Cretaceous Research 69 (2017) 113–118

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Bizzare wingless parasitic wasp from mid-Cretaceous Burmese amber (Hymenoptera, Ceraphronoidea, Aptenoperissidae fam. nov.)

A.P. Rasnitsyn [a, b, *], George Poinar Jr. [c], Alex E. Brown [d]

[a] Paleontological Institute, Russian Academy of Sciences, 117997 Moscow, Russia
[b] Natural History Museum, London SW7 5BD, UK
[c] Department of Integrative Biology, Oregon State University, Corvallis, OR 97331, USA
[d] 629 Euclid Avenue, Berkeley, CA 94708, USA

ARTICLE INFO

Article history:
Received 28 June 2016
Received in revised form
6 September 2016
Accepted in revised form 15 September 2016
Available online 15 September 2016

Keywords:
Aptenoperissus burmanicus sp. et gen. nov.
Mid-Cretaceous
Burmese amber
Bizarre hymenopteran

ABSTRACT

A strange wingless female parasitic wasp from mid-Cretaceous Burmese amber is described as *Aptenoperissus burmanicus* sp. et gen. nov. in the new family Aptenoperissidae (Hymenoptera, Ceraphronoidea). Diagnostic characters of the female *Aptenoperissus burmanicus* sp. et gen. nov. include its wingless, streamlined and heavily sclerotized body lacking any apparent trace of a wasp waist, and geniculate antenna composed of a long, thin, stick-like scape, standard pedicel and 22 uniform flagellomeres. Also the body has 9 externally visible segments with no evidence of segment fusion implying the presence of a completely hidden segment. All tibiae have paired spurs and the hind femora are saltatory and incrassate. The double fore-tibial spur combined with unquestionable diagnostic features of Apocrita (primarily an internalized needle-like thin and acute ovipositor) suggest placement within the superfamily Ceraphronoidea s.str. with the Maimetshidae as a sister group of the crown Ceraphronoidea, composed of the Ceraphronidae, Megaspilidae, Stigmaphronidae, and Radiophronidae. The fossil is hypothesized to live semicryptically on the forest floor or tree trunk and to parasitize immature holometabolous insects. Diagnostic features of a respective male are suggested to test the hypothesized position of the new taxon.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Mid-Cretaceous amber from the Hukawng Valley in Myanmar has provided a variety of fascinating invertebrates and plants from that important period in the earth's history. In fact, the arthropods found in that amber presently, which includes 252 families, is the richest known assemblage in all Cretaceous amber. Its taxonomic composition forms, along with the Levantine assemblage, a focal center of arthropod diversity in the warmer part of the Cretaceous non-marine realm, as opposed to the more temperate northern amber assemblages (Rasnitsyn et al., 2016). Interestingly, the Cretaceous amber arthropod assemblages demonstrate no clear trend of taxonomic composition in comparison to their age. Possible causes of this phenomenon are discussed in Rasnitsyn et al. (2016).

While many fossils from Burmese amber can be placed in extant families, many others are unique. Some are very bizarre creatures, such as *Haidamyrmex* Dlussky and related ants with grotesquely modified mandibles and lower head capsules (Perrichot et al., 2016), the scorpionfly *Parapolycentropus* Grimaldi & Rasnitsyn with a long piercing beak and a completely missing hind wing (Grimaldi and Johnston, 2014), and the lacewing *Paradoxosisyra* Makarkin, 2016 with a long sucking beak (Makarkin, 2016). Some of these aberrant fossils have no close descendants and must be placed in new families. That is the case with the present insect fossil that we describe below as *Aptenoperissus burmanicus* Rasnitsyn & Poinar, sp. et gen. nov. in the new family, Aptenoperissidae fam. nov. We ascribe the new family to the order Hymenoptera and to the superfamily Ceraphronoidea s.str. and treat it preliminary as a sister to the clade embracing the four families, Ceraphronidae, Megaspilidae, Stigmaphronidae, and Radiophronidae. Based on its wingless, streamlined body, we suspect that the fossil was a cryptic parasitoid that attacked insect stages hidden in narrow crevices.

* Corresponding author. Paleontological Institute, Russian Academy of Sciences, 117997 Moscow, Russia.
E-mail address: alex.rasnitsyn@gmail.com (A.P. Rasnitsyn).

http://dx.doi.org/10.1016/j.cretres.2016.09.003
0195-6671/© 2016 Elsevier Ltd. All rights reserved.

2. Materials and methods

The specimen originated from the Noije Bum 2001 Summit Site mine excavated in the Hukawng Valley in 2001 and located southwest of Maingkhwan in Kachin State (26°20′N, 96°36′E) in Myanmar. Based on paleontological evidence this site was dated to the late Albian of the Early Cretaceous (Cruickshank and Ko, 2003), placing the age at 97 to 110 Ma. A more recent study using U–Pb zircon dating determined the age to be 98.79 ± 0.62 Ma or at the Albian/Cenomanian boundary (Shi et al., 2012). Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit Site indicate an araucarian tree source for the amber (Poinar et al., 2007).

Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 800×. Helicon Focus Pro ×64 was used to stack photos for better depth of field. Line drawings were made with CorelDRAW software based on photographs.

LSID urn:lsid:zoobank.org:pub:135AD641-E78B-4DCB-B094-6549042F0636

3. Systematic paleontology

Order: Hymenoptera Linné, 1758
Suborder: Vespina Laicharting, 1781
Superfamily: Ceraphronoidea Haliday, 1833
Family: Aptenoperissidae Rasnitsyn & Poinar, fam. nov.
LSID urn:lsid:zoobank.org:act:49CA442E-6556-4341-9DE0-0988C9DA34C6
Type genus *Aptenoperissus* Rasnitsyn & Poinar, gen. nov.

Diagnosis. Female wingless, saltatory, streamlined (with no apparent trace of a wasp waist), heavily sclerotized and somewhat depressed, with ovipositor internalized. Antenna polymerous (with more than 15 flagellomeres), geniculate with scape long and thin, stick-like, attached on elevation(s) above mandibles. Eyes well developed, ocelli present, mouthparts as preserved with no peculiarities. Pronotum deeply excised posteriorly, short at midline, propleuron not elongate (not forming neck). Mesonotum preserved as simple semicircular plate with no suture/carina visible, all following terga uniform simple quadrangular plates except for apical long triangular metasomal tergum. Body with 9 externally visible segments with no evident trace of segment fusion, thus implying one completely hidden segment, putatively 1st metasomal. Legs ordinary except that all (!) tibiae with paired apical spurs, hind femur saltatory, incrassate, no trochantellus present except for small rudiment in hind leg; fourth tarsomere with modified plantula in all legs. Antennal cleaner (modified inner fore tibial spur and fore basitarsus) well developed. Apical metasomal tergum and sternum fit together enclosing ovipositor in repose. Male unknown.
Genera included. Type genus only.
Remarks. The new family displays a number of unusual or atypical combination of characters that prevents its straightforward assignment to a higher taxon. It is ascribed to the order Hymenoptera based primarily on the characteristic antenna cleaner formed with a specifically modified inner (fore) protibial apical spur, and the internalized, needle-like thin, sharp barbed ovipositor. Protibial cleaner occurs in Lepidoptera and some beetles but in a different form (with protibial apex rather than basitarsus employed opposing the spur) and are never combined with needle-like internalized ovipositor.

The most striking feature of the new family as a hymenopteron is a polymerous long-geniculate antenna of ant-like appearance but with numerous flagellomeres. In Hymenoptera, both polymerous and long-geniculate antennae are regular features, but these features only occur separately and never together. Being so unique, this character combination is not considered indicative of its taxonomic position and was not considered while seeking a sister taxon(s). Instead, as a key feature, we use the unique character of the fore tibia containing two apical spurs, one being modified as a calcar. Lower Symphyta hymenopterans equally possessing the double protibial spurs (Xyeloidea, Tenthredinoidea, and Pamphiliodea) are not considered to be closely related because of the internalized needle-like ovipositor in the fossil. The internalized ovipositor implies that the Aptenoperissidae is deeply rooted within Apocrita. This makes it hardly possible that it retained the outer (hind) protibial spur directly from basal Hymenoptera. That spur has been already lost by the common ancestor of the clade embracing Cephoidea, Siricoidea s.l., Orussoidea and Apocrita (Rasnitsyn, 1988). This implies that Aptenoperissidae could re-gain the double protibial spurs as a reversal. With this limitation, two fore tibial spurs are strongly indicative of crown Ceraphronoidea s.str. (Ceraphronidae, Megaspilidae, Stigmaphronidae, and Radiophronidae, but not Maimetshidae). Considering this similarity as a putative synapomorphy, we ascribe the new family to the superfamily Ceraphronoidea and treat it tentatively as a sister to the crown group Ceraphronoidea. Remaining as a putative synapomorphy of the entire superfamily Ceraphronoidea s.str. is the small, reduced first metasomal segment forming an articulatory ring between the meso- and remaining metasoma, which is hidden between the propodeum and second metasomal segment and invisible externally. The putatively sister position of Aptenoperissidae in respect to the crown Ceraphronoidea is supported by the oligomerous geniculate antenna of the latter groups as opposed to the polymerous geniculate antennae in the new family.

The only available alternative to Ceraphronoidea in possessing the double protibial spurs is possibly several advanced genera of Braconidae, *Bathyaulax* Szepligeti (including some *Bicentra* Achterberg & Sigwalt as a synonym) and *Rhamnura* Enderlein (Quicke, 1987 and Kaartinen and Quicke, 2007, respectively). However, the above braconid genera have no other characters in common with Aptenoperissidae, and so it is unlikely they have any phylogenetic relationship to the new family.

However the braconid genus *Streblocera* Westwood (of the subfamily Euphorinae and hence only distantly related to *Bathyaulax* and *Rhamnura* of the subfamily Braconinae) is unique for all the superfamily Ichneumonoidea in having the scape elongate, often very much so. However, this is only a superficial similarity with Aptenoperissidae, because these two adaptations are contrasting. The long geniculate antenna of the new family is unquestionably sensory, even though details of its function is expectably obscure in the fossil. In contrast, antenna of *Streblocera* represents a catching device aimed to grasp and manipulate the adult host (Chrysomelidae beetles) to secure a position for oviposition (Belokobylskij, 1996). As a result, the antennae of *Streblocera* represent a homoplasy in respect to the raptorial legs of praying mantida and dryinid wasps rather than to the geniculate antenna of Aptenoperissidae.

Genus *Aptenoperissus* Rasnitsyn & Poinar, gen. nov.
LSID urn:lsid:zoobank.org:act:991884F3-1A1E-424A-94BC-D135604E4463
Type species: *Aptenoperissus burmanicus* Rasnitsyn & Poinar, sp. nov.

Derivation of name. The generic name is derived from the Greek "aptenos" = wingless and the Greek "perissos" = strange.
Diagnosis. As for family (by monotypy).
Included species. Type species only.

Aptenoperissus burmanicus Rasnitsyn & Poinar, sp. nov.
LSID urn:lsid:zoobank.org:act:A76D48F4-E1C9-405B-ABE8-FEFFC2F3279B
Figs. 1–3

Derivation of name. The specific epithet refers to the location of the fossil.
Holotype. Female No. B-Hy-19 deposited in the Poinar amber collection maintained at Oregon State University. Complete, well-preserved specimen with only some scattered debris obscuring particular details; body dark, thus making it difficult to discern surface sculpture. Air bubbles present, including small ones extruded from mesothoracic and propodeal spiracles (Fig. 3I, arrows). A viscous deposit surrounding part of the metasoma distorts underlying structures and makes observations in that region difficult (Fig. 2A, arrows). Syninclusia (Fig. 3J–L): adjacent to the holotype are 12 multi-segmented spear-headed setae composed of long basal stalks ranging from 300 to 352 μm in length and short, expanded triangular tips ranging from 32 to 36 μm in length. These closely resemble hastisetae from the abdominal tergites of larvae of the subfamilies Anthreninae and Megatominae of the family Dermestidae (Peacock, 1993) and are putative signs of the presence of dermestid larva.
Type locality. Kachin (Hukawng Valley) of northern Myanmar.
Stratigaphic horizon. The lowermost Cenomanian (98.79 ± 0.62 Ma; Shi et al., 2012); mid-Cretaceous.
Diagnosis. As for family (by monotypy).

Description. Body and appendages black to dark brown as preserved. Surface sculpture predominantly rather densely punctate, from glabrous to densely pubescent when discernable.

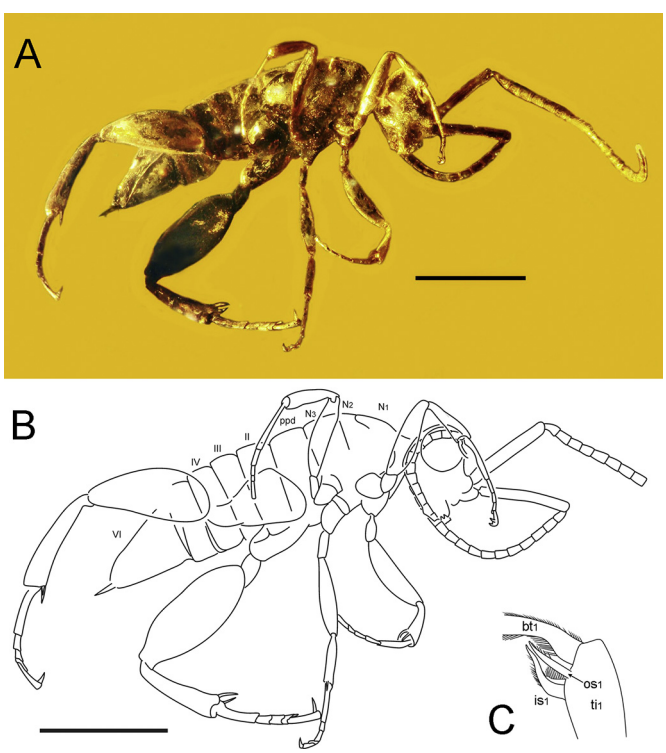

Fig. 1. *Aptenoperissus burmanicus* gen. et sp. nov. in Burmese amber. A. Ventral-lateral view. Scale bar = 1.0 mm. B. Same, interpretation. Scale bar = 1.1 mm. Drawing restrictions: contours on structures occurring nearer the observer (as with the legs) are continuous; those structures further behind on the body show interrupted contours due to the superimposed lines. C. Antennal cleaner. Explanation of symbols: II–VI – metasomal segments, bt_1 – fore basitarsus, is_1 – inner fore tibial spur, N_1 – pronotum, N_2 – mesonotum, N_3 – metanotum, os_1 – outer fore tibial spur, ppd – propodeum, ti_1 – apex of fore tibia.

Head transverse, of moderate size, with eyes large, subspherical, densely pubescent (Fig. 3A), located high on head sides; ocelli not distinct but apparently 3 (Fig. 3B); antennae attached to pair of adjacent lobes elevated above short, subvertical clypeus (Fig. 3C). Mandible moderately narrow, with three subequal teeth, with cutting edge subparallel to mandible rotational axis (Fig. 3C). Other mouthparts poorly preserved. Antenna (Fig. 1, 2, 3B) with scape straight, subcylindrical, slightly longer than head length, about as thick as pedicel and flagellum. Pedicel pear-shaped, about as long as average flagellomere. Flagellum filiform, 22-segmented, segments of nearly standard width, up to one and a half times as long as wide except apical one twice as long as wide, very slightly narrowed basally, with sensilla small, roundish (no multiporous plate sensilla visible) (Fig. 3D).

Mesosoma and three basal metasomal terga of equal width, further segments tapering toward acute apex. Pronotum with deep arcuate hind margin, possibly slightly attenuate forward, with posterolateral ends distant from posterior boundary of mesonotum by about 0.3 visible length of mesonotum, not distinctly modified in dorsal aspect. Mesonotum semicircular, flat, metanotum and propodeum subequal to each other, quadrangular with slightly rounded angles, about 0.8 times as long as mesonotum. Structure of lateral and ventral mesosoma insufficiently known. Legs of usual appearance except saltatory incrassate condition of hind coxa and femur (coxa 0.6 times as high as propodeal plate width, femur 0.4 times as wide as long); all tibiae with two apical spurs. Fore and mid coxae subequal in length, with fore coxa wider and more rounded, each less than half as long and as wide as hind coxa; mid coxa apparently wide basally. Trochanters elongate-ovate with attenuate base. Only hind trochantellus visible as small, strongly convex ring at femur base (Fig. 3E). Fore and mid femora and all tibiae ordinary, tibiae slightly shorter than respective femora. All spurs simple, acute, except for fore tibial longer (inner) spur bifid apically, with inner side bearing comb of long setae elevated on membranous flap (Fig. 1C, 3F; bifid apex of inner spur not visible in Fig. 1C because of improper orientation). Fore basitarsus excised basally, ventrally, with long comb of setae extending nearly to apex of segment (Fig. 3F). Basal and apical tarsal segments longer than normal in all legs (cf. measurements for details), segments 3 and 4 of pro- and mesotarsi with modified (cylindrical) plantula ventrally, apically (Fig. 3G). Claws symmetrical, acute, moderately bent, with long, low basal lobe bearing single long seta, with no subapical tooth (Fig. 3G). Arolium small or absent.

Metasoma with 5 visible segments, all terga appearing solid, slightly arching transversally, apical long triangular, all others uniform in general form and size (length varying because of slight telescoping, width slightly diminishing gradually posteriorly), all quadrangular with angles rounded (hind ones less so), and with subapical transverse impression line. Metasomal sterna agreeing in form and position with respective terga when discernible, with basal rather than subapical impressed line. Ovipositor as noted (apex of articulated stylets only, sheath not visible), barbed: with at least 3 distinct transverse notches on tapering apical part (Fig. 3H).

Measurements: Total body length, 3.6 mm; head length, 0.6 mm; head width, 0.7 mm; mesosoma length, 1.3 mm; metasoma length, 1.7 mm; scape length, 0.9 mm; flagellum length, 2.6 mm; length exposed portion of ovipositor, 0.2 mm; tarsal lengths, μm: protarsus; 1, 266; 2, 105; 3, 105; 4, 70; 5, 126: mesotarsus; 1, 218; 2, 155; 3, 115; 4, 52; 5, 86: metatarsus; 1, 430; 2, 126; 3, 86; 4, 52; 5, 230.

Remarks. The body with nine externally visible segments, four mesosomal and five metasomal, is interpreted as indicative of hidden first and seventh through tenth metasomal segments (at least their terga) for the following reasons. In female Hymenoptera,

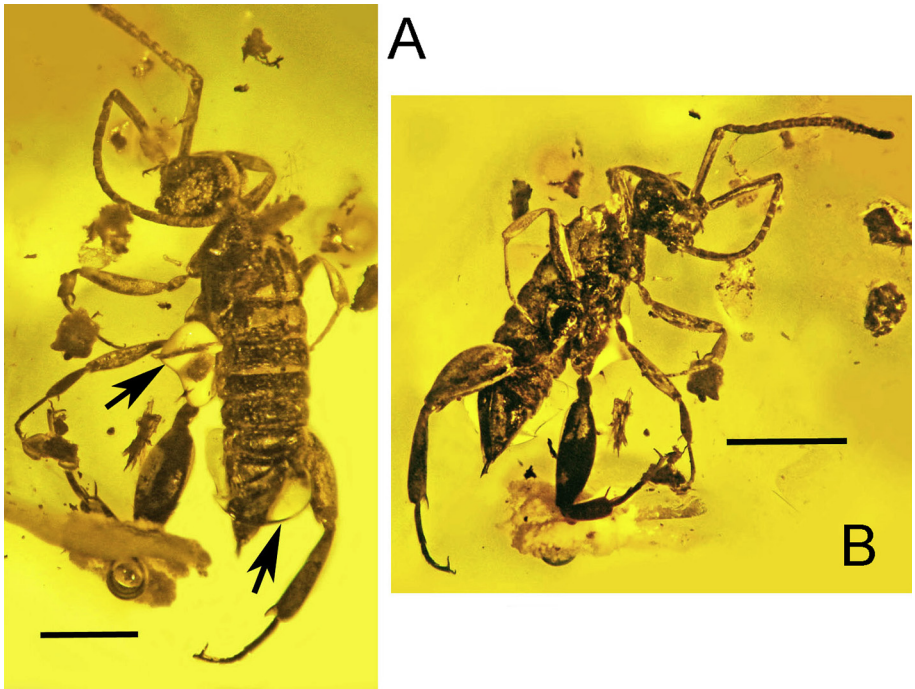

Fig. 2. *Aptenoperissus burmanicus* gen. et sp. nov. in Burmese amber. A. Dorsal-lateral view. Scale bar = 0.8 mm. Arrows indicate bubbles of viscous substance which form lenses distorting contours of underlying structures. B. Ventral-lateral view. Scale bar = 1.3 mm.

the apical sternum is normally the seventh abdominal (sixth metasomal) and never the eighth abdominal segment. Internalisation of the seventh metasomal sternum is possible (for instance in Chrysididae) but rare and additional evidence for this is not available in the present case. That is why we are stating that one metasomal tergum is lost externally and the five visible ones are ordinary terga and not a result of fusion. The first four visible terga are so similar in form and structure that only the apical one can be suspected of fusion. However, the apical tergum fits fairly well with its sternal counterpart, and both display no appreciable trace of fusion. That is why we prefer the above hypothesis of the first metasomal segment reduced to a short and narrow, ring-like petiole hidden between the propodeum and second metasomal segment. The presence of a hidden petiolar segment is characteristic of Maimetshidae (Rasnitsyn, 1975) as well as of the majority of other Ceraphronoidea s.str. (Radiophronidae, Stigmaphronidae and Megaspilidae; cf. figures in Ortega-Blanco et al., 2010, 2011; Goulet and Huber, 1993, fig. 209. 210). The external disappearance of the petiole is not uncommon among Chalcidoidea as well (Goulet and Huber, 1993, fig. 213–218, 221–225, etc.).

4. Discussion

Considering its streamlined sclerotized body and wingless condition, it is likely that *Aptenoperissus burmanicus* sp. et gen. nov. was a cryptic parasitoid that attacked insects hidden in narrow crevices or concealed habitats. Wings would be a hindrance and make it difficult to wedge the abdomen into small holes for egg deposition. The heavy armature of the cuticle would provide some protection. The immense metacoxae and metafemora provide the wasp with the leaping ability to escape from its enemies. The females of several extant hymenopterans that lack wings and have thick body walls, e.g. mutillids, bethylids, etc., are cryptic and spend much time within a substrate. The sturdy, serrated ovipositor indicates that the hosts may also have been armored, suggesting that the egg or pupal stages of wood boring or otherwise cryptic holometabolous insects may have been targeted. It is less likely that the ovipositor, even though comparatively thick and heavily barbed, was used penetrate through wood to reach the host. This function supposes, at least in Hymenoptera, the ability of the ovipositor to be directed more or less vertical to the body axis in order to receive sufficient pressure toward a substrate. The fossil under description has its ovipositor directed straight backwards, with limited ability to change the direction due to the rigid body impossible to be bent at an appreciable angle. The apical metasomal sternum appears to be of limited downward mobility as well and equally impossible to render the ovipositor sufficient freedom for a downward rotation. That is why the armed and comparatively thick ovipositor rather implies penetration of a more or less armored host (egg with hard chorion, pupa with thick integument or in a cocoon, or the like).

5. Concluding remarks

The presently described fossil demonstrates that even without any deep miniaturization (as in the case of the smallest adult insect male mymarid *Dicopomorpha echmepterygis* Mockford, cf. Polilov, 2015), an adult hymenopteran can be modified so greatly that its ordinal position becomes questionable. Nor does it need extreme desimaginisation (as in the female marine midge, *Pontomyia* Edwards, cf. Bretschko, 1982), or parasitism (as in the putative pterosaur parasites, the mecopteroid *Saurophthirus* Ponomarenko and its relatives, the dipteran *Strashila* Rasnitsyn, and the suggested chewing louse *Saurodectes* Rasnitsyn, Zherikhin; cf. Gao et al., 2014, Huang et al., 2013, and Rasnitsyn, Zherikhin, 2000, respectively). In our case, the only necessary prerequisite for such significant morphological transformations was apparently a cryptic way of life in a substrate that could have been completely cryptic or semicryptic. However, the obvious saltatory adaptations suggest that periodic movement of the fossil into open space also occurred. Semicryptic habits are commonplace in insects and in

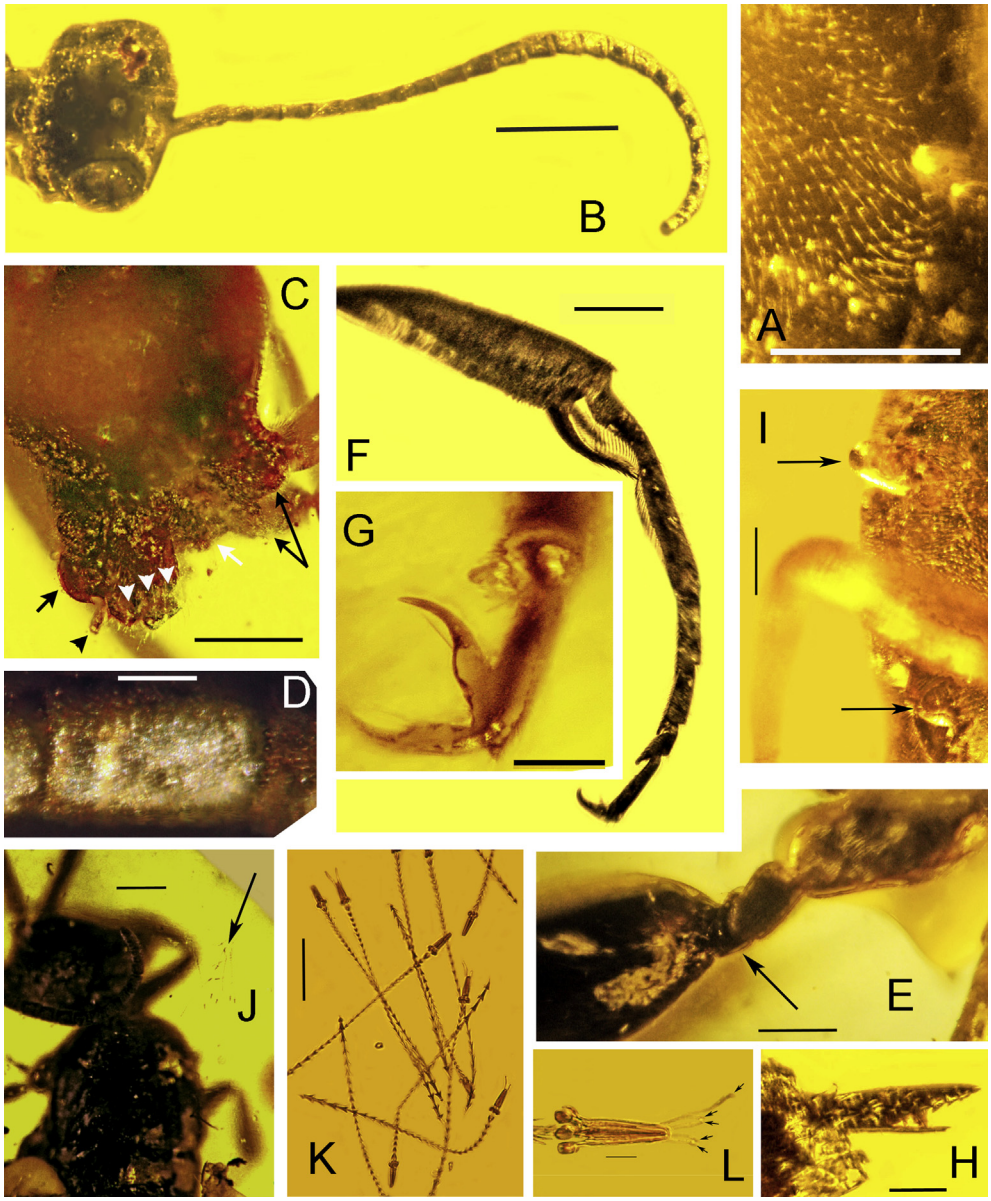

Fig. 3. Details of *Aptenoperissus burmanicus* gen. et sp. nov. in Burmese amber. A. Eye pubescence. Scale bar = 0.1 mm. B. Dorsal view of head and antenna. Scale bar = 0.5 mm. C. Head below and mouthparts: clypeus (white arrow), supraclypeal lobes (double black arrow), mandibular teeth (white arrowheads), prementum? (black arrow), labial (?) palp (black arrowhead). Scale bar = 0.2 mm. D. 16th flagellomere Scale bar = 0.046 mm. E. Hind trochantellus (arrow). Scale bar = 0.2 mm. F. Foreleg. Scale bar = 0.14 mm. G. Fourth and fifth fore tarsal segments with plantula and claws. Scale bar = 0.06 mm. H. Ovipositor apex. Scale bar = 0.07 mm. I. Air bubbles (arrows) from the pro- (above) and mesothoracic (below) spiracles, lateroventral view (cf. Fig. 2B). Scale bar = 0.2 mm. J. Syninclused dermestid setae (arrow). Scale bar = 0.3 mm. K. Same, enlarged. Scale bar = 0.08 mm. L. Seta head; arrows indicate pseudopodia-like extensions arising from tip of seta. Scale bar = 0.01 mm.

Hymenoptera particularly. In the present case, extant and unusual specialization occurred. To possess complete aptery, a hidden petiolar (first metasomal) segment and leaping adaptations, as well as a perfectly streamlined and highly sclerotized body lacking even a trace of the wasp waist is very unusual. The complete external similarity of the propodeum (the first abdominal tergum) with the other abdominal (metasomal) terga is simply unique, because this feature was lost early in the hymenopteran groundplan, since even the basal Hymenoptera have the first abdominal tergum modified (divided). Another unusual adaptation obtained in evolution of the fossil under discussion is its long geniculate and polymerous antenna indicative of intensified sensory (tactile and gustatory) function. According to Dlussky and Fedoseeva (1988), a long geniculate antenna is used to obtain long distance sensory signals (due to the total length of the antenna) and to supply fine manipulation (due to the possibility of bringing the tips of both antennae particularly close to the mouth where tactile and gustatory appendages occur). Dlussky and Fedoseeva mention aculeate wasps and particularly ants having oligomerous antennae able to reach the tips of their mouths. *Aptenoperissus* has polymerous antennae with long flagella that possibly had the ability to reach the mouth if there was sufficient flexibility of the flagellum (Fig. 1B). The long antennae could be associated with a close examination of a potential host before oviposition, and this hypothesis further suggests parasitism occurred in a host with limited if any mobility. Above it was suggested that the structure of the ovipositor, and the body in general, is modified for parasitizing a sclerotized egg or pupa, or else a host in a hard cocoon. While we can only speculate about

possible habitats and hosts, some unique insect trichomes in the amber adjacent to the wasp are very similar to those of extant dermestid larvae, suggesting that this insect group shared the habitat with *Aptenoperissus burmanicus* sp. et gen. nov. or even served as hosts. There are some previous reports of dermestid fossils in Burmese amber (cf Rasnitsyn et al., 2016, Sl) including a description of *Dermestes larvalis* Cockerell, 1917 (Cockerell, 1917). However, the correct taxonomic position of the latter fossil remains unknown at this time.

Another lesson acquired during the present study is how subtle the reasons can be for determining the taxonomic position of fossils. Hymenoptera are generally an order of insects that are comparatively easy to identify, yet with this fossil we depend solely on the structure of the antennal cleaner and ovipositor tip to determine the Order. A more precise taxonomic position was equally hypothesized based on characters such as the double protibial spurs together with the internalized needle-like ovipositor, which occurs only in the Ceraphronoidea. Further placement of the fossil is based on antennae that are already geniculate (synapomorphic with the crown Ceraphronoidea) and also polymerous (symplesiomorphic with Maimetshidae). This makes it useless to attempt a formal cladistic analysis and leaves the selected hypothesis somewhat questionable at this time. Further analysis would benefit by the discovery of a respective male even though that male might have nothing in common with the above described female in body structure. Thus we suggest two distinct and easily observable features least affected by sexual dimorphism for identification. One of these characters is the double protibial spurs, and the other is a polymerous antenna which is distinctly geniculate, or at least with the scape much longer than the other segments, a feature not characteristic of Maimetshidae as demonstrated by Rasnitsyn and Brothers (2009), Perrichot et al. (2011) and Perrichot (2013).

Acknowledgements

The authors acknowledge important help from two anonymous reviewers whose thorough examination and detailed comments have improved our evidence considerably. We are thankful to Sergei Belokobylskij (St.Peterburg) for supplying us with the relevant literature about *Streblocera.* For APR, the present study has been supported in part by Presidium RAS Program N° 22 «Evolution of the organic world and planetary processes».

References

Belokobylskij, S.A., 1996. Parasitism on the beetles (Coleoptera) as an important stage in the evolution of braconid wasps (Hymenoptera: Braconidae). II. Entomologicheskoe Obozrenie 75 (4), 790–814 (in Russian).

Bretschko, G., 1982. *Pontomyia* Edwards (Diptera: Chironomidae), a member of the coral reef community at Carrie Bow Cay, Belize. Smithsonian Contributions to Marine Science 12, 381–385.

Cockerell, T.D.A., 1917. Arthropods in Burmese amber. Psyche 24, 40–45.

Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21, 441–455.

Dlussky, G.M., Fedoseeva, E.B., 1988. [Origin and early evolution of ants]. In: Ponomarenko, A.G. (Ed.), Melovoj biocenoticheskij krisis I evolucija nasekomyh [Cretaceous biocenotic crisis and evolution of the insects]. Nauka Press, Moscow, pp. 70–144 (in Russian).

Gao, Taiping, Shih, Chungkun, Rasnitsyn, A.P., Xu, Xing, Wang, Shuo, Ren, Dong, 2014. The first flea with fully distended abdomen from the Early Cretaceous of China. BMC Evolutionary Biology 14, 168. http://www.biomedcentral.com/1471-2148/14/168.

Grimaldi, D.A., Johnston, M.A., 2014. The long-tongued Cretaceous scorpionfly *Parapolycentropus* Grimaldi and Rasnitsyn (Mecoptera: Pseudopolycentropodidae): new data and interpretations. American Museum Novitates 3793, 1–23. http://dx.doi.org/10.1206/3793.1.

Goulet, H., Huber, J.T., 1993. Hymenoptera of the World: an Identification Guide to Families. Agriculture Canada, Ottawa, p. vii+668.

Huang, D., Nel, A., Cai, C., Lin, Q., Engel, M.S., 2013. Amphibious flies and paedomorphism in the Jurassic period. Nature 495 (7439), 94–97. http://dx.doi.org/10.1038/nature11898.

Kaartinen, R., Quicke, D.L.J., 2007. A revision of the parasitic wasp genus *Bathyaulax* Szépligeti (Hymenoptera: Braconidae: Braconinae) from Africa and the Arabian Peninsula. Journal of Natural History 41, 125–212. http://dx.doi.org/10.1080/00222930601121221.

Makarkin, V.N., 2016. Enormously long, siphonate mouthparts of a new, oldest known spongillafly (Neuroptera, Sisyridae) from Burmese amber imply nectarivory or hematophagy. Cretaceous Research 65, 126–137. http://dx.doi.org/10.1016/j.cretres.2016.04.007.

Ortega-Blanco, J., Rasnitsyn, A.P., Delclòs, X., 2010. A new family of ceraphronoid wasps from Early Cretaceous Álava amber, Spain. Acta Palaeontologica Polonica 55 (2), 265–276. http://dx.doi.org/10.4202/app.2009.0014.

Ortega-Blanco, J., Delclòs, X., Engel, M.S., 2011. Diverse stigmaphronid wasps in Early Cretaceous amber from Spain (Hymenoptera: Ceraphronoidea: Stigmaphronidae). Cretaceous Research 32, 762–773. http://dx.doi.org/10.1016/j.cretres.2011.05.004.

Peacock, E.R., 1993. Adults and larvae of hide, larder and carpet beetles and their relatives (Coleoptera: Dermestidae) and of Derodontid Beetles (Coleoptera: Derodontidae), vol. 5. Royal Entomological Society of London. Handbooks for the Identification of British Insects, pp. 1–144.

Perrichot, V., 2013. New maimetshid wasps in Cretaceous amber from Myanmar (Insecta: Hymenoptera). Annales de paleontologie 2013 (99), 67–77. http://dx.doi.org/10.1016/j.annpal.2012.10.002.

Perrichot, V., Ortega-Blanco, J., McKellar, R.C., Delclòs, X., Azar, D., Nel, A., Tafforeau, P., Engel, M.S., 2011. New and revised maimetshid wasps from Cretaceous ambers (Hymenoptera, Maimetshidae). ZooKeys 130, 421–453. http://dx.doi.org/10.3897/zookeys.130.1453.

Perrichot, V., Wang, B., Engel, M.S., 2016. Extreme morphogenesis and ecological specialization among Cretaceous basal ants. Current Biology 26. http://dx.doi.org/10.1016/j.cub.2016.03.075.

Poinar Jr., G.O., Lambert, G.J.B., Wu, Y., 2007. Araucarian source of fossiliferous Burmese amber: spectroscopic and anatomical evidence. Journal of the Botanical Research Institute of Texas 1, 449–455. http://www.jstor.org/stable/41971435.

Polilov, A.A., 2015. Small is beautiful: features of the smallest insects and limits to miniaturization. Annual Review of Entomology 60, 103–121. http://dx.doi.org/10.1146/annurev-ento-010814-020924.

Quicke, D.L.J., 1987. The Old World genera of braconine wasps (Hymenoptera: Braconidae). Journal of Natural History 21, 43–157.

Rasnitsyn, A.P., 1975. Hymenoptera Apocrita of Mesozoic. Transactions of Paleontological Institute, Academy of Sciences of the USSR, vol. 147. Nauka Press, Moscow, 134 p. (in Russian).

Rasnitsyn, A.P., 1988. An outline of evolution of the hymenopterous insects (order Vespida). Oriental Insects 22, 115–145.

Rasnitsyn, A.P., Zherikhin, V.V., 2000 (1999). First fossil chewing louse from the Lower Cretaceous of Baissa, Transbaikalia (Insecta, Pediculida = Phthiriaptera, Saurodectidae fam. nov.). Russian Entomological Journal 8, 253–255.

Rasnitsyn, A.P., Brothers, D.J., 2009. New genera and species of Maimetshidae (Hymenoptera: Stephanoidea *s.l.*) from the Turonian of Botswana, with comments on the status of the family. African Invertebrates 50, 191–204.

Rasnitsyn, A.P., Bashkuev, A.S., Kopylov, D.S., Lukashevich, E.D., Ponomarenko, A.G., Popov, Yu.A., Rasnitsyn, D.A., Ryzhkova, O.V., Sidorchuk, E.A., Sukatsheva, I.D., Vorontsov, D.D., 2016. Sequence and scale of changes in the terrestrial biota during the Cretaceous (based on materials from fossil resins). Cretaceous Research 61, 234–255. http://dx.doi.org/10.1016/j.cretres.2015.12.025.

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yand, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37, 155–163. http://dx.doi.org/10.1016/j.cretres.2012.03.014.