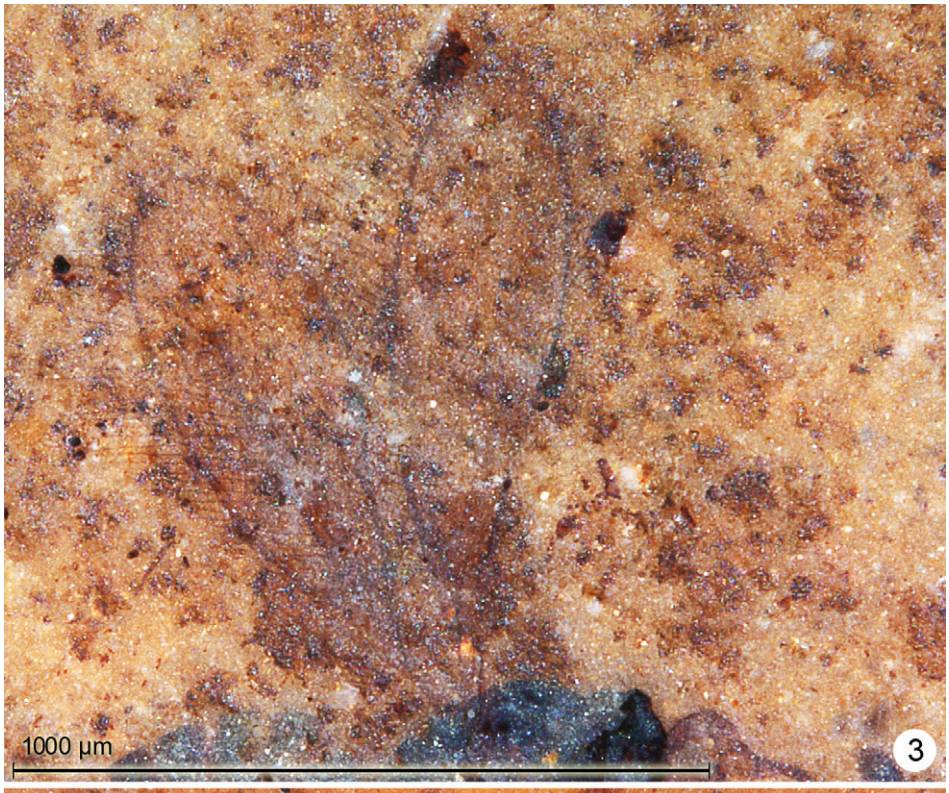
***Eoeustochus borchersi* Huber, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Eoeustochus_borchersi
Figs 5–8

Type material. Holotype female (NMNH) labelled "*Eoeustochus borchersi* Huber Holotype female #543759"

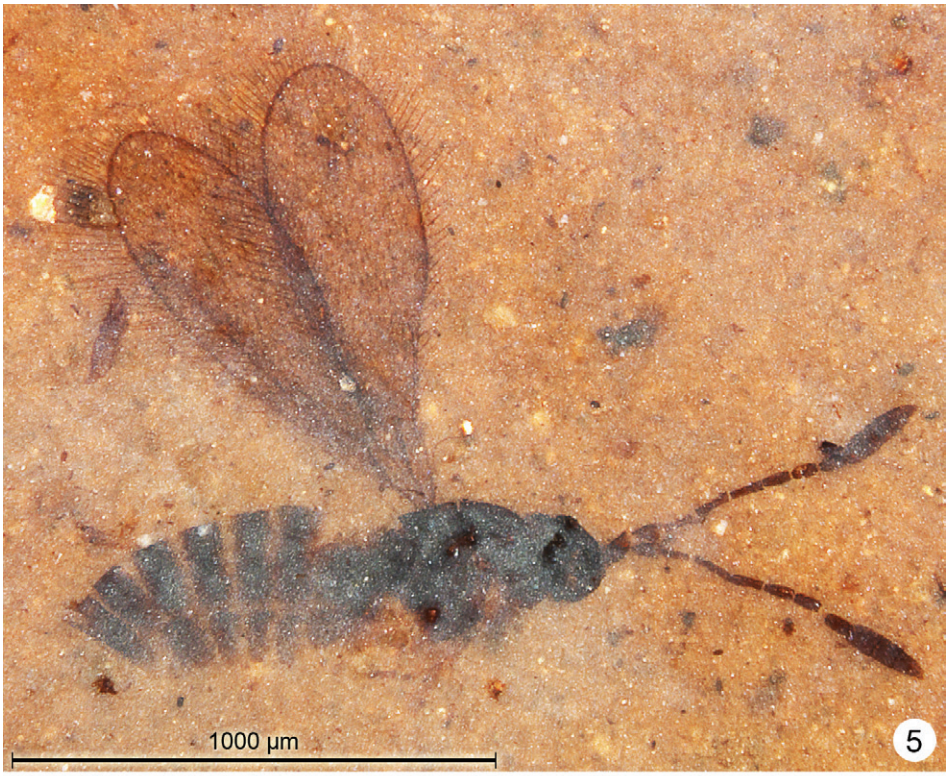
Paratype female (NMNH), labelled as for holotype but "paratype #543760".

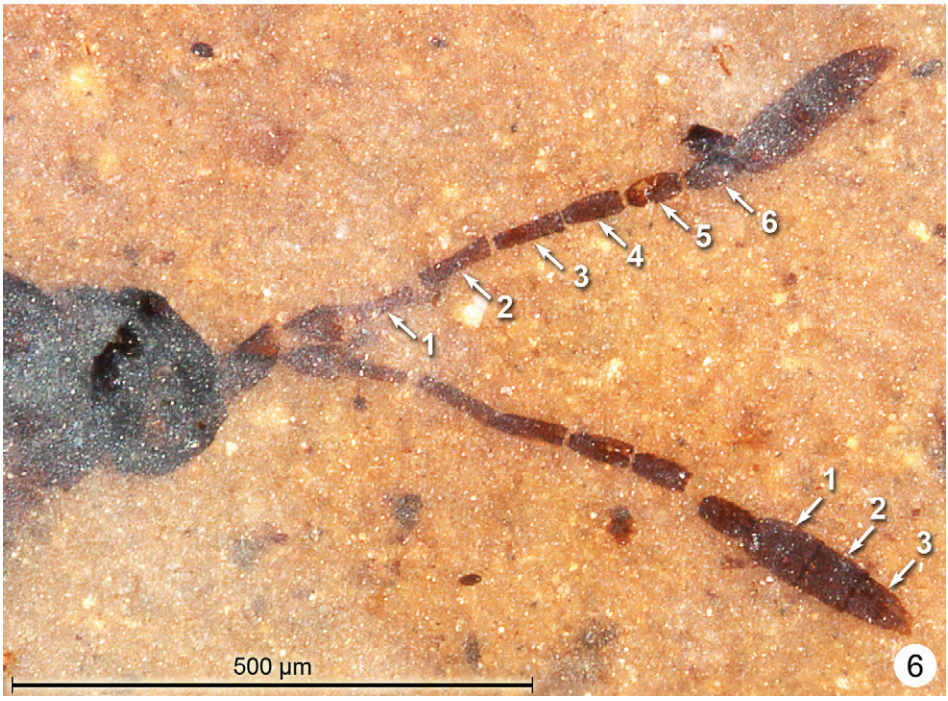


Figures 1–2. *Eoeustochus kishenehn*, holotype **1** habitus lateral **2** mesosoma, head, antennae.

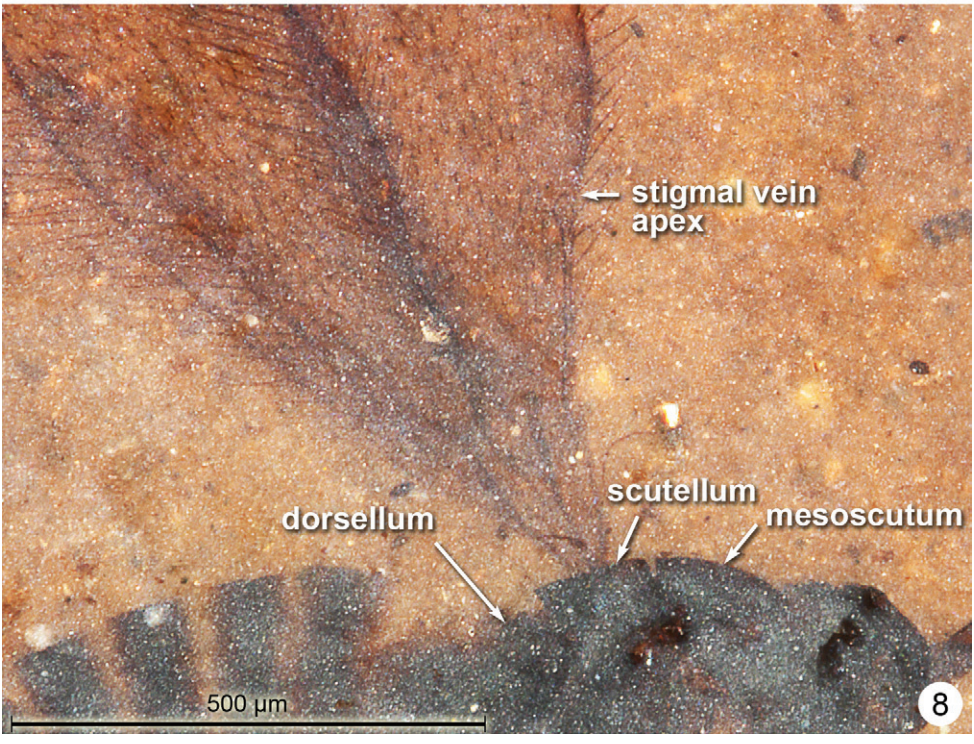


Figures 3–4. *Eoeustochus kishenehn* **3** wings, holotype **4** paratype, habitus dorsal.





Figures 5–6. *Eoeustochus borchersi*, holotype **5** habitus lateral **6** head and antennae.



Figures 7–8. *Eoeustochus borchersi*, holotype **7** wings **8** mesosoma and base of wings.

Description. Female. Colour dark brown, fore wing thinly margined with brown. Holotype (Fig. 5) measurements as follows. Body length 1094. Antenna (Fig. 6) with total funicle length 432; scape -, pedicel 58, fl_1 69, fl_2 78, fl_3 71, fl_4 64, fl_5 56, fl_6 54; clava 186, 0.47× funicle length. Fl_2 distinctly the longest segment and fl_6 the shortest. Fore wing (Fig. 7) length 948, width 312, length/width 2.72, longest marginal setae 188, venation (Fig. 8) length 395. Hind wing length 781, width 32. Ovipositor length 292, not exserted beyond apex of gaster.

Comments. This species differs from *E. kishenehn* by the longer funicle segments (funicle 2.31× clava length cf. 1.83× in *E. kishenehn*) and slightly wider fore wing (length/width at most 3.49 instead of at least 3.64 in *E. kishenehn*).

Derivation of species name. Named after Harold Borchers, professor of entomology and early mentor to the junior author at Bemidji State University, Bemidji, Minnesota.

Gonatocerus Nees

Figs 9–16

Gonatocerus is a worldwide group with numerous described extant species classified in several subgenera (Triapitsyn et al. 2010). Its members are often the most commonly collected Mymaridae in almost any habitat so it seems surprising that it has been recorded only once as a fossil, in Baltic amber by Meunier (1905).

The three species described below definitely belong to *Gonatocerus* based on the entire clava, 8-segmented funicle, similar sized gastral segments, short and probably narrow petiole, and 5-segmented tarsi (at least in the one species where they can be counted). Because they all appear to have a rhomboidal dorsellum they would be classified either in *G.* (*Gonatocerus*) or in *G.* (*Cosmocomoidea*), but not *G.* (*Lymaenon*), the most common extant subgenus because it has a narrow, strap-shaped dorsellum or *G.* (*Gastrogonatocerus*) because the ovipositor does not project forward under the mesosoma.

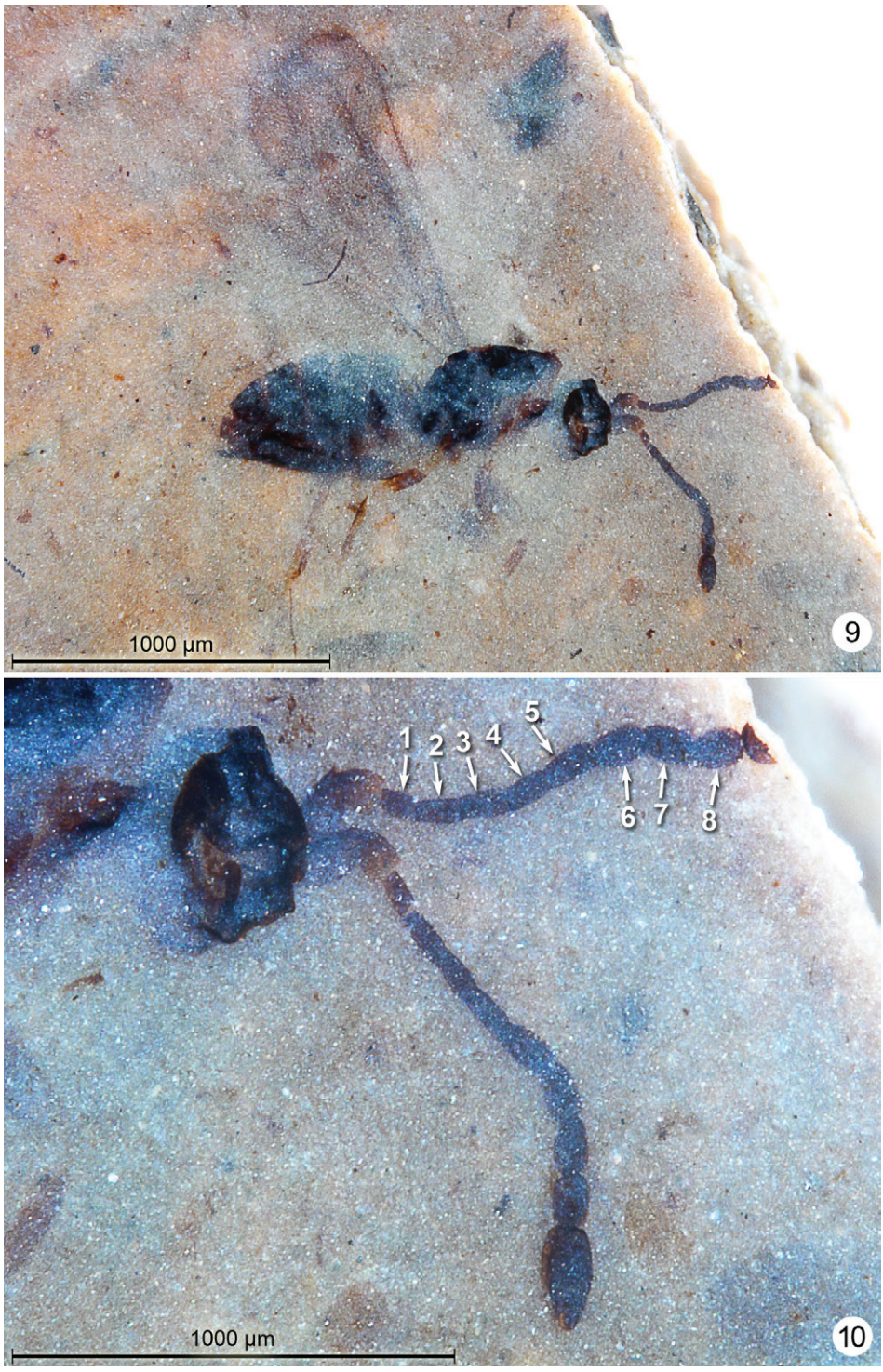
Gonatocerus kootenai Huber, sp. n.

urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Gonatocerus_kootenai

Figs 9–11

Type material. Holotype female (NMNH) labelled "*Gonatocerus kootenai* Huber Holotype female #543761".

Description. Female. Colour dark brown except pedicel laterally, pronotum, trochanters, base and apex of femora, base and apex of tibiae (at least of fore and middle legs) and tarsomeres except apical tarsomere of all legs whitish. Holotype (Fig. 9) measurements as follows. Body length 1270. Head height 246, length 157. Antenna (Fig.



Figures 9–10. *Gonatocerus kootenai*, holotype **9** habitus lateral **10** head and antennae.

10) with total funicle length 476; scape -, pedicel 57, fl_1 54, fl_2 57, fl_3 52, fl_4 59, fl_5 69, fl_6 64, fl_7 61, fl_8 60, clava 120. Mesosoma length 462. Fore wing length 1101, width 309, length/width 3.56, venation length 259, longest marginal setae 95. Hind wing length 729, width 35, longest marginal setae 67. Metasoma (Fig. 11) length 658. Ovipositor length 588.

Comments. *Gonatocerus kootenai* differs from the following two species by the relatively narrower wings and shorter funicle segments. I tentatively place it in *G.* (*Gonatocerus*) because of the relatively narrow fore wing and fairly long and relatively slender fl_3–fl_5. The reverse side of the shale piece contains a specimen of Trichoptera.

Derivation of species name. Named after the Kootenai tribe of the Flathead Nation in northwestern Montana, site of the Kishenehn shales.

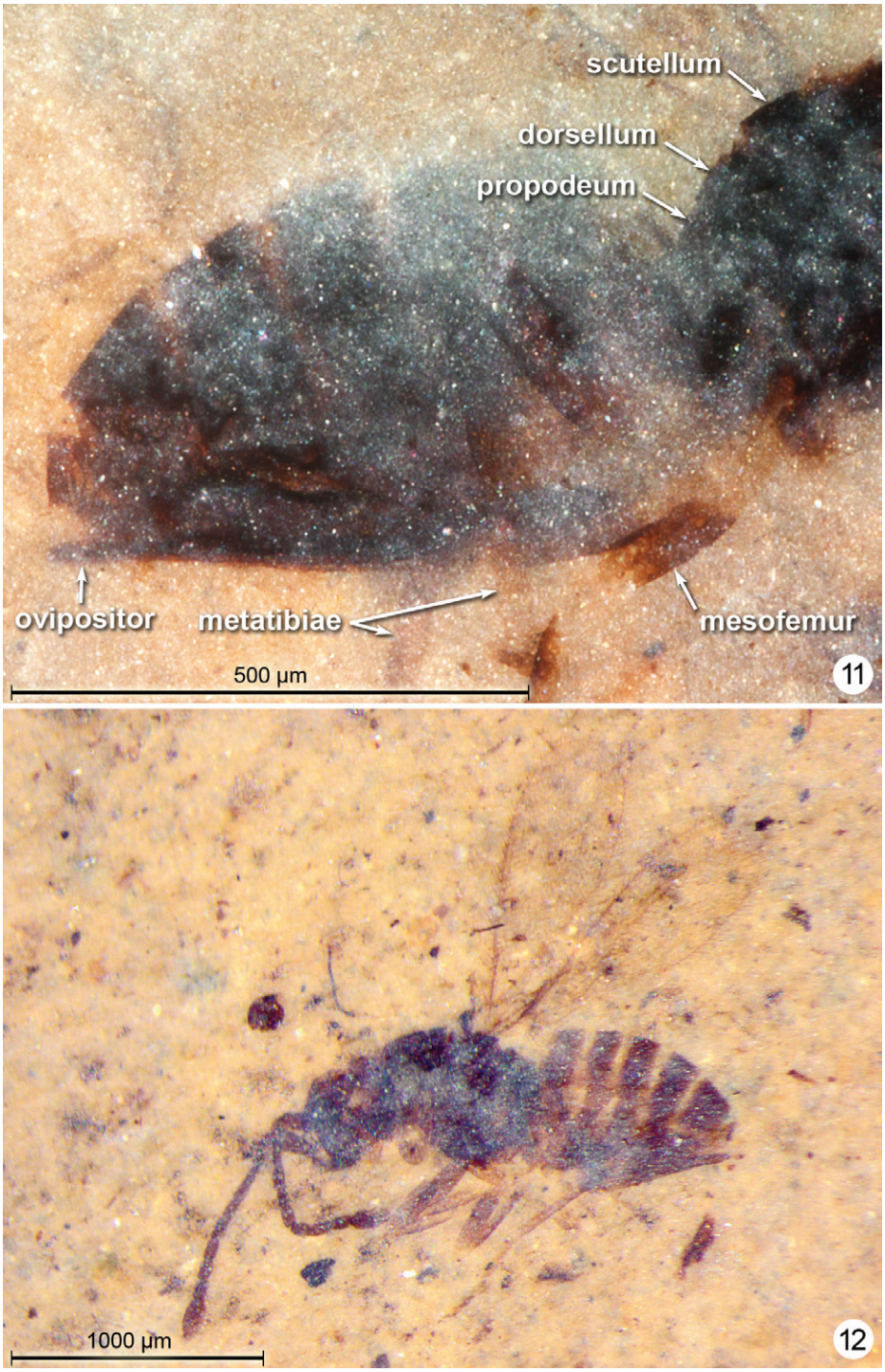
***Gonatocerus rasnitsyni* Huber, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Gonatocerus_rasnitsyni
Figs 12–13

Type material. Holotype female (NMNH) labelled "*Gonatocerus rasnitsyni* Huber Holotype female #543762".

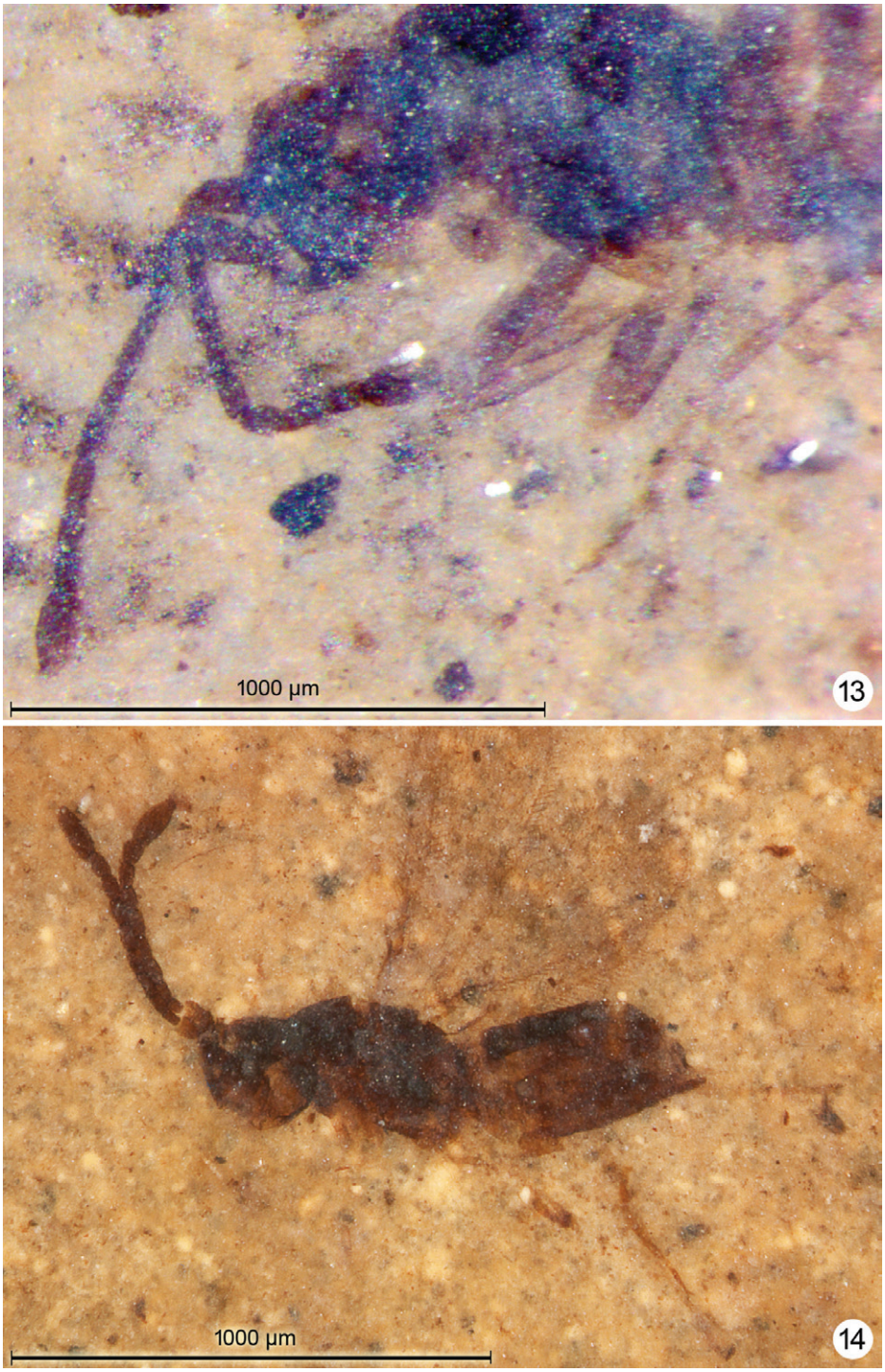
Description. Female. Colour dark brown except middle leg (others less clearly visible) with coxa, trochanter, apex of femur and base of tibia, and basal 4 tarsal segments yellowish. Holotype (Fig. 12) measurements as follows (measured in NMNH only). Body length 1046. Antenna (Fig. 13) with total funicle length 414: scape length and width 144/46, pedicel -, fl_1 44, fl_2 43, fl_3 55, fl_4 51, fl_5 65, fl_6 56, fl_7 58, fl_8 50, clava 113. At least on one antenna it appears that fl_3 is wider than fl_2 and fl_4. Mesosoma length (excluding pronotum) 375. Fore wing length 789 (775 from margin of mesosoma), width 243, length/width 3.25.

Comments. *Gonatocerus rasnitsyni* differs from *G. kootenai* by the relatively smaller size, shorter and wider fore wing, and colour of the antennal pedicel and legs. I tentatively place it in *G.* (*Cosmocomoidea*) because of the relatively wider fl_3 (on one antenna at least, suggesting it bears multiporous plate sensilla) compared to the slightly narrower fl_2 and fl_4. This resembles several extant members of this subgenus that also have alternately wider and narrower basal funicle segments.

Derivation of species name. Named in honour of A. P. Rasnitsyn, the world's foremost Hymenoptera palaeontologist, on the occasion of his 75th birthday.



Figs 11, 12. *Gonatocerus* spp. **11** *G. kootenai* holotype, posterior half of mesosoma and metasoma **12** *G. rasnitsyni* holotype, habitus lateral.



Figs 13, 14. *Gonatocerus* spp. **13** *G. rasnitsyni* holotype, mesosoma, head, antennae **14** *G. greenwalti* holotype, habitus lateral.

***Gonatocerus greenwalti* Huber, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Gonatocerus_greenwalti
Figs 14–16

Type material. Holotype female (NMNH) labelled "*Gonatocerus greenwalti* Huber Holotype female #543763".

Description. Female. Colour dark brown except apex of pedicel and legs beyond coxae lighter (yellowish). Holotype (Fig. 14) measurements as follows. Body length 926. Antenna (Fig. 15) with total funicle length 398; scape -, pedicel 51, fl_1 35, fl_2 42, fl_3 57, fl_4 54, fl_5 56, fl_6 55, fl_7 56, fl_8 54, clava 116. Mesosoma length 410. Fore wing (Fig. 16) length 730, width 273, length/width 2.67, longest marginal setae 58. Fore wing seemingly bare (without microtrichia) behind and just apical to the venation. Hind wing length 458, width 23, longest marginal setae 73. Metasoma length 460. Ovipositor length 417.

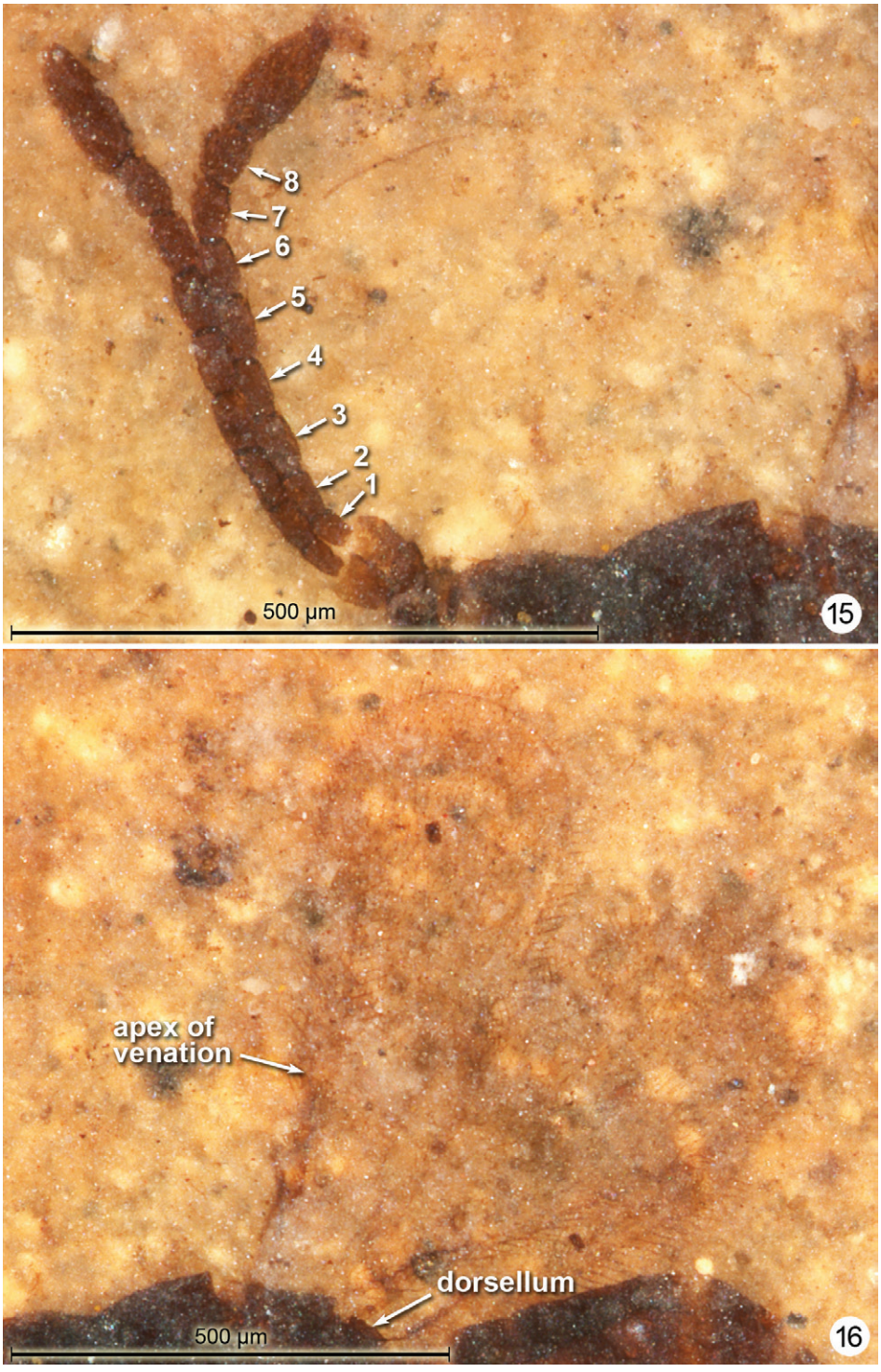
Comments. *G. greenwalti* differs from *G. kootenai* and *G. rasnitsyni* by the wider fore wing and thicker funicle segments. The apparent absence of microtrichia behind the venation, the wide fore wing, and fairly uniformly thick funicle segments suggest that *G. greenwalti* should be classified in *G.* (*Cosmocomoidea*).The shale fragment in which the fossil occurs contains several aquatic insects (e.g., Notonectidae), an indication of the lacustrine environment in which the mymarid lived (though it is not aquatic itself).

Derivation of species name. Named by the senior author in honour of the junior author, Dale Greenwalt, who collected and curated the insect fossils from Kishenehn shale.

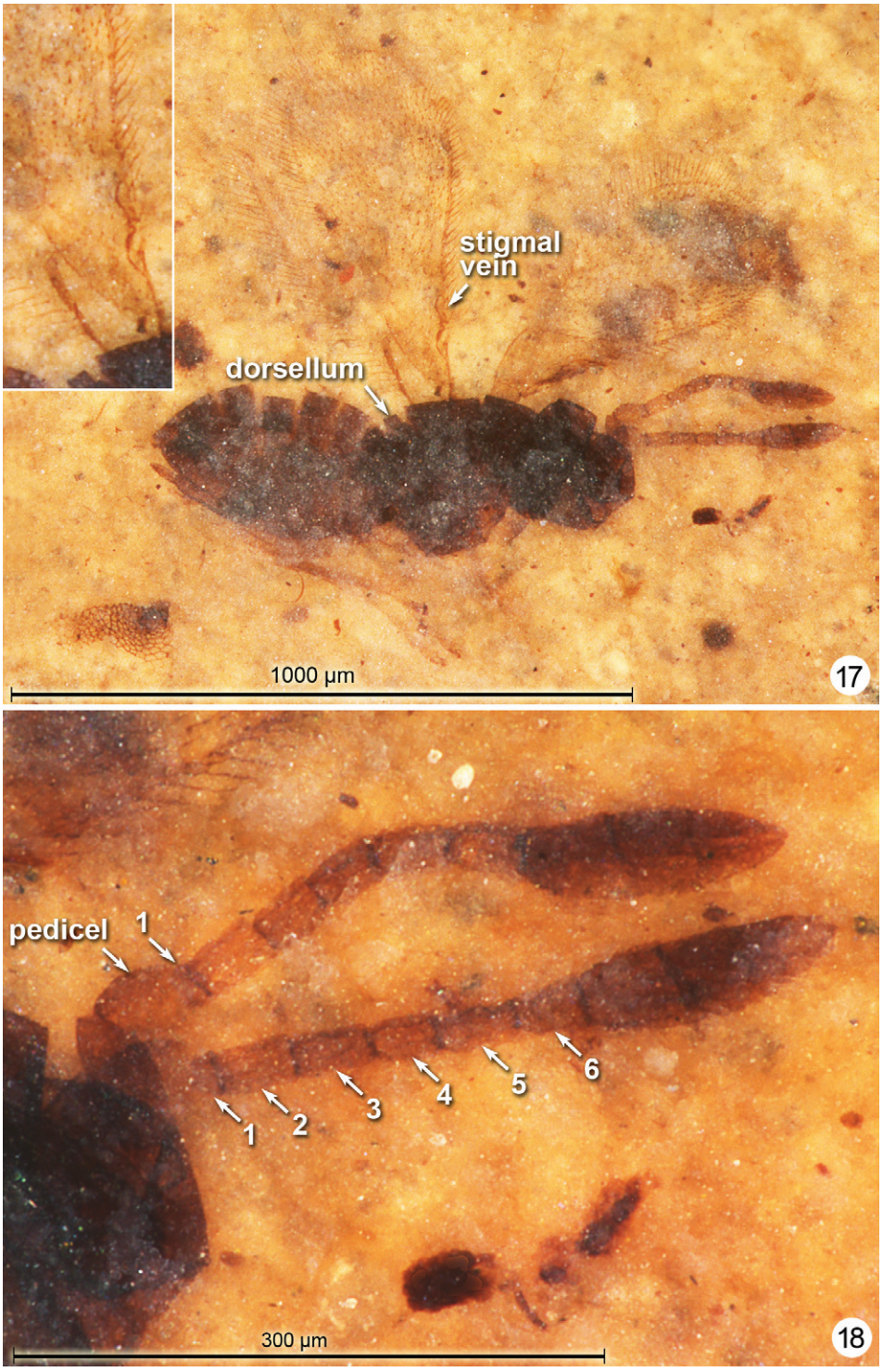
***Eoanaphes* Huber, gen. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Eoanaphes
Figs 17, 18

Description. Female. Body about 700. **Head**. About as wide as high (measured in frontal view). Malar space long, almost eye height. **Antenna.** Funicle 6-segmented, with fl_1 very short and remaining segments longer than wide; clava 3-segmented with the claval sutures almost perpendicular to claval length. **Wings**. Fore wing wide, slightly asymmetrical, with somewhat truncate apex; marginal fringe much shorter than fore wing width. Venation almost 1/3 fore wing length, with marginal vein fairly short, about as long as stigmal vein. Hind wing narrow; marginal fringe much longer than wing width and along posterior margin extending to base of membrane. **Mesosoma.** About 0.75 x gaster length. Mesoscutum length shorter than scutellum. Metanotum much shorter than scutellum, apparently with strap-like dorsellum. **Metasoma**. Apparently slightly constricted at base, probably with fairly wide, short petiole. Gastral terga similar in length. Ovipositor moderately short, apparently arising near base of gaster and its apex not exserted beyond gastral apex.

Type species. *Eoanaphes stethynioides* Huber, sp. n.



Figs 15, 16. *Gonatocerus greenwalti* holotype: antennae **16** wings.



Figs 17, 18. *Eoanaphes stethynioides*, holotype **17** habitus lateral (insert fore wing base) **18** antennae.

Derivation of generic name. The name is based on the extant genus *Anaphes*, which is also known from one extinct species in Baltic amber. The gender is masculine.

Discussion. *Eoanaphes* appears to be related to two genera, *Anaphes* and *Stethynium*. Four features suggest *Anaphes*: 1) in lateral view there is a distinct constriction dorsally between the mesosoma and metasoma, indicating that the propodeum slopes strongly down relative to the horizontal scutellum and dorsellum (in *Stethynium*, the entire dorsal margin of the mesosoma is horizontal and in line with the base of the metasoma, without a depression between the two parts); 2) the very short fl_1; 3) the apparent absence of a distinct rounded lobe on the posterior margin of the fore wing opposite the marginal + stigmal veins (one wing appears to have a rounded lobe but this is due to the membrane being partly folded over on itself); 4) the wing surface behind the marginal vein seems to be bare except for a few setae behind the stigmal vein and a faint suggestion of a hair line separating medial from marginal space. Two features suggest *Stethynium*: 1) the clearly 3-segmened clava; 2) the strap-like dorsellum (rhomboidal in *Anaphes*).

Eoanaphes stethynioides **Huber, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Eoanaphes_stethynioides
Figs 17, 18

Type material. Holotype female (NMNH) labelled "*Eoanaphes stethynioides* Huber Holotype female #543764".

Description. Female. Colour dark brown; pedicel, basal two funicle segments, and tarsi except perhaps apical tarsomere yellowish. Holotype (Fig. 17) measurements as follows. Body length 703. Head width 199. Antenna (Fig. 18) with total funicle length 189; scape -, pedicel 50, fl_1 15, fl_2 38, fl_3 38, fl_4 34, fl_5 40, fl_6 34, clava 132, about 0.66× funicle length. Mesosoma length (excluding pronotum) 293. Fore wing length 593, width 248, length/width 2.39, longest marginal setae 99; venation length 169, about 0.28× fore wing length. Hind wing length 485, width 34, venation length 115, longest marginal setae 84. Gaster length 372. Ovipositor length 322.

Discussion

Compression fossils in sedimentary rock are less informative morphologically than amber fossils. Fine details such as body setation and sculpture are not visible (wing setae may be visible), and body flattening during fossilization usually results in distortion. Measurements of body parts may therefore not be accurate though they can sometimes be more easily measured because they are flat. Appendages are the best source of useful diagnostic characters because some (legs, antenna) are less and some (wings) are not distorted. Because of the preservation method, compression fossils cannot be easily compared to amber fossils or extant genera and species. Nonetheless, they can be di-

agnosed moderately well and differentiated with reasonable certainty from each other and from other extinct and extant genera.

Among the 17 Kishenehn mymarids found, *Eoeustochus* is the most common, followed by *Gonatocerus* and *Eoanaphes*. It is surprising that no males were found; in extant genera males are less common than females but they are rarely almost completely absent. The compression fossils are of middle Eocene (Lutetian) age, as indicated above, and so are most Baltic amber fossils (Weitschat and Wichard 2010), i.e., about 41–49 my old. Incidentally, Meunier (1901), quoting A. Jentzsch, had noted that their age was lower Eocene, not lower Oligocene (yet the latter was stated again by Meunier 1909 and Doutt 1973). The Eocene had a warm humid climate, significantly warmer than the present (Zachos et al. 2001), allowing for development of subtropical and tropical rain forests to which the Baltic amber forests belong (Weitschat and Wichard 2010). Baltic amber forests were apparently rich in lentic water, flood plains, ponds, lakes with littoral habitats and temporary micro waters. Aquatic insects make up 25% of Baltic amber inclusions (Weitschat and Wichard 2010). The Middle sequence of the Coal Creek member of the Kishenehn Formation consisted of lacustrine sediments of a large permanent and shallow lake and associated lakeside and/or marsh, and has a high proportion of aquatic insect fossils (e.g., > 60% of all the fossil insects are Corixidae and Chironomidae). Because the climate and habitat of both Baltic and Kishenehn fossils was apparently similar it is not surprising that the genera of Mymaridae found in each are similar.

Meunier (1901) described most Baltic amber fossils of Mymaridae. Doutt (1973) described a few species from Mexican amber (Simojovel, Chiapas), dated as 15–20 my, and Thuróczy (1983) described one species. There is no indication from morphology that any of these or the mymarid compression fossils form a link between Cretaceous and Tertiary/Quaternary genera and species. Instead, they add support to the analysis by Rasnitsyn and Kulicka (1990) that showed Hymenoptera assemblages from Baltic amber seem to be more similar to the extant fauna than to the Late Cretaceous fauna.

One clear morphological tendency from Cretaceous to Tertiary and Quaternary (present) species can be seen — a reduction in the number of funicle or claval segments in females. A 3-segmented clava occurs in three of five (60%) Cretaceous genera, four of ten (40%) previously reported Tertiary genera from amber and shale (reported above), and 13 of 103 (about 8%) currently recognized extant genera. An 8-segmented funicle occurs in three of five (60%) Cretaceous genera, one of the 10 (10%) previously reported Tertiary genera, and five of the 103 (about 5%) extant genera. Except for *Gonatocerus,* which has eight funicle segments but an entire clava, all other Tertiary fossils have six (rarely fewer) funicle segments in females.

Spahr (1987) catalogued the literature and listed 11 mymarid genera from amber, three of them Cretaceous and eight Tertiary. He followed previous authors by including genera and species now correctly classified in Mymarommatidae (Gibson et al. 2007). Witsack (1986) described Palaeopatasson for one species from Dominican amber.

The senior author examined 16 Baltic amber pieces (SVT, UCRC) in 2005, 13 pieces (AMNH) in 2011, and three pieces (IPMGö., ZMUC) in about 2005. Only a few specimens could be referred confidently to an extant genus. These were four

specimens of *Gonatocerus,* and (less confidently) three specimens of *Anaphes* and two of *Stethynium*. If correctly identified, five more genera, all known from the extant fauna, are reported here for the first time as amber fossils. Having examined these 32 additional amber specimens and realizing that most of them cannot definitely be classified in an extant genus, the senior author has doubts about the correct generic placement of at least some of the specimens studied by past workers. None of those specimens were examined, however. Each Tertiary fossil genus is discussed briefly below.

Anagroidea (1 female, C.V. Henningsen, B-1 1956, ZMUC, examined) is no longer known from extant species in Europe and is rare in the Holarctic region (eastern Asia and south east USA).

Alaptus is known from at least two species in Miocene amber (Doutt 1973) that are probably correctly identified to genus.

Anaphes was known from three specimens in Baltic amber. *Anaphes splendens* Meunier is probably incorrectly classified. According to Meunier the ovipositor extends appreciably beyond the apex of the metasoma, unlike any extant *Anaphes*. The fore wing with a slight but distinct ventral lobe, its overall shape, the venation with a distinct stigmal vein, and the antenna with fl_1 almost as long as fl_2 also do not fit the genus. *Anaphes schellwieniens* Meunier is described from a male so it is impossible to determine its placement. Doutt (1973) examined a male from Chiapas amber and tentatively placed it in *Anaphes*. Three specimens examined here are fairly confidently placed in *Anaphes* (1 female, UCRC; 2 females, SVT). Additional specimens (2 females, SVT) examined are tentatively placed in *Anaphes*.

Arescon is known from two species in amber (Meunier 1901, 1905) that are probably correctly placed because of their 5-segmented funicle, though fore wing venation length, which is important information for correct generic placement, was not given by Meunier.

?*Camptoptera* (1 female, SVT), examined in 2005, if correctly classified, would be the first fossil specimen for this worldwide genus.

?*Dorya* (1 female, UCRC) is known only from extant species in Australia and New Zealand.

?*Eustochus* (1 female, AMNH). The gaster appears to be petiolate. This suggests a *Eustochus* with a distinct 3-segmented clava (most have a 2-segmented clava) though the wing shape and antenna suggests *Eoeustochus*.

?*Mimalaptus* (3 females, SVT; 2 females, UCRC; 1 female, box G 3.910 Hymenoptera #BST03124, IPMGö.) is known from extant species in Australia and New Zealand and possibly eastern Asia.

Gonatocerus was known from only one fossil specimen, *Gonatocerus henneberti* (Meunier 1905), which appears to belong to either *G*. (*Gonatocerus*) or *G*. (*Lymaenon*) as suggested by the narrow wings. However, the "écusson semilunaire" [semilunate shield], which I interpret from Meunier's drawing as being the dorsellum, appears to be rhomboidal in shape, which would eliminate *G*. (*Lymaenon*) as the correct subgenus. The small size of the specimen, only 1/3 mm long, is unusual; it is much smaller than the smallest extant *Gonatocerus* I have seen. A specimen of *Gonatocerus* (*Cosmocomoidea*) is reported here (1 male, Poinar collection, OSU) from Dominican amber, 15–20 my.

Litus is represented by two fossil species. *Litus elegans* Meunier (1901) may or may not be correctly classified because the description and illustration are insufficient to place it. It apparently differs considerably from *Litus mexicanus* Doutt (1973), which is likely correctly classified. Extant *Litus* species tend to have a bi-geniculate funicle, unlike that illustrated by Meunier. *Litus beneficus* Meunier from copal (recent) from Madagascar also needs to be re-examined; it is unlikely to be classified correctly.

Malfatia molitorae Meunier (1901) is based on a male and from the description alone it is impossible to determine how it relates to extant genera. Its status remains uncertain.

Palaeopatasson grollei Witsack (1986) is based on a female and may be related to Anaphes.

Polynemoidea mexicana Doutt (1973) from Chiapas amber was stated to be similar to *P. domestica* Girault, but the latter species is likely incorrectly placed in *Polynemoidea* (Lin et al. 2010). Consequently, I suspect that *P. mexicana* is also incorrectly classified; it does not have a strongly exserted ovipositor as in the type species of *Polynemoidea*.

Stethynium (1 female, S. Triapitsyn collection), if correctly identified, confirms that the genus occurs in Baltic amber, as reported by Thuróczy (1983).

Conclusions

1. Tertiary fossils of Mymaridae are clearly more related to the extant fauna than to the Cretaceous fauna.
2. Except for *Gonatocerus* and the two new genera described above, tertiary fossils of Mymaridae (except perhaps *Anaphes* and *Stethynium*) are for the most part doubtfully assigned to extant genera.
3. Several Eocene amber fossils, if correctly identified to genus, represent genera that no longer occur in Europe (*Anagroidea*, *Dorya*, *Mimalaptus*) or are very poorly represented in most of the Holarctic region (*Stethynium*). These genera are now distributed mostly in the tropics or southern hemisphere, supporting observations that the Eocene climate (in parts of the Holarctic region at least) was considerably warmer than at present.
4. If correctly identified, *Anagroidea*, *Eustochus*, and perhaps *Eoeustochus* would be the first fossil records of genera belonging to the extant tribe Mymarini *sensu* Annecke and Doutt (1961), likely the most derived lineage in Mymaridae.

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collection for study of the senior author. These were then purchased by AMNH, where they will be deposited.

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RESEARCH ARTICLE

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Revision of fossil species of *Deinodryinus*, with description of a new species (Hymenoptera, Dryinidae)

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Abstract

Deinodryinus velteni **sp. n.** is described from middle Eocene Baltic amber. The species differs from other fossil Palaearctic species of *Deinodryinus* Perkins owing to the shape of the antenna (clavate, with distal part very thickened), the large compound eyes, and the distal part of the stigmal vein much longer than the proximal part. A revision and a key to the fossil Palaearctic species of *Deinodryinus* Perkins, 1907 is presented.

Keywords

Taxonomy, *Deinodryinus velteni*, Baltic amber, key, Dryinidae, Anteoninae

Introduction

Dryinidae (Hymenoptera, Chrysidoidea) are parasitoids of Auchenorrhyncha (Guglielmino and Olmi 1997, 2006, 2007). The genus *Deinodryinus* Perkins, 1907 is present in all zoogeographical regions and a member of the subfamily Anteoninae. One hundred and forty-eight species of *Deinodryinus* have been described from throughout the world, of which only two are fossil species (Olmi 1984, 1999; Olmi et al. 2010;

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Ponomarenko 1975): *D. areolatus* (Ponomarenko, 1975), from Baltic amber, and *D. ? aptianus* Olmi, Rasnitsyn & Guglielmino, 2010, a compression fossil from Early Cretaceous marl of the Khurilt rock unit (Mongolia). The latter species is tentatively placed within *Deinodryinus* given that it is uncertain whether the attribution of this Early Cretaceous species to a modern genus is justified. Insufficient characters were preserved in *D.*? *aptianus* to support its placement in a new generic taxon.

Recently we have discovered an additional new fossil species of *Deinodryinus* from Baltic amber, and the taxon is described herein.

Material and methods

The descriptions follow the terminology used by Olmi (1984, 1994a, 1999). The measurements reported are relative except for the total length (head to abdominal tip, without the antennae) and the length of some parts of the body, which are expressed in millimetres.

The redescriptions of *D.? aptianus* and *D. areolatus,* respectively by Olmi et al. (2010) and Ponomarenko (1975), are provided for the sake of completeness. Information on the fossil deposits under consideration are provided by Rasnitsyn and Quicke (2002).

The material studied in the present paper is deposited in the following institutions:

PIN A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow (Russia).

SNMS Staatliches Museum für Naturkunde Stuttgart, Abt. Paläontologie–Sektion Bernstein, Stuttgart (Germany).

Systematic paleontology

Genus *Deinodryinus* Perkins, 1907
http://species-id.net/wiki/Deinodryinus

Deinodryinus Perkins, 1907: 45. Type species: *Deinodryinus paradoxus* Perkins, 1907, designated by Muesebeck and Walkley 1951.

Trisanteon Kieffer, 1913: 300 (synonymized by Olmi 1984); type species: *Trisanteon hirticornis* (Kieffer, 1911), monotypic and original designation.

Electrodryinus Ponomarenko, 1975: 126 (synonymized by Olmi 1984); type species: *Electrodryinus areolatus* Ponomarenko, 1975, monotypic.

Prioranteon Olmi, 1984: 589 (synonymized by Olmi 2007); type species: *Prioranteon casalei* Olmi, 1984, original designation.

Diagnosis. Female: macropterous or micropterous; palpal formula 6/3; in macropterous specimens forewing usually with distal part of stigmal vein longer than proximal

part, less frequently as long as, or shorter than proximal part; occipital carina complete; vertex frequently with two strong oblique keels connecting posterior ocelli to occipital carina; pronotum with distinct anterior collar and posterior disc; foreleg chelate; enlarged claw with inner proximal prominence not bearing bristles, with 1–2 bristles or peg-like hairs located further distally than proximal prominence; tibial spurs 1/1/2. Male: always macropterous (even if female micropterous); palpal formula 6/3; forewing usually with distal part of stigmal vein longer than proximal part, less frequently as long as, or shorter than proximal part; forewing usually with pterostigma four or more than four times as long as broad; antennal hairs usually much longer than breadth of segments, less frequently shorter than breadth of segments; vertex frequently with two strong oblique keels connecting posterior ocelli to occipital carina; paramere without dorsal process, usually with more-or-less large inner branch wrapping penis, less frequently with reduced inner branch; tibial spurs 1/1/2.

Distribution. Worldwide.

Hosts. Cicadellidae (Guglielmino and Olmi 2007).

Species. Presently with 152 living and fossil species.

Key to the fossil species of *Deinodryinus*

Females

1 Antenna filiform (Fig. 1); compound eye shorter than one-half length of head (Fig. 1)..... ***aptianus* Olmi, Rasnitsyn & Guglielmino**

– Antenna clavate (Figs 2, 3); compound eye longer than one-half length of head (Figs 2, 3) **2**

2 Distal part of stigmal vein much longer than proximal part (Fig. 3) .... ***velteni* sp. n.**

– Distal part of stigmal vein about as long as proximal part (Fig. 2) .... ***areolatus* (Ponomarenko)**

Males: Unknown.

***Deinodryinus? aptianus* Olmi, Rasnitsyn & Guglielmino**

Fig. 1

Deinodryinus? aptianus Olmi, Rasnitsyn & Guglielmino 2010: 30.

Material examined. Type: *Holotype*, female, MONGOLIA: Central Mongolia, Bayanhongor Aimag, 5–8 km N Bon Tsagan Nuur Lake, outcrop 87, bed 8, impressed in marl of the Khurilt rock unit probably of Aptian age (Early Cretaceous) (100–115 mybp)(PIN, No. 3559/4586).

Diagnosis. Female with antenna filiform and compound eye small (Fig. 1).

Redescription. *Female*: macropterous; length 6.2 mm; length of main regions: head: 0.87 mm; antennae: 3.06 mm; mesosoma: 1.37 mm; prothorax: 0.87 mm; me-

Figure 1. *Deinodryinus ? aptianus*. Female holotype (from Olmi et al. 2010). Length 6.2 mm.

sothorax + metathorax + propodeum: 1.37 mm; metasoma: 3.12 mm. Antenna filiform (Fig. 1); antennal segments in following proportions: 14:12:14:12:13:17:15:13:12:15; length/breadth ratio of antennal segments 8–10: 8th: 13:3; 9th: 12:3; 10th: 15:3. Head only visible from ventral side. Occiput very deeply excavated, with hipostomal bridge short (in ventral side, length of occiput: 0.62 mm; hipostomal bridge: 0.62 mm; oral fossa: 0.43 mm). Palpi not visible. Compound eye small (Fig. 1). Propleura normal (as in extant dryinids). Profemur very large, covering ventral side of mesothorax. Forewing hyaline, with three basal cells completely enclosed by pigmented veins. Marginal cell closed. Stigmal vein regularly curved, distal part much longer than proximal part. Pterostigma very narrow, with following length/breadth ratio: 35:7. Petiole very short. Ovipositor present. Legs only partly visible. Profemur very large (length/breadth ratio: 39:18), as in extant chelate female of dryinids. Chela present, hardly visible. Remainder of forelegs, partly missing. Mid- and hindlegs partly missing. Length of mesocoxa: 0.62 mm. Length of metacoxa: 0.81 mm. Tibial spurs not visible.

Male: unknown.

Hosts. Unknown.

Remarks. This fossil is only visible in ventral aspect and is difficult accordingly to place within a particular genus. In addition, the legs are partly missing and the chela is hardly visible. However, it is possible to identify tentatively this specimen as a species of the extant genus *Deinodryinus* given the shape of the pterostigma and stigmal vein

and for the presence in the forewing of three basal cells completely enclosed by pigmented veins. Among Anteoninae, the above characters may also place this specimen in *Lonchodryinus* Kieffer, 1905, but *Lonchodryinus* has the hypostomal bridge much shorter than in *Deinodryinus*. Given that the fossil exhibits the condition in the latter genus the authors placed the species in *Deinodryinus*. Among Dryinidae, the above characters of the forewing may also place this specimen in Dryininae and Gonatopodinae but because the occiput is less excavated in Dryininae and Gonatopodinae than in *Deinodryinus*, and in *D.*? *aptianus*, attribution to *Deinodryinus* is more justified. Another unusual character of *D.*? *aptianus* is the shape of the antennae: they are filiform, as in males of Dryinidae, whereas in females usually they are clavate (Olmi et al. 2010).

***Deinodryinus areolatus* (N. Ponomarenko)**
http://species-id.net/wiki/Deinodryinus_areolatus
Fig. 2

Electrodryinus areolatus N. Ponomarenko 1975: 128.
Deinodryinus areolatus (N. Ponomarenko): Olmi 1984: 121.
Deinodryinus areolatus (N. Ponomarenko): Olmi 1995: 268.
Deinodryinus areolatus (N. Ponomarenko): Olmi and Bechly 2001: 41.

Material examined. Type: *Holotype*, female, Eocene Baltic amber (40–45 mybp)(PIN, No. 964/60).

Diagnosis. Female with antenna clavate and compound eye large (Fig. 2); distal part of stigmal vein about as long as proximal part (Fig. 2).

Redescription. *Female*: macropterous; length 4.5 mm. Head black, except anterior region of face brown; clypeus testaceous, except central brown spot; mandible testaceous, except teeth and proximal region brown; antenna testaceous; mesosoma and metasoma black; legs brown-testaceous. Antenna 10-segmented, clavate, densely hairy, less than three times as long as head (157:63); antennal segments in following proportions: 17:10:30:22:18:15:11:11:10:13. Clypeus with anterior margin weakly emarginated. Antennal torulus distinctly separated from epistomal sulcus. Mandible with four teeth progressing larger from anterior one to posterior. Compound eye apparently bare, normally protruding. Subocular sulcus present. Occipital carina complete. Temple prominent. Posterior ocelli hardly visible, not touching occipital carina. Palpal formula 6/3. Pronotum not crossed by transverse impressions; pronotal tubercle reaching tegula; posterior margin of pronotum longer than anterior margin. Thoracic structure similar to that of extant *Deinodryinus*. Scutum shiny, finely punctate, longer than pronotum (20:15). Notauli complete, posteriorly separated. Propodeum reticulate rugose, with areolae very broad; dorsal surface approximately as long as posterior surface; posterior surface very steep, not distincly visible. Petiole distinct. Forewing hyaline, without dark transverse bands, with normal venation of Anteoninae; pterostigma narrow, more than four times as long as broad (40:8); marginal cell open; distal part of stigmal vein about

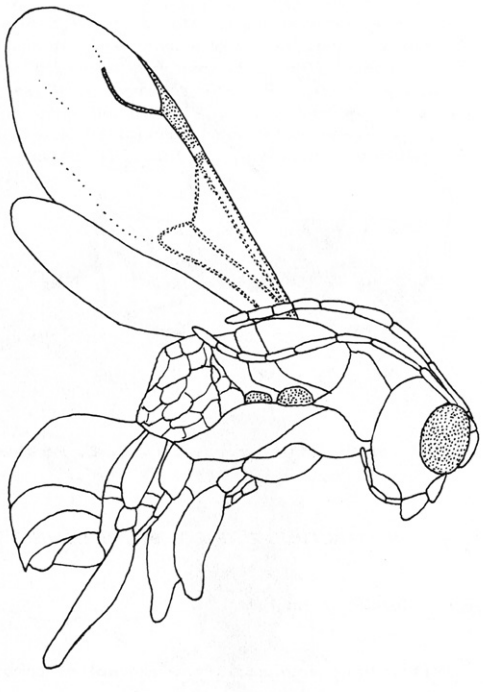

Figure 2. *Deinodryinus areolatus*. Female holotype (from Olmi 1984). Length 4.5 mm.

as long as proximal part (18:17); stigmal vein not S-shaped. Forewing with usual three basal cells clearly enclosed by pigmented veins (costal, median, and submedian cells). Shape of wings usual for *Deinodryinus*. Protrochanter not slender, without proximal slender stalk, slightly longer than broad (10:6). Segment 3 of protarsus produced into hook; segment 1 of protarsus slightly shorter than segment 4 (15:17). Forelegs chelate. Chela without rudimentary claw. Arolium much shorter than enlarged claw (7:32). Enlarged claw without subapical tooth and other teeth. Segment 5 of protarsus about as long as enlarged claw, with lamellae hardly visible. Tibial spurs 1/1/2.

Male: unknown.

Hosts. Unknown.

Remarks. In the holotype the sculpture of the vertex, face, and pronotum is hardly visible; the scutellum and metanotum are not visible.

***Deinodryinus velteni* Guglielmino & Olmi, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Deinodryinus_velteni
Fig. 3

Etymology. The species is named after Mr. Jürgen Velten (Idstein, Germany).

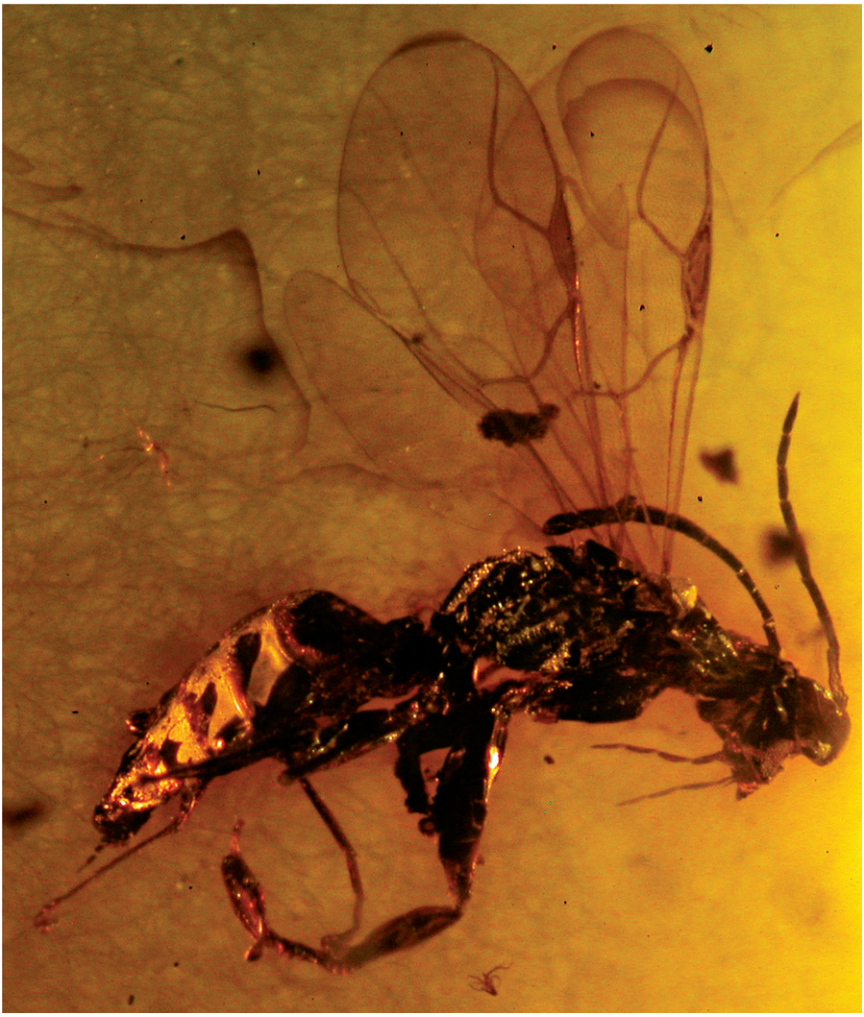

Figure 3. *Deinodryinus velteni*. Female holotype. Length 4.0 mm.

Material examined. Type: *Holotype*, female, Eocene Baltic amber (40–45 mybp) (SMSN).

Diagnosis. Female with antenna clavate and compound eye large (Fig. 3); distal part of stigmal vein much longer than proximal part (Fig. 3).

Description. *Female*: macropterous; length 4.0 mm. Colour apparently brown-black, except palpi testaceous. Antenna 10-segmented, clavate, short, covered with dense and short hairs, thickened distally; antennal rhinaria absent; antennal segments in following proportions: 5:7:8:13:10:9:8:6:6:9; antenna much shorter than body, approximately three times as long as head (head length dorsally measured from occipital carina behind ocelli to distal apex of mandible): 75:25. Head only partly visible, slightly convex, dull, apparently granulated and hairless; occiput excavated; compound eye normally bulging; ocelli partly visible; ocellar triangle apparently equilater-

al; temple distinct. Pronotum long, crossed by anterior strong transverse impression, with posterior disc, without posterior collar; pronotum apparently almost glabrous, shiny, slightly shorter than head (22:25); pronotal disc flat posteriorly, much longer than anterior collar; pronotal tubercle reaching tegula. Scutum dull, apparently glabrous, granulated, slightly shorter than pronotum (19:22). Notauli complete, posteriorly separated; minimum distance between notauli approximately as long as antennal segment 2. Scutellum very humped (Fig. 3), much shorter than scutum (8:19). Metanotum very humped (Fig. 3), shorter than scutellum (6:8). Propodeum longer than scutum (29:19), apparently reticulate rugose; sculpture of dorsal and posterior surfaces visible only laterally. Metapleura dull, rugose and partly sculptured by transverse keels. Epicnemium present. Shape of head, scutum, scutellum, metanotum and propodeum usual for Anteoninae. Forewing apparently completely weakly darkened, with usual venation of Anteoninae. Pterostigma long and narrow, much longer than broad (30:6). Pterostigma shape similar to that of extant *Deinodryinus*. Marginal cell open. Stigmal vein not S-shaped, with distal part much longer than proximal part (20:14); stigmal vein forming an angle between proximal and distal parts. Forewing with usual three basal cells clearly enclosed by pigmented veins (costal, median and submedian cells). Hindwing apparently slightly darkened. Hindwing shape usual for Anteoninae. Foreleg segments in following proportions: 30 (coxa): 7 (trochanter): 43 (femur): 29 (tibia): 7 (tarsomere 1): 3 (tarsomere 2): 5 (tarsomere 3): 11 (tarsomere 4): 24 (tarsomere 5). Foreleg chelate. Enlarged claw slightly shorter than tarsomere 5 (22:24). Protrochanter short, slightly longer than broad (7:5). Protrochanter shape similar to that of Anteoninae. Tarsomeres 2 and 3 of protarsus produced into a hook. Rudimentary claw absent. Arolium much shorter than enlarged claw (8:22). Distal apex of enlarged claw apparently pointed. Tarsomere 5 of protarsus with numerous lamellae on inner margin and distal apex. Midleg segments in following proportions: 12 (coxa): 8 (trochanter): 26 (femur): 24 (tibia): 22 (tarsomere 1): 9 (tarsomere 2): 6 (tarsomere 3): 4 (tarsomere 4): 6 (tarsomere 5). Hindleg segments in following proportions: 19 (coxa): 5 (trochanter): 33 (femur): 32 (tibia): 23 (tarsomere 1): 10 (tarsomere 2): 8 (tarsomere 3): 4 (tarsomere 4): 6 (tarsomere 5). Petiole shape and length usual for Anteoninae. Palpal formula 6/3. Shape, length and breadth of wings usual for Anteoninae. Shape and morphology of body usual for Anteoninae. Tibial spurs 1/1/2.

Male: unknown.

Hosts. Unknown.

Remarks. In the holotype the clypeus, mandibular teeth, frontal line, occipital carina, POL, OL, OOL, OPL, TL, and posterior surface of the propodeum are not visible; the sculpture of the pronotum, scutellum, metanotum, and mesopleura is not distinct; the enlarged claw is only partly visible because of a closed chela so that it is not possible to see if there are subapical teeth and lamellae; and tarsomere 5 of the protarsus is only partly visible so that it is impossible to count the lamellae and to see if there are one or two rows of lamellae.

Discussion

With 152 species, the genus *Deinodryinus* is present in all zoogeographical regions: six species are Palaearctic; 22 Afrotropical; nine Oriental; three Nearctic; 110 Neotropical; and two Australian. The only known fossil species have been found in the Palaearctic region, and all have been summarized in the present paper. Because of its geographic distribution, *Deinodryinus* is considered a 'Pangean' genus (Olmi 1994b). The genus perhaps originated in Central and South America, where the greatest number of extant species are present (110), although centres of origin do not always reside in areas today harboring the greatest species diversity and so this hypothesis requires phylogenetic testing. Almost all species live in tropical or subtropical countries. Very few are the species living in temperate countries: two in the Palaearctic region [*Deinodryinus biroi* (Olmi, 1984) and *D. hispanicus* (Olmi, 1991)], and one in the Nearctic region [*Deinodryinus atriventris* (Cresson, 1872)]. The presence of fossil species in Baltic amber and Early Cretaceous Mongolia marl perhaps indicates that these areas had relatively warm climates in the past, conclusions supported by other faunal and floral elements in these deposits, and that the genus had a much wider distribution.

From a morphological standpoint, *D. areolatus* and *D. velteni* do not exhibit significant differences from extant species of the genus. This is common with many fossil dryinids. By contrast, *D.? aptianus*, visible only in ventral aspect, with legs partly missing and the chela hardly distinct, is difficult to interpret. As mentioned above, attribution to *Deinodryinus* is only tentative and based on the shape of the pterostigma and stigmal vein and by the presence in the forewing of three basal cells completely enclosed by pigmented veins. However, the presence of filiform antennae, a character present in very few females of dryinids and rare in *Deinodryinus* (only the females of *D. benoiti* Olmi, 1984, from Madagascar, and *D. colombianus* Olmi, 1984, from South America, have filiform antennae), makes this attribution somewhat suspect. Accordingly, our assignment of this species to *Deinodryinus* remains speculative and we hope for the eventual discovery of more completely preserved material so as to clarify the generic status of this ancient taxon.

Acknowledgements

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RESEARCH ARTICLE

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Revision of fossil species of *Dryinus* belonging to *lamellatus* group, with description of a new species (Hymenoptera, Dryinidae)

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Abstract

Dryinus rasnitsyni **sp. n.** is described from amber collected in the Dominican Republic. A revision and a key to the fossil Neotropical species of *Dryinus* Latreille, 1804 belonging to the *lamellatus* species group is presented.

Keywords

Taxonomy, *Dryinus rasnitsyni*, amber, Dominican Republic, key, *Dryinus lamellatus* group, Dryininae

Introduction

Dryinidae (Hymenoptera: Chrysidoidea) are parasitoids of Auchenorrhyncha (Guglielmino and Olmi 1997, 2006, 2007). *Dryinus* Latreille, 1804, belonging to Dryininae, is present in all zoogeographical regions. Two hundred and seventy-eight species of *Dryinus* have been described from all over the world, of which seventeen are fossil species (Olmi 1984, 1995, 1999; Olmi and Bechly 2001; Olmi et al. 2010). According to Olmi (1993), *Dryinus* is divided into four groups: *constans*, *ruficauda*, *lamellatus* and

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autumnalis. In the *lamellatus* group only one fossil species has been described: *Dryinus grimaldii* Olmi, 1995.

In 2010 the authors have found a further new fossil species of the *lamellatus* group, which is described herein.

Material and methods

The descriptions follow the terminology used by Olmi (1984, 1994, 1999). The measurements reported are relative, except for the total length (head to abdominal tip, without the antennae), which is expressed in millimetres. In the descriptions, POL is the distance between the inner edges of the lateral ocelli; OL is the distance between the inner edges of a lateral ocellus and the median ocellus; OOL is the distance from the outer edge of a lateral ocellus to the compound eye; OPL is the distance from the posterior edge of a lateral ocellus to the occipital carina; TL is the distance from the posterior edge of an eye to the occipital carina.

A redescription of *D. grimaldii* is provided for completeness in this updated treatment of all fossil species of the *lamellatus* group.

The material studied herein is deposited in the following institutions:

AMNH American Museum of Natural History, New York (USA).
GPJC Private collection of George Poinar, Jr., c/o Department of Entomology, Oregon State University, Corvallis, Oregon (USA).
SNMS Staatliches Museum für Naturkunde Stuttgart, Abt. Paläontologie–Sektion Bernstein, Stuttgart (Germany).

Systematics

Genus *Dryinus* Latreille, 1804

http://species-id.net/wiki/Dryinus

Diagnosis. Female: macropterous; mandible with 1–4 teeth; occipital carina complete, or incomplete, or absent; antenna without tufts of long hairs on segments 5–10, usually with rhinaria, occasionally without; antennal segment 3 less than five times as long as segment 2; occasionally antennal segment 3 more than five times as long as segment 2 (in this case, notauli occasionally complete and scutum completely sculptured by numerous and parallel longitudinal keels); palpal formula 6/3; pronotal tubercle reaching or not tegula; forewing with three cells enclosed by pigmented veins (costal, median and submedian); protarsus chelate; chela with rudimentary claw; segment 5 of protarsus less than twice as broad as enlarged claw; enlarged claw as long as, or shorter

than protibia; tibial spurs 1/1/2, rarely 1/1/1. Male: macropterous; mandible with 1–3 teeth; palpal formula 6/3; occipital carina complete or incomplete; lateral regions of prothorax not continuous with mesopleura; epicnemium visible; mesosternum fused with mesopleura and not distinct; forewing with three cells enclosed by pigmented veins (costal, median and submedian); paramere without dorsal process; tibial spurs 1/1/2.

Distribution. Worldwide.

Hosts. Acanaloniidae, Cixiidae, Dictyopharidae, Flatidae, Fulgoridae, Issidae, Lophopidae, Ricaniidae, Tropiduchidae (Guglielmino and Olmi 1997, 2006, 2007)

Species. Two hundred and seventy-nine.

Remarks. The Neotropical species of *Dryinus* are divided into four groups, according to the following key (Olmi 1993):

1 Enlarged claw very reduced, approximately as long or slightly longer than arolium ..... ***autumnalis* group**
– Enlarged claw not reduced, much longer than arolium **2**
2 Enlarged claw without subapical tooth, or with at least 2 subapical teeth; rarely with one only subapical tooth, but then with a very broad apical lamella ..... ***lamellatus* group**
– Enlarged claw with 1 subapical tooth, never with a broad apical lamella **3**
3 Notauli at least partly present ..... ***constans* group**
– Notauli absent ..... ***ruficauda* group**

Key to fossil species of the *lamellatus* group

Females (males unknown)

1 Enlarged claw not spatulate (Figs 1, 2) ..... ***grimaldii* Olmi**
– Enlarged claw spatulate (Fig. 4) ..... ***rasnitsyni* sp. n.**

Dryinus grimaldii Olmi

http://species-id.net/wiki/Dryinus_grimaldii

Figs 1–3

Dryinus grimaldii Olmi 1995: 254.
Dryinus grimaldii Olmi: Olmi 2000: 65.
Dryinus grimaldii Olmi: Olmi and Bechly 2001: 45.

Type material. *Holotype*, female, Early Miocene amber from the Dominican Republic (16–19 Ma) (AMNH, No. DR-10-1426); same locality label, 1 female paratype (AMNH, No. DR-10-1423).

Additional specimens examined. same locality, three female specimens (GPJC).

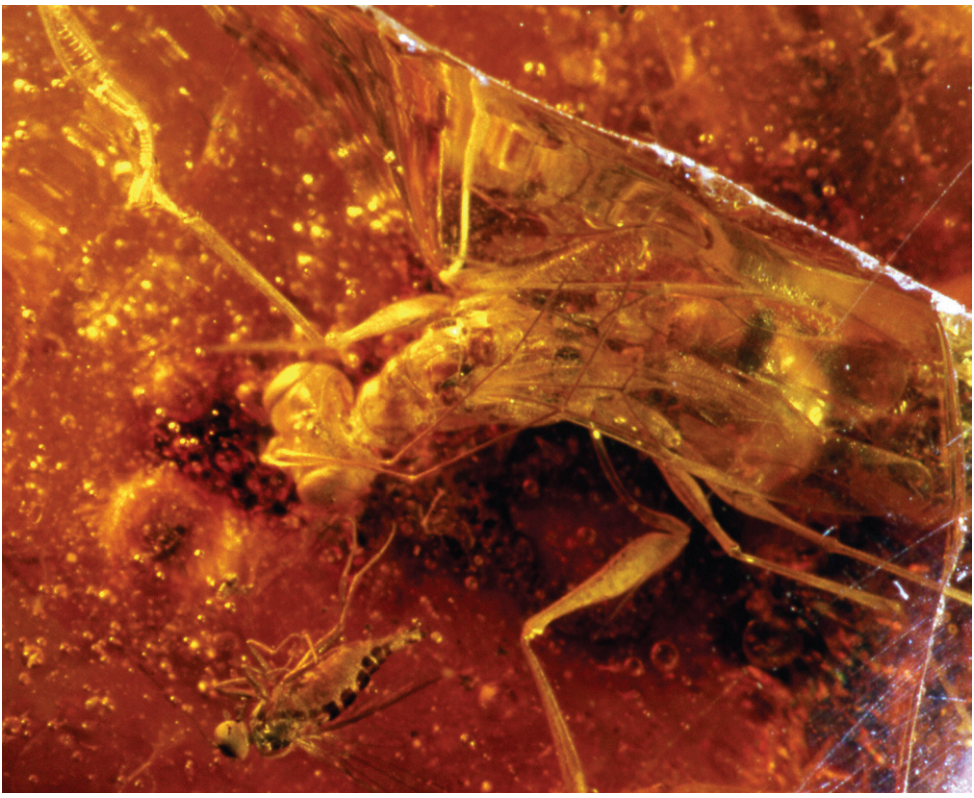

Figure 1. *Dryinus grimaldii*. Female holotype (from Olmi 1995). Length 4.3 mm.

Diagnosis. Female with enlarged claw not reduced and not spatulate (Figs 1, 2), longer than arolium; enlarged claw with two subapical teeth. Male unknown.

Redescription. *Female*: macropterous; length 4.3–6.3 mm. Colour difficult to discern, apparently testaceous, except two dark lateral spots on sides of pronotal disc, scutum, scutellum, propodeum and tegula dark; metasoma with dark transverse band. In paratype, legs with dark spots on coxae and clubs of femora; scutum apparently without dark lateral spots. In one specimen of GPJC labelled H-10-100, apparently scutum without lateral dark spots, scutellum not darkened, posterior surface of propodeum darkened. In two specimens of GPJC labelled H-10-23C, body totally testaceous, except petiole black and two brown spots on sides of scutum. Antenna 10-segmented, long and very slender, filiform, not thickened distally, covered with dense and short hairs; antennal segments of holotype in following proportions: 10:5:44:57:38:21:9:9:9:17; antenna more than nine times as long as head (length of head dorsally measured from occipital carina behind ocelli to distal apex of mandible): 219:22. Head weakly convex, apparently shiny, finely punctate, without apparent sculpture among punctures; clypeus and mandible not distinct; occipital carina apparently complete; occiput deeply excavated; eye normally bulging; POL = 2; OL = 1.5; OOL = 10; OPL = 1.5; TL = 5; greatest breadth of posterior ocellus longer than POL

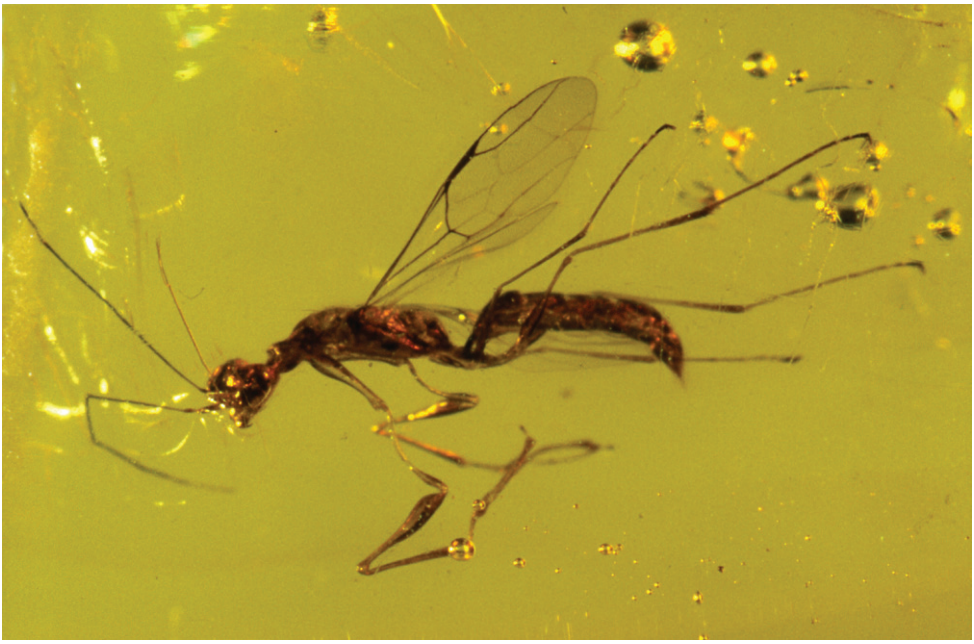

Figure 2. *Dryinus grimaldii*. Female specimen in lateral view (in GPJC, No. H-10-100). Length 6.3 mm.

(4:2); frontal line absent. Maxillary palpi not evident, apparently 6-segmented. Labial palpi not distinct. Pronotum apparently shiny, finely punctate, about as long as head, crossed by anterior strong transverse impression between anterior collar and disc; disc humped; posterior collar very short; pronotal tubercle reaching tegula. Scutum apparently shiny, finely punctate, slightly shorter than pronotum (19:22). Notauli complete, posteriorly separated; minimum distance between notauli about as long as greatest breadth of posterior ocelli. In one specimen of GPJC labelled H-10-100, notauli apparently almost complete, not reaching posterior margin of scutum. Scutellum apparently shorter than scutum (10:19), with sculpture not evident. Metanotum shorter than scutellum (6:10), with sculpture not evident. Propodeum longer than scutum (39:19), reticulate rugose, areolae very broad; posterior surface with two complete longitudinal keels; sculpture of median area of posterior surface not evident. In one specimen of GPJC labelled H-10-100, dorsal surface of propodeum with two median longitudinal and almost parallel keels. Shape of pronotum, scutum, scutellum, metanotum and propodeum usual for Dryininae. Forewing hyaline, without dark transverse bands, with usual venation of Dryininae; pterostigma narrow, much longer than broad (32:4); marginal cell apparently open; distal part of stigmal vein longer than proximal part (16:11); stigmal vein not S-shaped, forming angle between proximal and distal parts; forewing with usual three basal cells clearly enclosed by pigmented veins (costal, median and submedian cells). Hindwing hyaline, without dark transverse bands. Foreleg segments in following proportions: 55 (coxa): 53 (trochanter): 61 (femur): 60 (tibia): 18 (tarsal segment 1): 5 (tarsal segment 2): 8 (tarsal segment 3): 55 (tarsal

Figure 3. *Dryinus grimaldii*. Female specimen in dorsal view (in GPJC, No. H-10-100). Length 6.3 mm.

segment 4): 78 (tarsal segment 5); foreleg chelate; enlarged claw much shorter than segment 5 of protarsus (42:78); protrochanter more than four times as long as broad (53:5)(greatest breadth measured on distal club), with long and slender proximal stalk, broadened after half-way; segments 2 and 3 of protarsus produced into hooks; rudimentary claw present; arolium much shorter than enlarged claw (8:42); enlarged claw with two strong subapical teeth and 1 row of 8 lamellae; subapical teeth of enlarged claw very strong, such as in *Plesiodryinus*; distal apex of enlarged claw not spatulate. Segment 5 of protarsus with 2 rows of approximately 50 lamellae; distal apex with group of at least 20 lamellae (number of lamellae not evident). Midleg segments in following proportions: 22 (coxa): 7 (trochanter): 41 (femur): 60 (tibia): 17 (tarsal segment 1): 15 (tarsal segment 2): 15 (tarsal segment 3): 14 (tarsal segment 4); segment 5 of mesotarsus not distinct. Hindleg segments in following proportions: 27 (coxa): 11 (trochanter): 48 (femur): 80 (tibia); segments of metatarsus not distinct in holotype; segments of metatarsus of paratype in following proportions: 37 (tarsal segment 1): 19 (tarsal segment 2): 13 (tarsal segment 3): 10 (tarsal segment 4): 11 (tarsal segment 5). Metasoma without distinct and slender petiole. Shape and length of petiole usual for Dryininae. Shape, length and breadth of wings usual for Dryininae. Shape of body usual for Dryininae. Tibial spurs of holotype hardly visible, apparently 1/1/1; in one specimen of GPJC labelled H-10-100, tibial spurs distinctly 1/1/2.

Male: unknown.

Hosts. Unknown.

***Dryinus rasnitsyni* Olmi & Guglielmino, sp. n.**
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http://species-id.net/wiki/Dryinus_rasnitsyni
Figs 4–6

Holotype. Female, Oligo-Miocene amber from Dominican Republic (15–40 mybp) (SMSN).

Diagnosis. Female with enlarged claw spatulate, not reduced, with large distal apex (Fig. 6), longer than arolium. Male unknown.

Description. *Female*: macropterous; length 7.4 mm. Colour not distinct, apparently brown, except head, palpi and chela partly testaceous. Antenna 10-segmented, long and very slender, weakly thickened distally, covered with dense and short hairs; antennal segments in following proportions: 20:8:28:27:35:39:28:19:15:13; antenna about five times as long as head (length of head dorsally measured from occipital carina behind ocelli to distal apex of mandible): 90:18. Head weakly convex, apparently dull, granulated; occipital carina and occiput not distinct; eye normally bulging; frontal line not evident. Palpal formula apparently 6/3. Pronotum apparently shorter than head (8:18), crossed by anterior strong transverse impression between anterior collar and disc; disc humped; sculpture, posterior collar and pronotal tubercle not distinct. Scu-

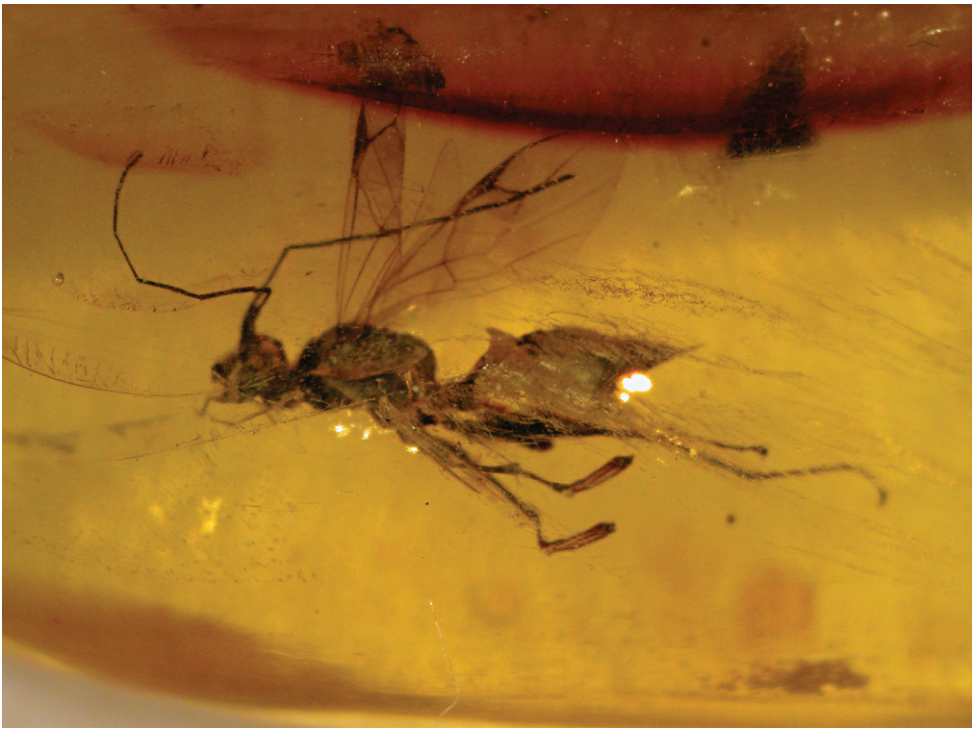

Figure 4. *Dryinus rasnitsyni*. Female holotype. Length 7.4 mm.

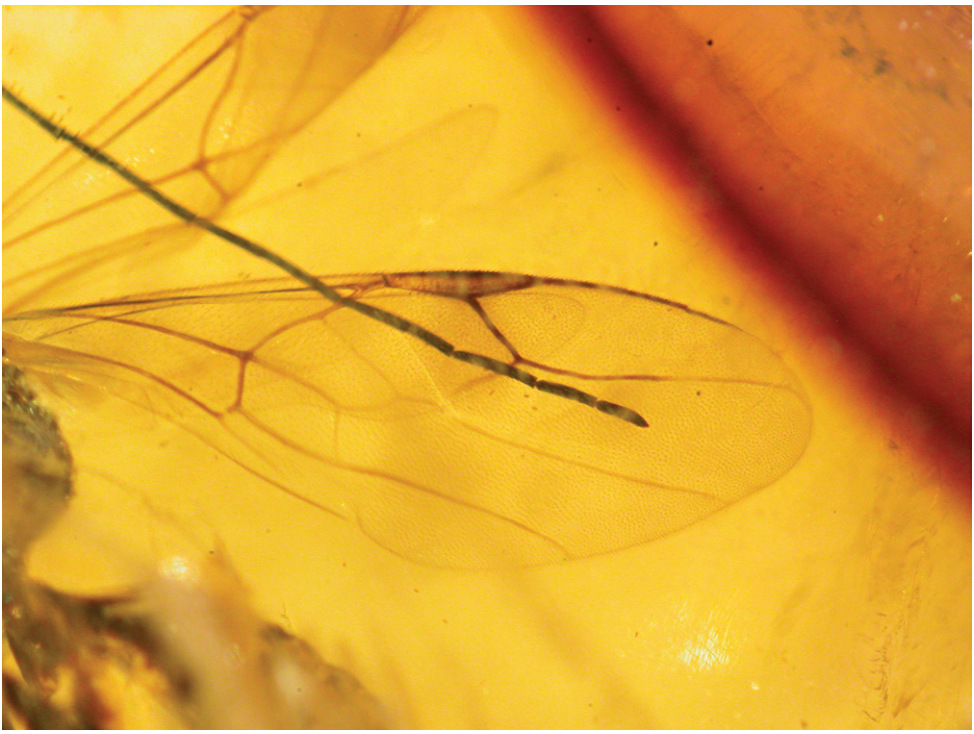

Figure 5. *Dryinus rasnitsyni*. Female holotype. Forewing.

tum apparently slightly longer than pronotum (9:8), with sculpture and notauli not distinct. Scutellum apparently shorter than scutum (4:9), with sculpture not distinct. Metanotum about as long as scutellum, with sculpture not distinct. Propodeum longer than scutum (15:9), with lateral regions reticulate rugose, with dorsal surface longer than posterior surface (10:5); sculpture of rest of propodeum and posterior surface not distinct. Shape of pronotum, scutum, scutellum, metanotum and propodeum apparently usual for Dryininae. Forewing (Figs 4, 5) completely weakly darkened, with usual venation of Dryininae; pterostigma narrow, much longer than broad (36:7); marginal cell open; distal part of stigmal vein longer than proximal part (34:18); stigmal vein very weakly S-shaped, forming angle between proximal and distal parts; forewing with usual three basal cells clearly enclosed by pigmented veins (costal, median and submedian cells). Hindwing completely weakly darkened. Foreleg segments in following proportions: 29 (coxa): trochanter not visible: 57 (femur): 46 (tibia): 27 (tarsal segment 1): 5 (tarsal segment 2): 8 (tarsal segment 3): 26 (tarsal segment 4): 46 (tarsal segment 5); foreleg chelate; enlarged claw slightly shorter than segment 5 of protarsus (42:46); protrochanter not distinct; segments 2 and 3 of protarsus produced into hooks; rudimentary claw present; arolium much shorter than enlarged claw (6:42). Enlarged claw (Fig. 6) spatulate, with large distal apex. Segment 5 of protarsus apparently with 1 or 2 rows of proximal and medial lamellae (number of lamellae not distinct); distal apex

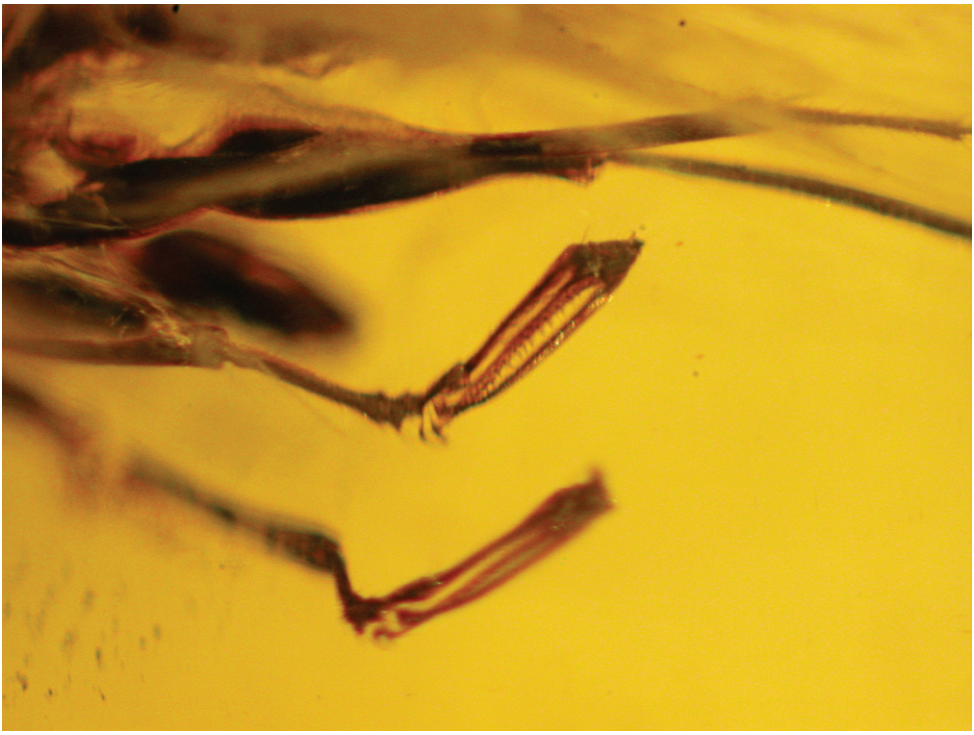

Figure 6. *Dryinus rasnitsyni*. Female holotype. Forelegs.

with a group of few lamellae (number of lamellae not distinct). Midleg segments in following proportions: 18 (coxa): 10 (trochanter): 62 (femur): 70 (tibia): 31 (tarsal segment 1): 13 (tarsal segment 2): 9 (tarsal segment 3): 4 (tarsal segment 4): 8 (tarsal segment 5). Hindleg segments in following proportions: 20 (coxa): 12 (trochanter): 87 (femur): 88 (tibia): 36 (tarsal segment 1): 16 (tarsal segment 2): 12 (tarsal segment 3): 7 (tarsal segment 4): 13 (tarsal segment 5). Metasoma with a short petiole. Shape and length of petiole usual for Dryininae. Shape, length and breadth of wings usual for Dryininae. Shape of body usual for Dryininae. Tibial spurs 1/1/2.

Male: unknown.

Etymology. The species is named after Dr. Alex Rasnitsyn.

Hosts. Unknown.

Remarks. In the holotype the head is partly crushed; the clypeus and mandible are only partly visible in lateral view so that it is not possible to count the number of teeth of the mandible and to see if the anterior margin of the clypeus is rounded or bidentate; the ocelli are only partly visible in lateral view and it is not possible to measure POL, OL, OOL and OPL; the temple is not distinct; the pronotum is only partly visible because of crushing; the scutum, scutellum, metanotum and propodeum are only visible in lateral view; both chelae are closed, so that it is not possible to see if the enlarged claw has lamellae and teeth.

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RESEARCH ARTICLE

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A new Late Cretaceous family of Hymenoptera, and phylogeny of the Plumariidae and Chrysidoidea (Aculeata)

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Abstract

The taxonomic placement of an enigmatic species of wasp known from two specimens in Late Cretaceous New Jersey amber is investigated through cladistic analyses of 90 morphological characters for 33 terminals ranging across non-Aculeata, non-Chrysidoidea, most subfamilies of Chrysidoidea and all genera of Plumariidae (the family to which the fossils were initially assigned), based on use of exemplars. The fossil taxon is apparently basal in Chrysidoidea, most likely sister to Plumariidae, but perhaps sister to the remaining chrysidoids, or even sister to Chrysidoidea as a whole. It is described as representing a new family, Plumalexiidae **fam. n.**, containing a single species, *Plumalexius rasnitsyni* **gen. et sp. n.** Previous estimates of relationships for the genera of Plumariidae and for the higher taxa of Chrysidoidea are mostly confirmed. The importance of outgroup choice, and additivity and weighting of characters are demonstrated.

Keywords

amber; fossil; Plumalexiidae; *Plumalexius rasnitsyni*; new genus; new species; classification

Introduction

The phylogeny of the Hymenoptera, and particularly the Aculeata, has recently been investigated critically by several authors (Brothers 1999; Ronquist 1999; Ronquist

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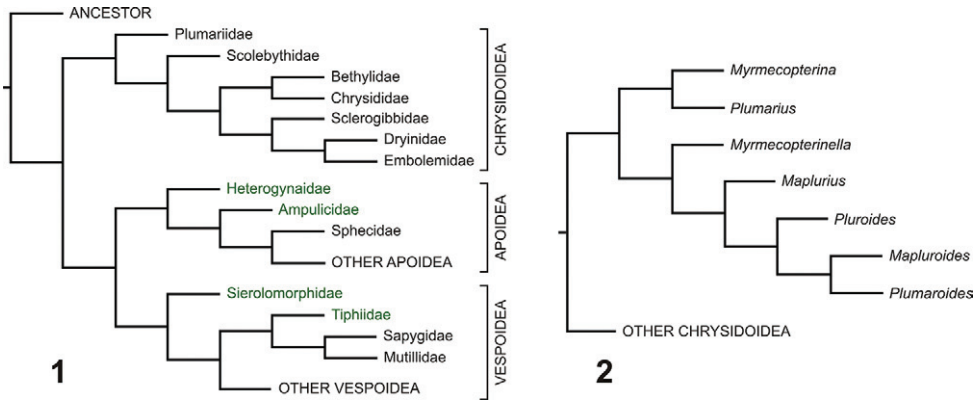
et al. 1999; Sharkey 2007; Davis, Baldauf and Mayhew 2010; Heraty et al. 2011). Generally, recent authors agree that the Aculeata is monophyletic and comprises two monophyletic lineages, the Chrysidoidea and the (Apoidea + Vespoidea), the latter group sometimes called the "Aculeata sensu stricto (s.str.)". All also agree that the Plumariidae is the sister group of the remaining Chrysidoidea (see also Carpenter 1999). This paper concentrates on the Chrysidoidea, and the relevant relationships so far established are shown in Figure 1.

As chrysidoids, plumariids are very unusual morphologically, the males having broad wings with a relatively rich wing venation including well developed accessory veins in the apical membrane similar to those of many of the very distantly related Mutillidae (Vespoidea) and Heterogynaidae (Apoidea) (the latter consequently mistakenly assigned to Plumariidae by Brothers 1974), and the females being wingless with the thorax highly modified (in particular with the propleura fused into a tube and a deep ventral constriction at the base of the laterally expanded metathorax-propodeum). No females have been directly associated with males and the correspondence is putative although very strongly supported on distributional and morphological grounds (Evans 1967; Brothers 1984). (The supposed female of *Plumaroides tiphlus* Diez, 2008 is actually a member of the genus *Pseudisobrachium* Kieffer, Bethylidae, according to Quintero and Cambra 2010.) Plumariids occur in the more arid regions of the southern hemisphere, the males often being attracted to lights and the females having been collected under stones or in pitfall traps, but nothing further is known of their biology. There are seven modern genera: *Plumarius* Philippi, 1873, *Plumaroides* Brothers, 1974, *Maplurius* Roig-Alsina, 1994, *Mapluroides* Diez, Fidalgo and Roig-Alsina, 2007 and *Pluroides* Diez, Roig-Alsina and Fidalgo, 2010 from South America, and *Myrmecopterina* Bischoff, 1914 and *Myrmecopterinella* Day, 1977 from southern Africa. Phylogenetic analyses of generic relationships within the family (Roig-Alsina 1994; Carpenter 1999; Diez, Roig-Alsina and Fidalgo 2010) have shown that each southern African genus is most closely related to one or more of the South American genera rather than their being most closely related to each other (Figure 2). The distribution is unusual and putatively Gondwanan, with each of the two primary lineages occurring on both continents and therefore probably having arisen before the breakup of Gondwana. There are no records from the other major Gondwanan continent, Australia, nor from India or the Middle East (other Gondwanan derivatives with arid environments) however.

Within the Chrysidoidea, the family which apparently arose next (after the Plumariidae had diverged) is the Scolebythidae (see Figure 1). This also has a putatively Gondwanan distribution, based on modern representatives, with *Pristapenesia* Brues, 1933 in the neotropics, *Clystopsenella* Kieffer, 1911 in the neotropics and Australia, *Ycaploca* Nagy, 1975 in South Africa, Australia, Fiji, New Zealand and New Caledonia, and *Scolebythus* Evans, 1963 in Madagascar and South Africa (Engel and Grimaldi 2007; CSIRO 2011; Brothers *pers. obs.*); the recent description of a species of *Pristapenesia* from Thailand and China (Oriental and Palaearctic regions) (Azevedo, Xu and Beaver 2011) has cast doubt on the validity of the previous statement, though. Again, the closest relationships are between genera separated by long distances, with



Figures 1–2. Previous estimates of relationships. **1** Aculeata, superfamilies, and families of Chrysidoidea (modified from Brothers 1999); aculeate taxa used as outgroup for analysis shown in green **2** Genera of Plumariidae (redrawn from Diez, Roig-Alsina and Fidalgo 2010)

Clystopsenella and *Scolebythus* being sister groups, as are *Ycaploca* and *Pristapenesia*, as shown by Engel and Grimaldi (2007). However, fossil species of Scolebythidae (including two *Pristapenesia*) have been found in Early Cretaceous Lebanese amber, Late Cretaceous New Jersey amber, Eocene French amber, Eocene Baltic amber and Miocene Dominican amber (Engel and Grimaldi 2007), demonstrating that the family was much more widespread in the past. Strikingly, the fossil members generally are more derived with more reduced wing venation than most modern members. The other ("higher") families of Chrysidoidea are all also known from fossils, in each case, as for Scolebythidae, the earliest being from the Early Cretaceous (see Engel and Grimaldi 2006; Rasnitsyn 2010; Ortega-Blanco, Delclòs and Engel 2011).

No fossil Plumariidae have yet been described, but two conspecific male specimens from Late Cretaceous New Jersey (USA) amber were recently stated to be members of the family (Rasnitsyn in Grimaldi, Shedrinsky and Wampler 2000; Brothers and Rasnitsyn 2000a,b) and this interpretation has been incorporated in some general accounts (e.g. Rasnitsyn 2002: 244, 2010), although some others (e.g. Grimaldi and Engel 2005: 430; Engel and Grimaldi 2006; Quintero and Cambra 2010) have reflected my subsequent view (Brothers 2003, 2004) that they may represent a new family. The long setae on the flagellomeres, reduced pronotum, large propleura and broad wings with a large pterostigma are particularly reminiscent of Plumariidae, although none of these features is unique to that family. The specimens differ from all modern male plumariids in having much simpler wing venation, lacking the accessory veins and with the second submarginal cell broadly sessile anteriorly, a much smaller anal (vannal/plical) lobe on the hind wing, the clypeus simple, the mandible truncate and four-toothed, the metanotum short and the mesopleuron less swollen. Preliminary analyses using the characters and taxa from Brothers and Carpenter (1993) had indicated their placement in Chrysidoidea (Brothers *pers. obs.*), but a more focused study in the context of the Chrysidoidea as a whole is required to establish their true relationship, and

coincidentally confirm or refute existing estimates of the relationships of the chrysidoid families. As reported and discussed below, it is concluded that they represent not only a new genus and species, but are indeed most appropriately allocated to a new family.

Materials and methods

The two amber pieces (Figures 3–4), each embedded in epoxy as described by Nascimbene and Silverstein (2000), were studied using standard methods and illustrated using stacked photographs taken with a Canon Powershot G10 digital camera adapted to Wild M7 and Wild M11 microscopes using a Clearshot 600 adapter kit (Alexis Scientific) and combined with CombineZP software (Hadley 2010). Drawings were done using a drawing tube and a Wild M8 microscope and subsequently digitised and corrected with reference to photographs, using CorelDraw X4. As with all fossils, some character states were not absolutely clear, but the most-probable states inferred (as explained in the species description) are those used in the analyses; if such states could not be inferred then they are coded as unknown. The specimens used for the analyses are listed in Appendix A. Terminology has been adapted from previous relevant studies.

Previous cladistic analyses of the Chrysidoidea and Plumariidae (e.g. Brothers, 1999; Carpenter 1999; Diez, Roig Alsina and Hidalgo 2010) have all rooted the trees using hypothetical ancestors with all-primitive states, based on comparisons with either Aculeata s.str. or other chrysidoids, and have utilised groundplans. For this analysis I used exemplars of the various taxa, both outgroup and ingroup, and thus made no a priori assumptions about probable direction of state changes, and thereby also included estimates of polymorphisms. Exemplars rather than groundplans were utilised, as advocated by Prendini (2001), but scorings for individual specimens were often combined to produce "summary" terminals with specified polymorphisms (see Table 1) rather than maintaining them as separate terminals. Since Chrysidoidea is the sister group of Aculeata s.str. (a clade with more-derived states for many characters, as shown by previous analyses), using only members of Aculeata s.str. as outgroups may have been misleading. In addition to other aculeates, I therefore included specimens representing various non-aculeate taxa which have previously been suspected as close relatives of Aculeata (Ichneumonidae, Trigonalidae and Evanioidea). Separate analyses were done using only Aculeata s.str. representatives as outgroup (similar to the approach of Carpenter 1999) and using the expanded outgroup to investigate the influence of using more- or less-distant taxa as outgroups. For the ingroup, in addition to the two fossil specimens, specimens of all genera of Plumariidae and most subfamilies or (for the smaller families) genera of the other families of Chrysidoidea were examined (Appendix A). In all cases, only males were used since we have no idea what the females of the fossil taxon were like, and there is often considerable sexual dimorphism in chrysidoids and aculeates in general. In a few cases states were derived from or checked in the literature (e.g.,

Olmi 1984, 1995, 2005; Gauld and Bolton 1988; Kimsey and Bohart 1990; Brothers and Carpenter 1993; Finnamore and Brothers 1993; Huber and Sharkey 1993; Prentice, Poinar and Milki 1996; Brothers and Janzen 1999; Terayama 2003b) specially where the condition of the specimens caused uncertainty, or states were scored as unknown ("?") for taxa where I had only one or two specimens which could therefore not be dissected. The 90 characters used (see Appendix B) were chosen from those used in previous analyses for plumariid genera, chrysidoid families and aculeates in general, as well as a few newly discovered. The range of characters was thus greater than used in previous analyses.

Parsimony analyses by TNT (Goloboff, Farris and Nixon 2008a, b) were performed using the default settings unless otherwise noted (traditional search, 10 000 replications, tree memory 100 000 trees); implied weighting was implemented using various values of k but only those for $k = 2.5$ are reported (this seems to be a reasonable value for the size of the matrix and level of homoplasy found, see Goloboff et al. 2008). Where several most-parsimonious cladograms (MPCs) were found, only the strict consensus is reported. WinClada (Nixon 2002) was used for tree analysis and drawing; branch lengths reflect optimisation of unambiguous states only, with branches unsupported by such states collapsed. In addition to analyses where most characters were considered to be additive (as shown in Appendix B), analyses were also done considering all characters non-additive to investigate the effects of removing all hypotheses of evolutionary direction. Relative group support for all analyses, using GC values which are frequency differences (Goloboff et al. 2003), was estimated by symmetric resampling using TNT (new technology search using ratchet, drift and tree fusing, 10 000 replications, tree memory 100 000 trees).

Systematic palaeontology

Family Plumalexiidae Brothers, fam. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Plumalexiidae

Type genus. *Plumalexius* Brothers, new genus.

Diagnosis. Male. Pronotum forming a short convex band reaching tegula; propleura closely associated, anterodorsally exposed as a short neck, posteriorly swollen and transversely truncate; prosternum short and scarcely exposed medially; mesopleuron large and swollen; metasternum somewhat depressed. Forewing with pterostigma very large, seven closed cells (costal, basal, subbasal, marginal, first and second submarginals, first discal), second submarginal cell with long anterior margin, no accessory veins in apical membrane. Hind wing with closed cells (basal and subbasal at least), anal (vannal/plical) lobe well developed; jugal lobe absent. Coxae subglobose, trochanters inserted apically.

Female. Unknown.

Genus *Plumalexius* Brothers, gen. n.
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Plumalexius

Type species: *Plumalexius rasnitsyni* Brothers, new species

Etymology: The genus name, which is masculine, is derived from "Plumariidae", to which it was first assigned, and "Alexandr", the first name of Professor Dr Rasnitsyn, honoured in this Festschrift.

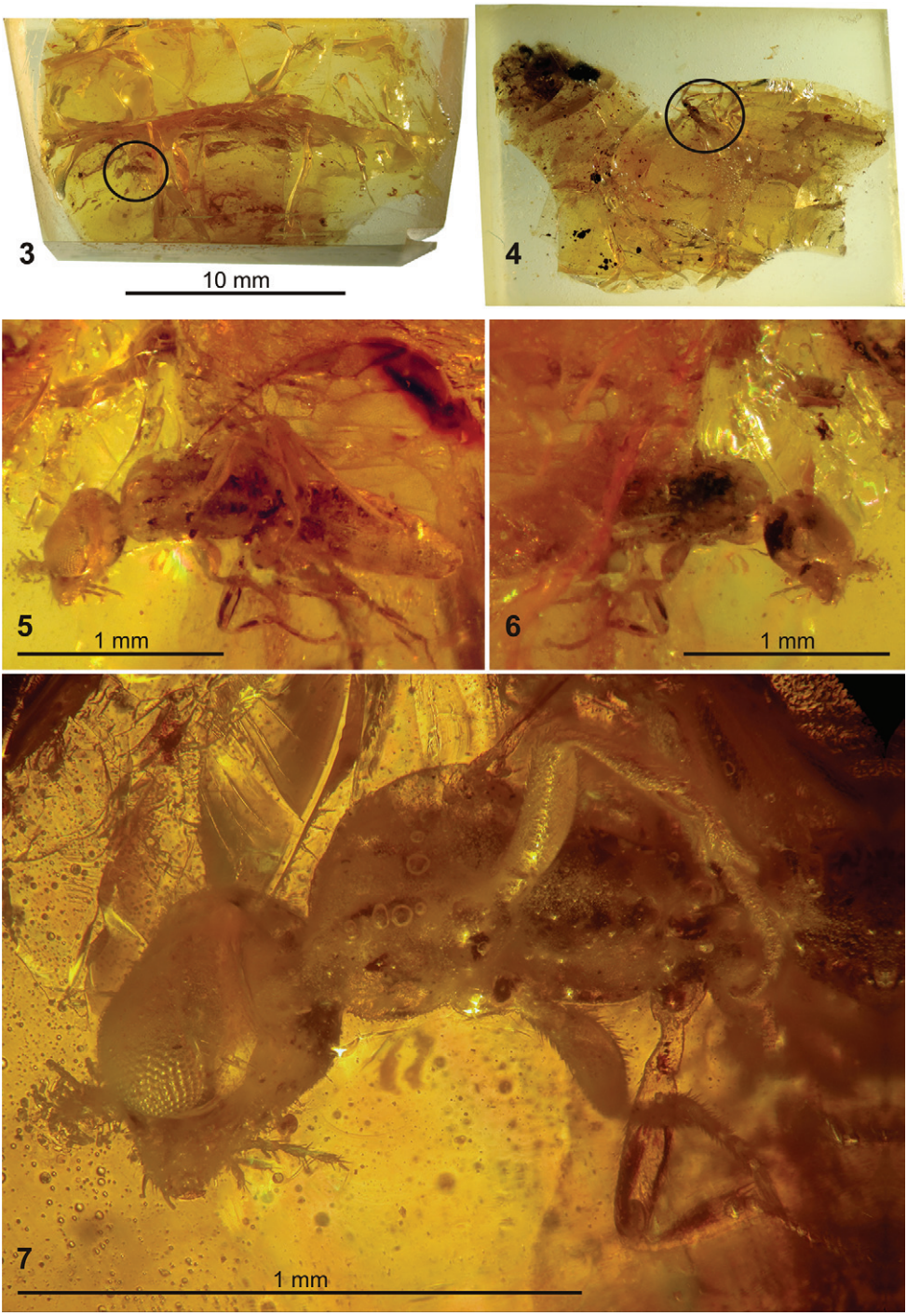
Diagnosis: Male. Compound eye oval with convex inner margin; antenna with many long fine erect setae (number of antennomeres unknown); mandible with four apical teeth along truncate apical margin; maxillary palp at least 5-segmented; labial palp at least 3-segmented. Pronotum much shorter than mesoscutum, with slight anterior collar (flange) and posteroventral angle rounded; mesoscutum transverse; notaulus distinct, complete; tegula small, convex; metapostnotum apparently about as long as metanotum; propodeum long, weakly constricted apically; meso-metapleural suture straight. Hind wing with two closed cells, vein C present only basally, anal (vannal/plical) lobe less than half length of wing. Tibiae without spines or strong setae; tibial spurs 1–2–2; basitarsomeres much longer than other tarsomeres; arolia large; claws simple. Metasoma ovoid, sessile basally, apical tergum apparently simple, seventh sternum reduced, hypopygium simple with convex apex.

Female. Unknown.

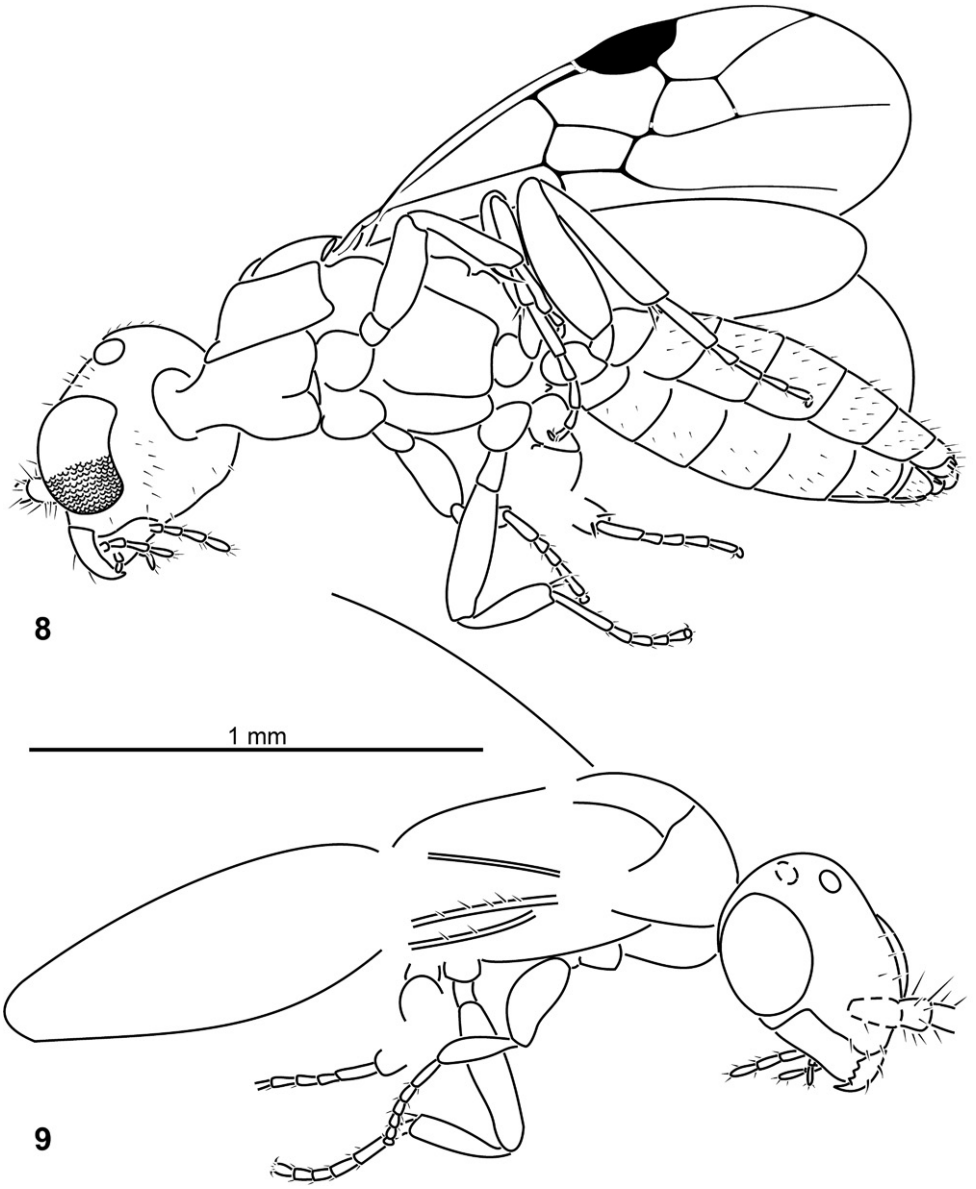
***Plumalexius rasnitsyni* Brothers, sp. n.**
urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Plumalexius_rasnitsyni
Figs 3–13

Type material: Holotype male (Figures 3, 5–9), in heavily fractured block of yellowish amber embedded in a trapezoidal epoxy matrix about 22 × 10 × 7 mm, with labels as follows: "NEW JERSEY Amber: / Late Cretaceous / NEW JERSEY: Middlesex Co / Sayreville, White Oaks Pit / 1995, coll.Paul Nascimbene / AMNH no. NJ-695", "NEW JERSEY Amber: / Late Cretaceous / AMNH no. NJ-695 / HYMENOPTERA:", "Plumariidae" [Rasnitsyn's handwriting], "HOLOTYPE / Plumalexius / rasnitsyni ♂ / D.J. Brothers, 2011" [red label, printed].

Paratype male (Figures 4, 10–13), in heavily fractured block of yellowish amber embedded in a rectangular epoxy matrix about 18.5 × 13.5 × 9 mm, with labels as follows: "NEW JERSEY Amber: / Late Cretaceous / NEW JERSEY: Middlesex Co / Sayreville, White Oaks Pit / 1995, coll.Paul Nascimbene / AMNH no. NJ-175", "NEW JERSEY Amber: / Late Cretaceous / AMNH no. NJ-175 / HYMENOPTERA: / Family? (PN-2a) / Plumariidae" [Rasnitsyn's handwriting], "?Family / Det. L. Masner 1996", "PARATYPE / Plumalexius / rasnitsyni ♂ / D.J. Brothers, 2011" [yellow label,



Figures 3–7. New Jersey amber containing specimens of *Plumalexius rasnitsyni* sp. nov. **3** Specimen NJ-695, holotype (circled) **4** Specimen NJ-175, paratype (circled) **5–7** Specimen NJ-695, holotype **5** Ventrolateral view **6** Dorsolateral view **7** Detail, ventrolateral view.

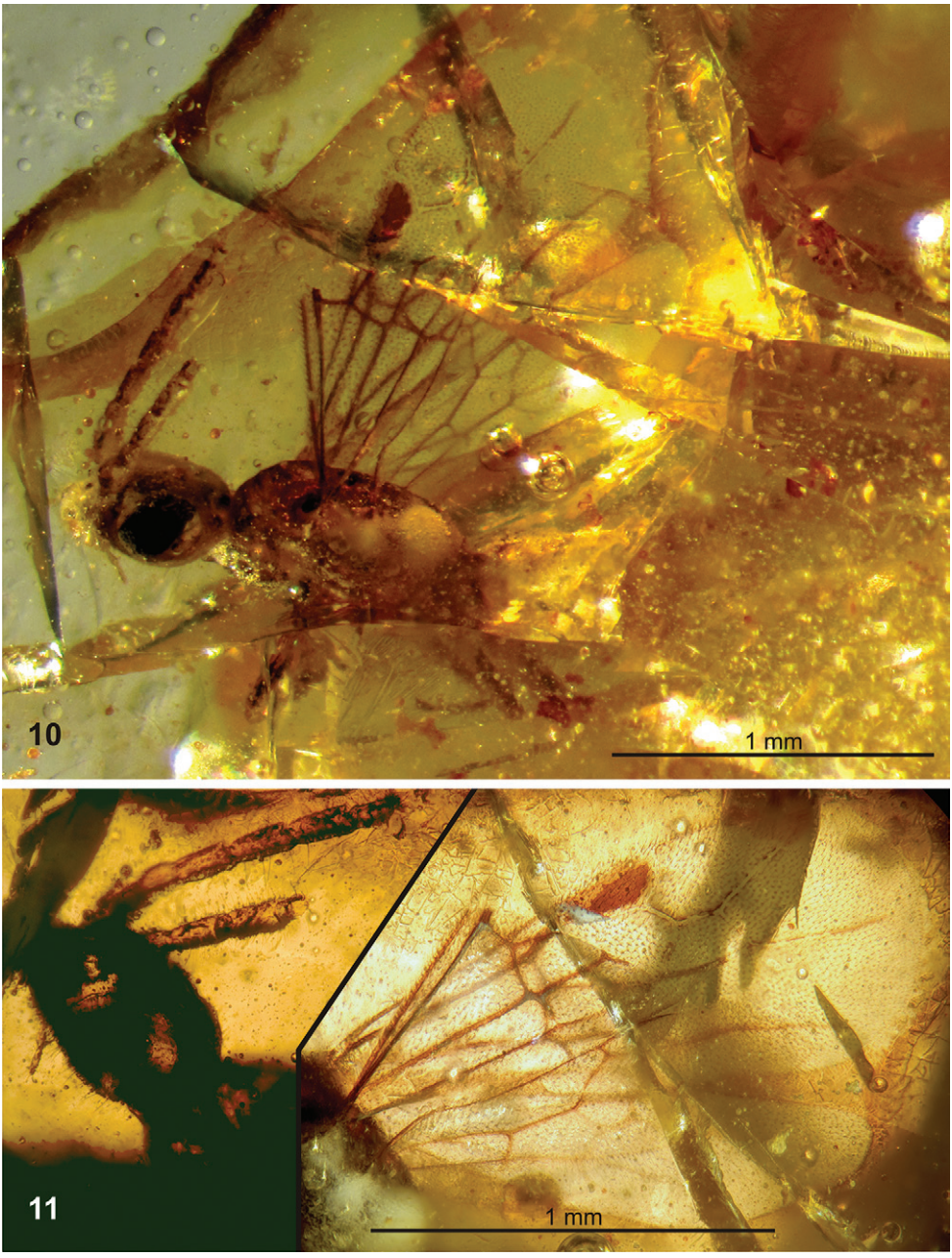


Figures 8–9. *Plumalexius rasnitsyni* sp. nov., holotype. **8** Ventrolateral view **9** Dorsolateral view.

printed]. (This specimen is presumed to be a male because of its similarity to the holotype even though the metasoma is mostly not visible.)

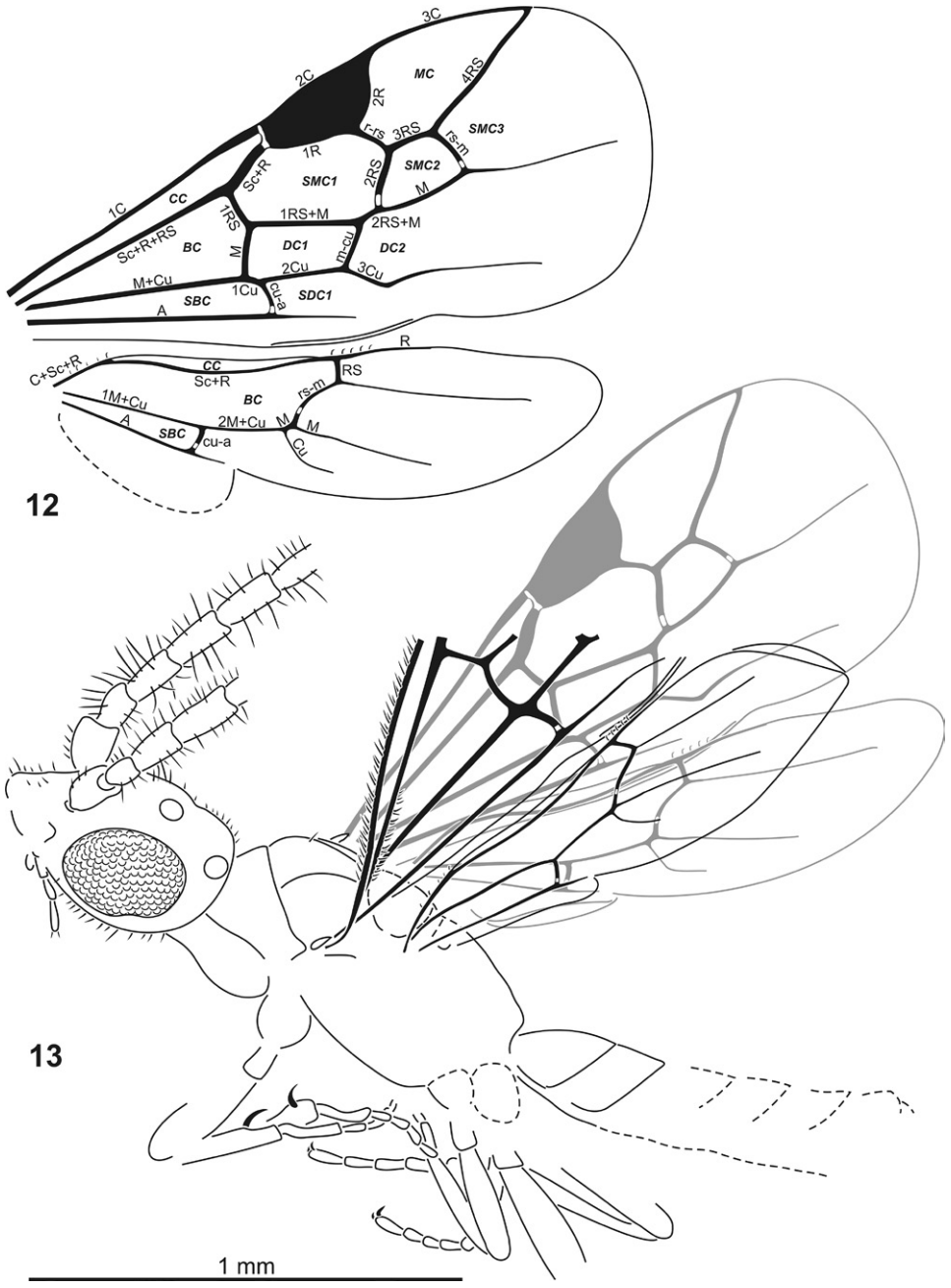
Etymology: The species name, a noun in the genitive case, honours Professor Dr Alexandr Rasnitsyn, who first recognised the significance of the specimens.

Description (based on holotype, paratype data in parentheses where different or feature not visible in holotype): **Male.** Entirely pale yellowish (reddish) brown with venation slightly darker. Head and body length as preserved 2.03 (2.37) mm; estimated



Figures 10–11. *Plumalexius rasnitsyni* sp. nov., specimen NJ-175, paratype. **10** Dorsolateral view **11** Details, dorsolateral view.

head length 0.24 (0.29) mm; estimated mesosoma length 0.80 (0.77) mm; estimated metasoma length 0.90 (0.89) mm; approximate forewing length 1.32 (1.46) mm; approximate hindwing length 1.03 (1.17) mm. Head and metasoma with scattered fine



Figures 12–13. *Plumalexius rasnitsyni* sp. nov. **12** Wings, based on both specimens **13** Paratype, dorsolateral view, right wings in grey. Abbreviations. Wing veins: A = anal, C = costa, Cu = cubitus, M = media, R = radius, RS = radial sector, Sc = subcosta (numerals indicate abscissae, all lower-case indicates crossveins); cells: *BC* = basal cell (cell R), *CC* = costal cell (cell C), *DC* = discal cell (cells 1M, 2M), *MC* = marginal cell (cell 2R1), *SBC* = subbasal cell (cell 1Cu), *SDC* = subdiscal cell (cell 2Cu), *SMC* = submarginal cell (cells 1R1, 1Rs, 2Rs).

short erect setae, mesosoma almost glabrous, antennal pedicel and flagellomeres with fine long erect setae; legs with dense recumbent setae and scattered semi-erect setae.

Head: Hypognathous; about as wide as high; vertex evenly rounded. Eye ovate with convex inner margin, moderately protuberant, apparently glabrous, ommatidia distinct. Ocelli ovate, large. Occipital carina distinct. Frons and clypeus weakly convex; clypeus transverse with convex anterior/apical margin. Gena simple. Antennal sockets simple, apparently about as close to eyes as to each other, apparently close to posterior/dorsal margin of clypeus. Antennal scape about as long as wide (distinctly flattened posterolaterally and broadened towards apex), with several erect setae; pedicel (about half length of scape and of first flagellomere), with many fine long erect setae; (flagellomeres 1–4 becoming slightly longer sequentially, with many fine long erect setae). Mandible long, evenly broad and curved; two prominent short curved setae on lateral surface; apex truncate with four similar sharp teeth, apical tooth the longest. Maxillary palp at least 5-segmented; labial palp at least 3-segmented [palp bases concealed by foam but segmentation inferred from assumed points of origin].

Mesosoma ovate, about twice as long as wide/high. Pronotum forming a curved oblique ribbon anterolateral to mesoscutum, broader medially than posterolaterally; posterodorsal margin evenly concave; posterolateral margin strongly emarginate and approaching tegula dorsally; posteroventral angle broadly rounded; anteroventrally with slight collar (flange) but leaving propleura exposed anteriorly. Propleura closely associated or fused; anteriorly produced as a short neck; swollen posteriorly; posterior margin apparently almost straight but exposing small part of prosternum medially; forecoxae approximated. Mesoscutum shorter than wide, moderately convex; notaulus distinct and complete, weakly diverging anteriorly; tegula small and convex. (Mesoscutellum apparently almost as long as scutum, weakly convex.) Mesopleuron large and convex; meso-metapleural suture distinct, almost straight. Mesosternum with posteromedial margin almost straight and apparently slightly overhanging mesocoxal base; mesocoxae slightly separated. (Metanotum short and transverse, flattened, not constricted medially. Metapostnotum apparently as long as metanotum, slightly depressed.) Metasternum apparently somewhat depressed. Metacoxae slightly separated. Propodeum slightly longer than mesoscutum, weakly convex but more strongly so posteriorly although without any defined posterior declivity; incision between mesosoma and metasoma weak.

Forewing broad, about 2.2 × as long as wide, about 1.7 (1.8) × as long as mesosoma, with seven closed cells, veins approaching but not reaching margin. Costal cell well developed, broad. Pterostigma large, about 0.19 × as long and 0.17 (0.20) × as wide as wing, entirely sclerotised. Marginal cell about 2.38 (2.17) × as long as wide, 1.41 (1.52) × as long as pterostigma, apex acute. First submarginal cell about 2.08 (2.61) × as long as wide, 0.81 (0.80) × as long as marginal cell. Second submarginal cell almost as large as pterostigma, broadly sessile anteriorly, about 0.64 (0.57) × as long as first submarginal cell. Veins tubular except for nebulous free apical sections of M, Cu and A. No trace of any accessory vein(s) in apical membrane. Prestigmal vein (Sc+R) scarcely swollen, about 1.33 (1.37) × as long as vein 1Rs. Crossvein cu-a distinctly

postfurcal, about 1.33 (1.75) × as long as 1Cu. Vein Cu2 absent, first subdiscal cell broadly open apically.

Hind wing about 0.8 × as long as forewing. (Basal and subbasal cells closed by tubular veins; costal cell open anteriorly, vein C present only basally. Veins tubular except for nebulous free apical sections of Rs, M, Cu and A. A few basal hamuli present in a cluster; about five apical hamuli. Crossvein rs-m long, about 2.67 × as long as 1Rs. Vein 1M very short, about 0.13 × as long as 2M+Cu. Crossvein cu-a distantly antefurcal, 2M+Cu about 0.57 × as long as 1M+Cu. Anal (vannal/plical) lobe apically delimited by moderate incision, lobe about 1.19 × as long as submedian cell, about 0.4 × as long as wing.) Jugal lobe absent.

Legs well developed, moderate in size; trochanters well developed and cylindrical; no trochantelli; tibiae without any spines or strong setae; basitarsomeres long, about as long as next three tarsomeres combined; all arolia large and flattened; claws simple ventrally. Foreleg with coxa subglobose, trochanter inserted apically; femur slightly swollen, with inner/anterior surface flattened; tibia with simple, weakly curved, bladelike calcar subapically. Mid- and hind legs with coxae globose, hind coxa somewhat larger than mid-coxa; tibiae each with two straight simple apical spurs, inner spur somewhat longer than outer.

Metasoma elongate oval, about 2.6 (indeterminable in paratype) × as long as wide/high; terga subequal in length. First tergum broad, weakly contracted toward base, profile evenly merging with second. First sternum apparently simple and evenly overlapping second. Seventh tergum apparently simple with apical margin convex. Seventh sternum apparently reduced and mostly concealed. Hypopygium simple, weakly convex, with narrowly rounded apical margin. Cercus apparently present, cylindrical. Genitalia with paramere apparently broadly rounded apically.

Female. Unknown.

Results and discussion

Table 1 shows the distribution of character states across the taxa.

The cladograms resulting from the analyses using an aculeate outgroup (illustrated using Anthoboscinae, but the relationships within the Chrysidoidea were not affected by changing this to any of the other three aculeates) are shown in Figures 14–17. The consensus tree from the "equally weighted additive" analysis (Figure 14) shows Chrysidoidea as monophyletic, all chrysidoid families also as monophyletic (although with their relationships often not convincingly resolved, as shown by several apparent clades having no or very low relative resampling support), *Plumalexius* sister to Plumariidae (this clade sister to the remaining chrysidoids), and the plumariid genera with similar relationships to those found earlier (see Figure 2). In contrast, although the consensus tree from the "equally weighted non-additive" analysis (Figure 15) also shows Chrysidoidea as monophyletic, all chrysidoid families also as monophyletic (with their relationships even less resolved), and the same relationships for the plumariid genera,

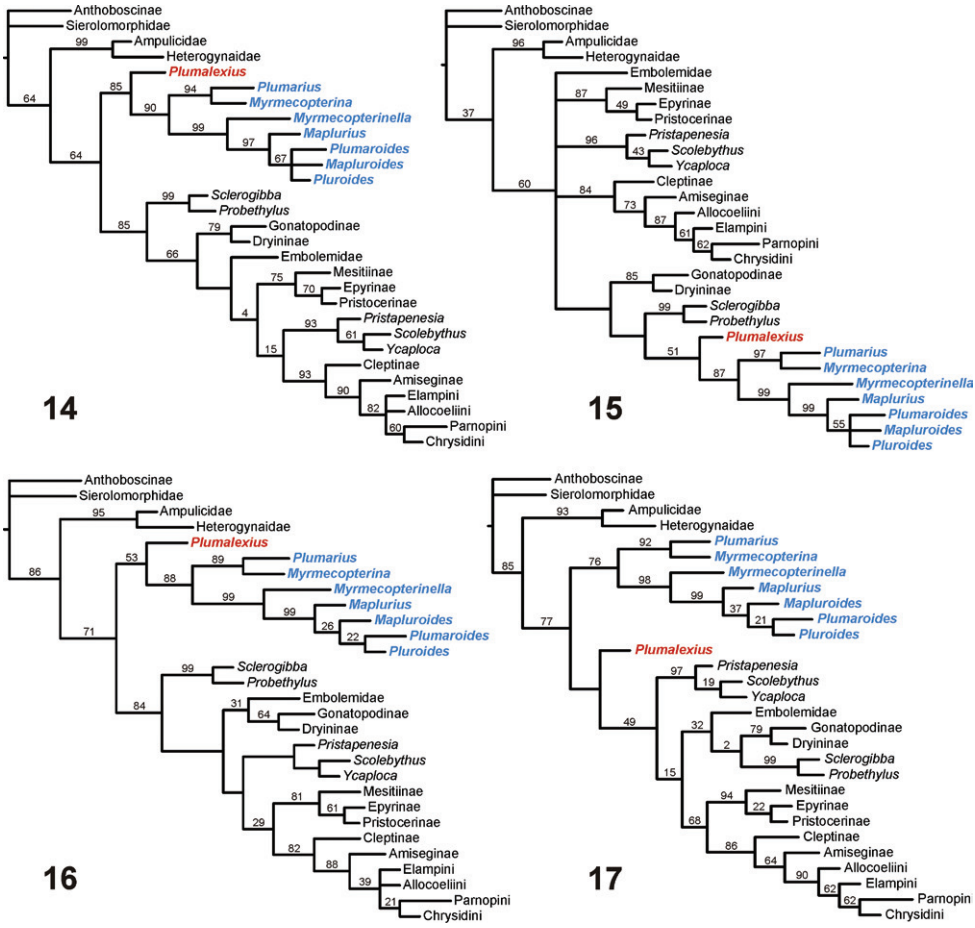
Table 1. Data matrix for analyses of relationships of members of Chrysidoidea.
(Specimens used shown in Appendix A, characters in Appendix B. Values between square brackets indicate polymorphisms.)

Characters	1 - 10	11 - 20	21 - 30	31 - 40	41 - 50	51 - 60	61 - 70	71 - 80	81 - 90
Taxa									
*Ichneumonidae	010100000[012]	000021000[01]	001[01]000202	000[01]1000[03]0	001[01]21[01]00[12]	[45]02?00010[12]	0[34]00000100	002001000[02]	0000000000
*Trigonalidae	1100010012	0000[01]01000	0010000202	0011100030	1000201001	000000000[01]	0301000100	0000000000	0000022200
*Evaniidae	0001100100	0000000001	0010100202	0011101033	5021011001	200-001103	1402100000	00000[01]0000	1000001020
*Gasteruptiidae	0211000100	0000100101	1100000202	0011211033	0011011001	620-000103	1412100100	0001000000	1000001020
Anthoboscinae	0110001112	0001200000	1002100100	1002100030	3300000001	0000000000	0400010000	0001020000	0000121001
Sierolomorphidae	111001111[02]	0001100000	1002100100	0001200012	3112000010	100-001001	1401000100	0011020000	0000002301
Ampulicidae	[01]110000110	0001200001	0000100011	1011120043	221[12]0101[01]1	0000000000	[01][04]01000[01]00	0[01]2[23]0[12]0004	010002[12]021
Heterogynaidae	0110000100	0001200001	0000100011	2011121043	2211010111	300-110100	1101010100	0023000004	0000020221
Plumalexius	1??0000?02	20100??100	1?0?1?0???	00001?001?	????1?0010	6100000011	1401010110	1023000000	0??001000?
Plumarius	0001100111	2131101101	1100100000	0000100111	4412211000	6101010011	0001010100	002201[01][01]03	0100010000
Plumaroides	0000011102	0001112220	1001111200	1000100120	3422211000	6101111010	1001011110	1123020000	011211100?
Myrmecopterina	0[12]10100111	2011101101	1100100000	0000100102	44[12][12]211000	6102110011	1001010110	1022011003	0101011000
Myrmecopterinella	0000001202	2001213200	0001111200	11001?1132	?411211010	620-011011	1301010110	0013220000	010001010?
Maplurius	0000011102	2121113220	1001111200	1000100120	3412211010	6101011011	1001011110	1122020010	010111020?
Mapluroides	0000011102	0001112220	1001121200	10000?0120	?411211000	6101011012	0001011110	1122020000	010111020?
Pluroides	0000011102	0001113210	1001111200	10001?0120	?411211000	6101011011	0001011110	1122020000	010211100?
Scolebythus	1110000100	2000000100	0020001000	1000101020	3301000011	620-001012	2222110111	0002000000	0100021020
Pristapenesia	1??0000100	0000[02]00100	00200010??	[12]0001?10??	?322000111	65[01]-00101?	2222110111	0002100000	0100010020
Ycaploca	1110000100	1000000100	0020001000	1000101020	3312000010	620-001012	2222110111	0012100000	0100021020
Mesitiinae	1130000122	20[01]0001000	0000100010	0011011032	4122010111	651-000012	2522110100	0021000004	0100020210
Epyrinae	111000012[02]	0000001000	0000100000	1011011032	4122010111	651-001111	2522110100	0021020004	0100010010
Pristocerinae	1[01][012]0000120	[02]0[01]0[02]01000	0000100000	101101[01]032	4122010111	651-001111	2522110100	0021020004	0100020210
Cleptinae	1000000100	0000111000	1010001000	0011110133	3122001111	651-001111	2211110100	0012000004	0100022020
Amiseginae	1110001100	0000221000	1010000010	0011210[01]33	4122001011	651-001011	1222110100	0013000003	0100022020
Elampini	1110001100	0001011001	1010000000	00111?0033	?222001011	65[01]-001110	1322110100	0013000004	0100022??0
Allocoeliini	111000?100	0001211001	1010000000	00111?0033	?222001011	651-001110	1222110100	0013000001	0?000222?0
Parnopini	111000110[02]	0001244001	1010001000	00111?0033	?[02]22001012	651-000112	1322110110	0113010004	0100022??0
Chrysidini	1110001100	0001211001	1010000000	0011[12]10[01]33	4[02]12001011	651-00111[013]	13[12][12]110110	0013000004	0100022020
Sclerogibba	0220001020	1001111100	1000100010	0011100022	5121110012	630-000012	2223110100	1022010002	0100010010
Probethylus	0220001020	1001132100	1000110010	0011100012	5121110012	630-000012	2223110100	1022010002	0100010010
Gonatopodinae	1220001310	10001[02][12]201	0010000000	0001100132	5022100010	650-001112	1423110110	1022100002	0100022020
Dryininae	1[12][12]0000310	1000101[12]01	0000100000	0011100132	5022[01]00010	650-001112	2523110100	1022100002	0100022020
Embolemidae	[01]1[12]1000300	[01]0000[123][12]001	0000120012	0011101[01]32	5[23]12100111	6[45][01]-00[01][01]1[012]	1423110110	0022000002	01000[12]1020

*Non-aculeate outgroup taxa excluded from some analyses (see text)

(*Plumalexius* + Plumariidae) now groups with Sclerogibbidae and Dryinidae, although without relative support. The consensus tree from the "implicitly weighted additive" analysis (Figure 16) shows similar relationships as the equally weighted version (Figure 14), except that there is slightly greater resolution for the families of Chrysidoidea and Scolebythidae is no longer sister to Chrysididae which is now monophyletic with Bethylidae, although some branches lack positive relative support values; there is also greater resolution for the plumariid genera. Similarly, the single MPC from the "implicitly weighted non-additive" analysis (Figure 17) produced improved resolution, showing (Bethylidae + Chrysididae) as monophyletic, but *Plumalexius* is grouped with the chrysidoids other than Plumariidae (although without positive relative branch support). The differences from previous analyses, most strikingly involving Scolebythidae and Sclerogibbidae (see Figure 1), are probably due to two factors: the use of exemplars instead of groundplans (introducing polymorphisms), and the position of the Aculeata s.str. outgroup taxa as relatively more derived than the Chrysidoidea.

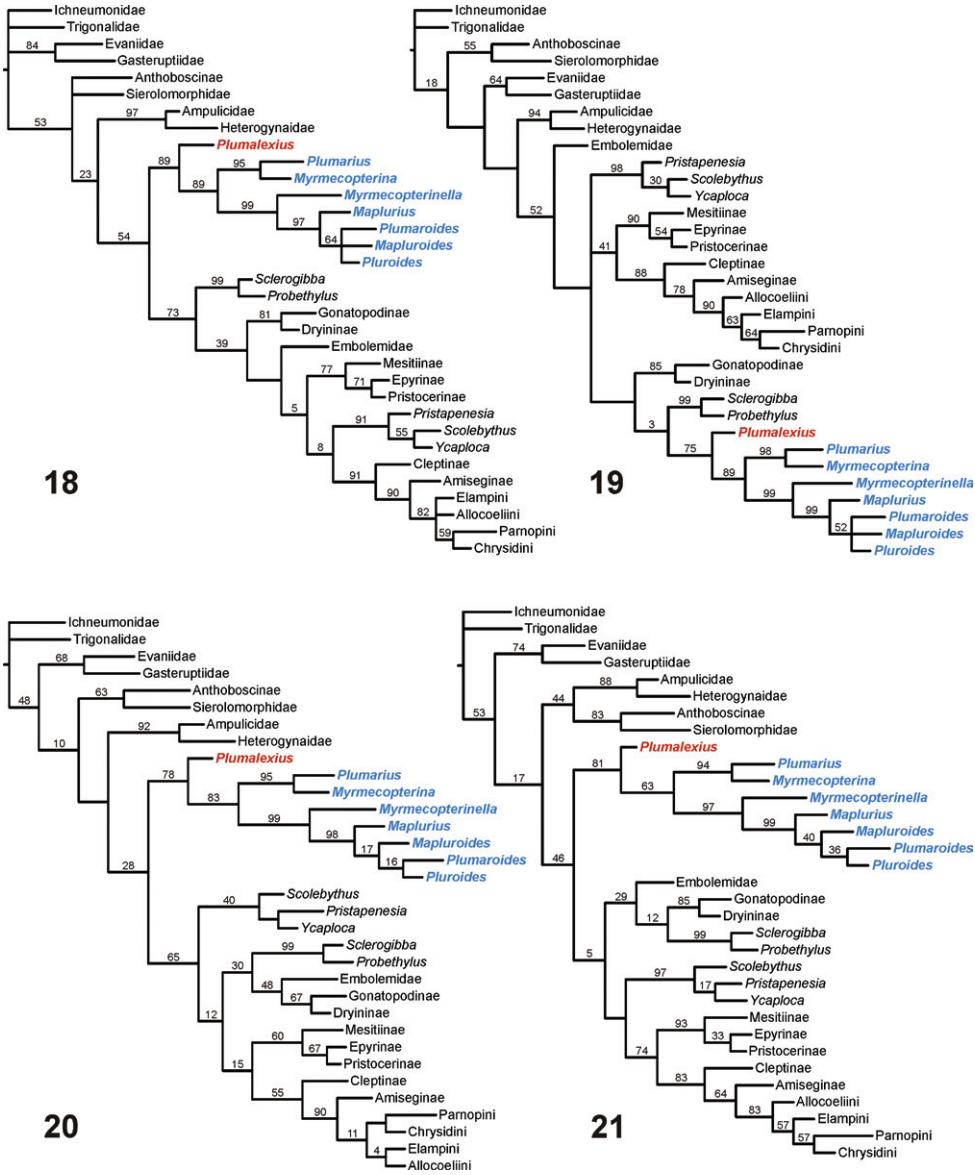
To try to address the second of the above concerns, analyses were done using four non-Aculeata as outgroup. The resulting cladograms (Figures 18–21) are presented with Ichneumonidae as outgroup, but using any of the other three non-aculeates made no difference to the relationships shown for the Chrysidoidea. The consensus tree from the "equally weighted additive" analysis (Figure 18) shows Chrysidoidea as monophyletic, all chrysidoid families also as monophyletic (but their relationships still sometimes unconventional), *Plumalexius* basal to Plumariidae (with high support), and the plumariid genera with similar relationships to those found earlier. Although the study was not intended to reflect the relationships amongst the outgroup taxa, it is interesting that Aculeata s.str. (Vespoidea and Apoidea) appears as paraphyletic in this analysis. The consensus tree from the "equally weighted non-additive" analysis (Figure 19) also shows Chrysidoidea as monophyletic (but with Embolemidae as basal), all chrysidoid families also as monophyletic but with most relationships very different from previous findings (except that Bethylidae and Chrysididae are well supported as monophyletic, and many of the family relationships have no positive relative branch support), with Plumariidae (and *Plumalexius* sister to it) appearing as most closely related to Sclerogibbidae and Dryinidae; the relationships for the plumariid genera remain consistent. Aculeata s.str. now appears as polyphyletic, with Evanioidea interpolated between Vespoidea and Apoidea. The single MPC resulting from the "implicitly weighted additive" analysis (Figure 20) is fully resolved, shows Chrysidoidea as monophyletic, all chrysidoid families as monophyletic, Plumariidae (and *Plumalexius* sister to it) as sister to the remaining chrysidoids, and the relationships of those families as found by previous analyses (see Figure 1); the relationships of the plumariid genera also agree with previous analyses (see Figure 2), except that *Plumaroides* appears as sister to *Pluroides* rather than *Mapluroides*. Aculeata s.str. is paraphyletic but with the apparent sister-group relationship of Apoidea to Chrysidoidea not supported (the resampling analysis instead showed a monophyletic Aculeata s.str. as supported with a value of 12). The "implicitly weighted non-additive" analysis also produced a single MPC (Figure 21) with a monophyletic Chrysidoidea, monophyletic chrysidoid families, *Plumalexius* sis-



Figures 14–17. Chrysidoidea relationships using Aculeata s.str. (Anthoboscinae) as outgroup **14** Characters equally weighted, some characters additive (strict consensus of 4 MPCs, raw lengths 383, CI = 0.41, RI = 0.71) **15** Characters equally weighted, all characters non-additive (strict consensus of 4 MPCs, raw lengths 349, CI = 0.45, RI = 0.71) **16** Characters implicitly weighted (k = 2.5), some characters additive (strict consensus of 2 MPCs, raw lengths 386, CI = 0.41, RI = 0.71) **17** Characters implicitly weighted (k = 2.5), all characters non-additive (1 MPC, raw length 352, CI = 0.44, RI = 0.70). Notes: *Plumalexius* shown in red, genera of Plumariidae shown in blue. Numbers are estimated GC branch-support values (see text); branches without numbers showed no positive support under the resampling protocol used.

ter to Plumariidae, and Bethylidae and Chrysididae forming a monophyletic group but apparently sister to Scolebythidae (but without relative branch support); relationships for the plumariid genera are the same as for the "additive" analysis. Aculeata s.str. is now monophyletic (with good support) and sister to Chrysidoidea (with some positive support). It is notable that the chrysidoid relationships shown are more similar to those for the "additive" analyses than those seen in the "unweighted non-additive" analysis.

At first sight, consideration of all of the above results, involving not only the placement of *Plumalexius* but even more the relationships amongst the other chrysidoids,



Figures 18–21. Chrysidoidea relationships using non-Aculeata (Ichneumonidae) as outgroup **18** Characters equally weighted, some characters additive (strict consensus of 12 MPCs, raw lengths 468, CI = 0.35, RI = 0.68) **19** Characters equally weighted, all characters non-additive (strict consensus of 4 MPCs, raw lengths 423, CI = 0.39, RI = 0.67) **20** Characters implicitly weighted (k = 2.5), some characters additive (1 MPC, raw length 473, CI = 0.35, RI = 0.68) **21** Characters implicitly weighted (k = 2.5), all characters non-additive (1 MPC, raw length 426, CI = 0.38, RI = 0.67). Note: *Plumalexius* shown in red, genera of Plumariidae shown in blue. Numbers are estimated GC branch-support values (see text); branches without numbers showed no positive support under the resampling protocol used.

has produced a slightly confused picture, perhaps not unexpected for a set of analyses using exemplars and considerable polymorphism, and also based on characters which have previously been used at very different levels. The limitation of having to exclude all characters restricted to females (many of which have proved extremely informative in previous analyses, and one of which, the presence of an articulation within gonocoxite IX, is probably the most significant unique synapomorphy for Chrysidoidea) has also had an effect. Nevertheless, it is gratifying that the results of most previous studies have been confirmed, or at least not convincingly contradicted. Accordingly, I consider that the cladogram which agrees best with those results, one using an expanded outgroup and additive characters, and derived using implied weighting (an approach advocated by Goloboff et al. 2008), should be considered the preferred current estimate of the relationships of the families of Chrysidoidea and the genera of Plumariidae. This is shown in Figure 22, elaborated and adjusted from Figure 20, with Aculeata s.str. shown as monophyletic (which increased the length of the tree by a single step) and the relationships of the tribes of Chrysidinae resolved to reflect that found (and supported) most often in all analyses (which did not alter the tree length). It must be noted that, although for each family some subfamilies, tribes and genera are also shown, and their apparent relationships often (but not always) agree with other recent studies (such as Carpenter 1999; Terayama 2003a; Engel and Grimaldi 2007; Carr, Young and Mayhew 2010), not all subfamilies or tribes are represented by exemplars, nor are all genera included (except for the Plumariidae), and the characters used did not necessarily include all those which have been found useful within all of the families, so these results are incomplete in that respect; the aim of including the exemplars used was to reflect the variation found within the families rather than to discover intra-family relationships (except for Plumariidae).

Plumalexius seems convincingly indicated as sister to the Plumariidae, although one analysis was ambiguous about this; trees with it placed as sister to the remaining chrysidoids or as sister to the Chrysidoidea as a whole differ in length from that shown in Figure 22 by only 4 and 5 steps respectively (lengths 478 and 479 compared with 474), emphasising its relatively basal position. It does not share any unique synapomorphies with Plumariidae, however (the five unambiguous states supporting the sister relationship to Plumariidae are 11-2: flagellomere setae conspicuous and erect; 21-1: pronotal posteroventral margin strongly concave; 45-1: metasternum weakly depressed anteromedially; 50-0: pterostigma large and prominent; and 87-0: hypopygium completely exposed or almost so, all states found elsewhere in relatively distantly related taxa). The long erect flagellar setae of *Plumalexius* and some Plumariidae have been indicated as a putative synapomorphy for the family (Rasnitsyn 2002: Fig. 331). The arrangement of the setae in *Plumalexius* is most similar to that in *Myrmecopterina*, although the setae are less dense and considerably longer in *Plumalexius*, but the present analysis has shown that other plumariid genera lack such setae and, conversely, they are also present in some Scolebythidae and Bethylidae at least; prominent flagellomere setae are actually found widely in the Chrysidoidea. The other most obvious similarity, more extensive venation in both wings than in other chrysidoids, is a symplesiomorphy.

Figure 22. Preferred cladogram of families of Chrysidoidea and genera of Plumariidae (raw length 474, CI = 0.35, RI = 0.68) showing only unambiguous character-state changes. Notes: open hashmarks indicate homoplasious states, black hatchmarks indicate unique states; character numbers above, state numbers below (polymorphisms separated by commas).

It is thus evident that there is no key apomorphy associating *Plumalexius* with the Plumariidae sufficient to assign it to that family. Were that to be done, the expanded family would lose its present defining features, such as the presence of apical accessory

veins in the wing membrane, the reduced second submarginal cell and the tapered mandibles with few apical teeth. In view of this, I conclude that the best solution is to propose a new family for it, as has been done above, something which also emphasises its distinctiveness. In contrast to the specialised morphology of Scolebythidae, showing several adaptations enabling the effective parasitisation of wood-boring beetle larvae, the morphology of *Plumalexius* provides little clue as to its biology, specially since the female is unknown. The male looks like a very generalised wasp, probably very similar to the form ancestral to Chrysidoidea as a whole.

Apart from the above results, the variety of analyses performed has shown that the use only of an outgroup which is sister to the ingroup, and which may have many characters with relatively more-derived states than the ingroup, may produce misleading or ambiguous results (Figs 14–17 all show different relationships from the preferred result). Instead, the outgroup should be expanded to include taxa similarly related to both the ingroup and its sister group. Furthermore, the use of additive characters where reasonable inferences of additivity can be made is likely to produce better-resolved cladograms than if all characters are considered non-additive, and it seems that using implied weighting not only improves the results obtained under both scenarios, but also reduces the uncertainty induced by considering all characters non-additive. The results obtained here, therefore, indicate that wherever possible additive characters and a method (such as implied weighting) which gives greater weight to the more reliable characters should be used.

Whether *Plumalexius* is sister to Plumariidae or not affects the estimated minimum age of Plumariidae: if it is, then Rasnitsyn's (2002, 2010) estimate remains reasonable (after all, the common ancestor of two lineages must be at least as old as either lineage), but if it is sister to the remaining chrysidoids or to Chrysidoidea as a whole, then that estimate for Plumariidae is poorly founded. Since all other chrysidoid lineages date from the Early Cretaceous (Engel and Grimaldi 2006; Rasnitsyn 2010), that would also be the estimated minimum age for Plumariidae itself if it is considered to be sister to the other chrysidoids rather than to *Plumalexius*. In any case, the presence of a group apparently closely related to Plumariidae in North America in the Cretaceous requires reassessment of ideas on the geographic origin of Plumariidae, making it unlikely that the group arose on Gondwanaland. Like the Scolebythidae, it is probable that the modern members are scattered relicts of a group with a previously much more extensive distribution. The discovery of fossils clearly attributable to Plumariidae will be critical in solving the puzzle, but such fossils are not very likely to be found if members of the family have always been adapted to arid environments, probably being parasitoids of subterranean hosts (Evans 1967), most likely beetle larvae. In contrast, Scolebythidae tend to be found in wooded or forest habitats as parasitoids of wood-boring beetle larvae, and thus have often been entombed in exuded resin and become inclusions in amber, facilitating their later discovery. Both *Plumalexius* and *Boreobythus* Engel and Grimaldi 2007 (Scolebythidae) were found in the same amber deposits, putatively derived from temperate coastal or deltaic swamps of coniferous trees (Grimaldi, Shedrinsky and Wampler 2000), an environment very different from those where modern Plumariidae exist.

Acknowledgments

I am most grateful to Alex Rasnitsyn for bringing the New Jersey fossils to my attention; it is with the greatest pleasure that I dedicate this paper to him in commemoration of his 75th birthday. I am also grateful to David Grimaldi (American Museum of Natural History, New York) for lending the specimens to me and for comments on some characters; to Arturo Roig-Alsina (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires) for the donation of specimens of *Maplurius*, *Mapluroides*, *Plumaroides* and *Pluroides*; to Simon van Noort (Iziko South African Museum, Cape Town) for the loan of a specimen of *Myrmecopterinella*; and to several other colleagues who have donated specimens of wasps over the years or provided useful insights. Doug Lundberg of Ambericawest (USA) very kindly gave me a piece of Dominican amber containing a specimen of *Pristapenesia inopinata*. Jim Carpenter (American Museum of Natural History) provided useful advice on some procedures for the analyses. Financial support from the University of KwaZulu-Natal Research Office is gratefully acknowledged.

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Appendix A. Specimens (all males) utilised for derivation of Table 1

All specimens are in D.J. Brothers' collection (to be deposited in Iziko South African Museum, Cape Town (SAM), in due course) unless otherwise stated.

Ichneumonoidea:

Ichneumonidae: Cryptinae sp. (S. Africa), Pimplinae spp. (2, Malawi, S. Africa)

Trigonaloidea:

Trigonalidae: *Taeniogonalos maculata* (Smith), *Trigonalys* ?*micanticeps* (Strand)

Evanioidea:

Evaniidae: *Evania* sp. (S. Africa), *Acanthinevania* sp. (Australia)

Gasteruptiidae: *Gasteruption* spp. (2, Botswana, S. Africa)

Vespoidea:

Tiphiidae, Anthoboscinae: *Anthobosca* spp. (2, S. Africa)

Sierolomorphidae: *Sierolomorpha bicolor* Evans, *S. canadensis* (Provancher)

Apoidea:

Ampulicidae: *Ampulex* spp. (2, S. Africa), *Dolichurus carbonarius* Smith

Heterogynaidae: *Heterogyna protea* Nagy, *H. nocticola* Ohl, *H. madecassa* Day

Chrysidoidea:

Plumalexiidae: *Plumalexius rasnitsyni* sp. nov. (AMNH)

Plumariidae: *Plumarius striaticeps* (André), *Plumarius* spp. (2, Argentina); *Plumaroides andalgalensis* Brothers, *Plumaroides brothersi* Diez and Roig-Alsina; *Myrmecopterina* spp. (3, Botswana, Namibia, S. Africa); *Myrmecopterinella* sp. (S. Africa) (SAM); *Maplurius spatulifer* Roig-Alsina; *Mapluroides ogloblini* Diez, Hidalgo and Roig-Alsina; *Pluroides porteri* Diez, Roig-Alsina and Hidalgo

Scolebythidae: *Scolebythus madecassus* Evans; *Pristapenesia primaeva* Brues, *P. inopinata* (Prentice and Poinar in Prentice, Poinar and Milki); *Ycaploca evansi* Nagy

Bethylidae: Mesitiinae: *Pilomesitius* ?*madagascarensis* Moczar, *Sulcomesitius* ?*pondo* (Benoit), *S.* ?*schoutedeni* (Benoit); Epyrinae: *Epyris* spp. (2, S. Africa); Pristo-

cerinae: *Acrepyris fraterna* (Evans), ?*Pristocera* sp. (S. Africa), *Apenesia* sp. (S. Africa)

Chrysididae: Cleptinae: *Cleptes alienus* Patton; Amiseginae: *Amisega similis* Kimsey, *A. flavicrus* Kimsey, *Bupon pashoanus* Kimsey; Chrysidinae: Elampini: *Hedychrum nobile* (Scopoli), *H.* sp. (S. Africa); Allocoeliini: *Allocoelia capensis* (Smith); Parnopini: *Parnopes fischeri* Spinola, *P. edwardsii* (Cresson); Chrysidini: *Chrysis ignita* Linnaeus, *Chrysura pacifica* (Say), *Stilbum cyanurum* (Förster)

Sclerogibbidae: *Sclerogibba africana* Kieffer, *S. berlandi* Benoit, *S.*?*magrettii* (Kieffer), *Probethylus schwarzi* Ashmead

Dryinidae: Gonatopodinae spp. (2, S. Africa); Dryininae spp. (2, S. Africa)

Embolemidae: *Embolemus collinsi* (Olmi), *E. confusa* (Ashmead), *E. magna* (Olmi), *E.* sp. (New Caledonia), *E. brothersi* Olmi

Appendix B Characters used for analysis of relationships of Chrysidoidea, all (except last) applicable to males only, treated as additive except where noted otherwise

1. Compound eye, inner margin: sinuate = 0, convex = 1;
2. Compound eye, pores and setae: no pores or setae = 0, scattered pores and/or setae = 1, dense pores and/or setae = 2;
3. Compound eye, setae: absent = 0, minute = 1, short = 2, long = 3;
4. Antennal socket, distance from epistomal suture: less than socket width = 0, more than 1.5 × socket width = 1;
5. Clypeus, shape: transverse, without prominent median lobe = 0; with long median lobe narrower than intermandibular area = 1;
6. Clypeus, form: platelike, apical margin not deflexed = 0, convex, thickened, apical margin deflexed medially = 1;
7. Occipital carina: present = 0, absent = 1;
8. Antenna, antennomere number: more than fourteen = 0, thirteen = 1, twelve = 2, ten = 3;
9. Antenna, radicle-scape axis and insertion: axis nearly straight, simple annular constriction = 0, axis angled, simple annular constriction = 1, axis angled, radicle under flangelike expansion of scape = 2;
10. Antenna, scape form: simple, more or less cylindrical = 0, basally expanded ventromesally = 1, apically expanded ventromesally = 2 (NON-ADDITIVE);
11. Antenna, flagellomere setae orientation: inconspicuous and decumbent = 0, conspicuous and semi-decumbent, some erect = 1, conspicuous and erect = 2;
12. Antenna, flagellomere setae distribution: evenly developed, scattered = 0, better developed ventrally, in irregular transverse rows = 1;
13. Antenna, flagellomere setae length: much less than flagellomere width = 0, about 0.5–1 × flagellomere width = 1, about 1.5–2 × flagellomere width = 2, about 3–4 × flagellomere width = 3;

14. Mandible, form: apical margin truncate (chewing type) = 0, apical margin strongly tapering (cutting type) = 1;
15. Mandible, apical teeth: four or more = 0, three = 1, two or fewer = 2;
16. Maxillary palp, segments: six = 0, five = 1, four = 2, three = 3, one = 4;
17. Labial palp, segments: four = 0, three = 1, two = 2, one = 3, absent = 4;
18. Pronotum, anterior collar (flange): present, covering propleura = 0, present but reduced and exposing propleura = 1, extremely reduced to slight ridge, effectively absent = 2;
19. Pronotum, posterolateral lobe: simple = 0, with preapical vertical blunt carina, posteriorly depressed = 1, with preapical vertical lamella, posteriorly concave = 2;
20. Pronotum, posteroventral angle: rounded = 0, narrowly acute = 1;
21. Pronotum, posteroventral margin: straightish = 0, strongly concave = 1;
22. Propleura, dorsally: separated by membranous region = 0, closely approximated although not fused = 1;
23. Propleura, posterior margin: almost straight, propleura almost entirely contiguous mesad = 0, indented on medial halves, propleura partially separated = 1, mostly indented, propleura almost entirely separated = 2;
24. Proepimeron: clearly distinguishable at outer angle and along posterior margin = 0, reduced, discernible only at outer angle = 1, indistinguishable = 2;
25. Prosternum, form: mostly in a single plane = 0, distinctly biplanar, mostly depressed posteriorly = 1;
26. Prosternum, ventral view: well developed with apophyseal pit(s) = 0, visible as triangular sclerite without apophyseal pit = 1, reduced, scarcely visible = 2;
27. Procoxae, contiguity: contiguous basally = 0, well separated basally = 1;
28. Prepectus, form: very well developed, long (nearing midline) and broad = 0, well developed, short (far from midline) and broad = 1, reduced, short (far from midline) and narrow = 2;
29. Prepectus, midventrally: halves divided, free from each other = 0, halves fused midventrally = 1;
30. Prepectus, fusion: entirely articulating or surrounded by membrane = 0, fused with mesopleuron = 1, fused with pronotum = 2 (NON-ADDITIVE);
31. Notauli: diverging anteriorly = 0, parallel = 1, absent = 2 (NON-ADDITIVE);
32. Scutellum: simple = 0, produced posterodorsally as sharp-edged flange = 1;
33. Mesepimeron, development: well developed, flangelike, overlapping metepisternum = 0, much reduced, abutting metepisternum = 1;
34. Mesosternum, form posteriorly: smoothly truncate = 0, mesad with short transverse carina or weak tooth = 1, mesad with lamella projecting over mesocoxal base = 2;
35. Mesocoxae, contiguity: broadly separated = 0, slightly separated = 1, contiguous = 2;
36. Mesosoma, second dorsal phragma: strongly oblique, muscles 2ph-3ph anterior = 0, scarcely oblique posteriorly, muscles 2ph-3ph anterior = 1, scarcely oblique posteriorly, muscles 2ph-3ph posterior = 2 (NON-ADDITIVE);

37. Metanotum, shape: mesally about as long as laterally or longer = 0, mesally half as long as laterally or shorter = 1;
38. Metanotum, lateral length: less than half medial length of scutellum = 0, more than two-thirds medial length of scutellum = 1;
39. Metapostnotum, development: distinctly lengthened laterally = 0, evenly long throughout = 1, distinctly shortened laterally = 2, shortened throughout = 3, greatly expanded posteromedially = 4 (NON-ADDITIVE);
40. Metapostnotum, hind margin: entirely distinct = 0, distinct medially, indistinct laterally = 1, obliterated medially, indistinct laterally = 2, entirely obliterated = 3 (NON-ADDITIVE);
41. Mesosoma, third dorsal phragma: forming distinct even flange = 0, forming narrow even flange = 1, forming narrow even flange laterally only = 2, medially reduced but distinguishable = 3, absent medially = 4, entirely absent = 5 (NON-ADDITIVE);
42. Metapleuron, endophragmal pit and sulcus: pit posteriorly placed, sulcus angled or rounded ventral to pit = 0, pit posteriorly placed, sulcus acutely extended ventral to pit = 1, pit posteriorly placed, sulcus entirely dorsal to pit and curved = 2, pit anteriorly placed, sulcus entirely dorsal to pit and straight = 3, pit anteriorly placed, sulcus acutely extended ventral to pit = 4 (NON-ADDITIVE);
43. Metathoracic-propodeal pleural suture, dorsally: distinct and complete = 0, reduced but partly discernible = 1, obliterated = 2;
44. Metathoracic-propodeal pleural suture, ventrally: distinct and complete = 0, reduced but partly discernible = 1, obliterated = 2;
45. Metasternum, form anteromedially: not depressed = 0, weakly depressed = 1, entirely depressed = 2;
46. Metacoxal cavities: open = 0, closed = 1;
47. Propodeum, length: longer than high = 0, shorter than high = 1;
48. Propodeum, declivity: imperceptibly merging with disk, not identifiable = 0, distinct from disk = 1;
49. Forewing, tubular/nebulous veins: reaching apical margin = 0, ending before apical margin = 1;
50. Forewing, pterostigma: large and prominent = 0, medium to small but distinct = 1, very small, indistinct or absent = 2;
51. Forewing, closed cells and cell 2Cu (variable 1): ten (C, R, 1Cu, 1R1, 1M, 2Cu, 2R1, 1Rs, 2M, 2Rs) = 0, seven (C, R, 1Cu, 1R1+1Rs, 1M, 2Cu, 2R1) = 1, seven (C, R, 1Cu, 1R1, 1M, 2Cu, 2R1)= 2, six (C, R, 1Cu, 1R1, 2Cu, 2R1) = 3, seven (R, 1Cu, 1R1+1M+1Rs, 2Cu, 2R1, 2Rs, 2M) = 4, six (R, 1Cu, 1R1+1M+1Rs, 2Cu, 2R1, 2M) = 5, seven or fewer (cells 2Cu, 2M and 2Rs open or lost) = 6 (NON-ADDITIVE);
52. Forewing, closed cells and cell 2Cu (variable 2): six or more (2Cu present and closed) = 0, seven (C, R, 1Cu, 1R1, 1M, 2R1, 1Rs) = 1, six (C, R, 1Cu, 1R1, 1M, 2R1) = 2, five (C, R, 1Cu, 1R1, 2R1) = 3, four (C, R, 1Cu, 1M) = 4, three (C, R, 1Cu) = 5;

53. Forewing, costal cell: broad, wider than thickness of bounding veins = 0, narrow, as wide as thickness of bounding veins or less = 1, eliminated, veins C and Sc+R+RS fused = 2;
54. Forewing, 2nd submarginal cell (1Rs) shape (absent coded "-"): anteriorly broadly sessile = 0, shortened and anteriorly briefly sessile to briefly petiolate = 1, much reduced and anteriorly strongly petiolate = 2;
55. Forewing, marginal cell anterior margin: more than 0.7 × pterostigma width = 0, less than 0.5 × pterostigma width = 1;
56. Forewing, apical accessory vein ("RS2"): absent, not even spectral = 0, present, nebulous or spectral = 1;
57. Forewing, prestigma (vein Sc+R) form: narrow, apically less than 1.5 × width of 1Sc+R = 0, broad, apically more than 1.8 × width of 1Sc+R = 1;
58. Forewing, prestigma (vein Sc+R) length: at least as long as 1RS = 0, less than 0.5 X length of 1RS = 1;
59. Forewing, vein Cu2: present = 0, absent = 1;
60. Hind wing, basal hamuli: several, dispersed along costal margin = 0, few, concentrated into cluster = 1, one = 2, absent = 3;
61. Hind wing, tubular/nebulous veins: reaching apical margin = 0, into apical half of wing but not reaching apical margin = 1, restricted to basal half of membrane = 2;
62. Hind wing, veins C and Sc+R: both long and separated, cell C closed = 0, both long and fused = 1, C short, Sc+R absent except at base = 2, C short but distinct, Sc+R long = 3, C absent except at base, Sc+R long = 4, C absent except at base, Sc+R short = 5 (NON-ADDITIVE);
63. Hind wing, vein M+Cu: well developed, tubular = 0, distinguishable but nebulous = 1, absent = 2;
64. Hind wing, anal veins: A1 well developed, A2 present = 0, A1 well developed (more than half length anal lobe), A2 absent = 1, A1 short (less than half length anal lobe), A2 absent = 2, A1 minute, A2 absent = 3;
65. Hind wing, veins rs-m and cu-a: both present = 0, both absent = 1;
66. Hind wing, incised anal (vannal/plical) lobe: absent, at most indicated by slight notch = 0, present, distinct acute incision = 1;
67. Hind wing, anal (vannal/plical) lobe length: short, less than 0.5 × length of wing = 0, long, more than 0.6 × length of wing = 1;
68. Hind wing, jugal lobe: present, delimited apically by incision = 0, absent = 1;
69. Tarsal claws, form ventrally: toothed = 0, simple = 1;
70. Protrochanter, basal insertion: apical on coxa = 0, basolateral on coxa = 1;
71. Foretarsus, arolium: narrower than tarsal apex and shorter than claws = 0, at least as broad as tarsal apex and at least as long as claws = 1;
72. Meso- and metatarsi, arolia: well developed = 0, vestigial = 1;
73. Mesocoxa, subdivision and insertion: large basi- and disticoxites, cavities large = 0, reduced basicoxite and large disticoxite, cavities moderate = 1, much-reduced basicoxite and large disticoxite, cavities small = 2;

74. Mesotrochantellus: distinctly present = 0, reduced but discernible as complete ring = 1, much reduced, almost indiscernable, ventrally only = 2, absent = 3;
75. Mesotibia, spurs: two = 0, one = 1, none = 2;
76. Mesotibia, scattered spines: absent = 0, weak = 1, moderately strong = 2;
77. Metacoxa, specialised area of setae on ventral surface: absent = 0, present = 1;
78. Metatrochanter, specialised area of setae on ventral surface: absent = 0, present = 1;
79. Metafemur, apex: simple = 0, with toothlike projection on each side at tibial articulation = 1;
80. Metatibia, inner apical spur: simple, similar to outer spur = 0, forming calcar with weak simple dorsal carina = 1, forming calcar with dorsal setose carina = 2, forming calcar with dorsal setal fringe only = 3, forming calcar with fine dorsal pectination = 4 (NON-ADDITIVE);
81. Metasoma-propodeum attachment: ventral, between hind coxae = 0, dorsal, distant from hind coxae = 1;
82. Metasoma, T1 articulation with S1: overlapping and articulating with base of S1 = 0, narrowed and fused with base of S1 dorsolaterally = 1;
83. Metasoma, T7 surface: simple, ecarinate = 0, longitudinally carinate = 1;
84. Metasoma, T7 apical flange: absent = 0, present, narrow = 1, present, broad, 0.33 × as long as tergum = 2;
85. Metasoma, S1: ecarinate = 0, with strong median longitudinal carina = 1;
86. Metasoma, S7: well developed and exposed = 0, reduced and partly exposed = 1, much reduced and concealed = 2;
87. Metasoma, hypopygium (S8) concealment: completely exposed or almost so = 0, partially concealed = 1, completely concealed or almost so = 2;
88. Metasoma, hypopygium (S8) shape: simple with blunt to rounded apex = 0, triangular with pointed apex = 1, truncate with weakly emarginate apex = 2, peglike = 3 (NON-ADDITIVE);
89. Metasoma, cercus: present, well developed, cylindrical = 0, present but much reduced, cylindrical = 1, absent or vestigial flattened setose disk = 2;
90. Sexual dimorphism, antennomere number: absent = 0, present (♂ 13, ♀ 12) = 1.