

Short communication

Three new female *Aptenoperissus* from mid-Cretaceous Burmese amber (Hymenoptera, Stephanoidea, Aptenoperissidae): Unexpected diversity of paradoxical wasps suggests insular features of source biome

Alexandr P. Rasnitsyn^{a, b, *}, Christoph Öhm-Kühnle^c

^a A.A. Borissiak Palaeontological Institute, Russian Academy of Sciences, 117647 Moscow, Russia

^b Natural History Museum, Cromwell Road, London SW7 5BD, UK

^c Kirchgasse 11, 71083 Herrenberg, Germany



ARTICLE INFO

Article history:

Received 15 March 2018

Received in revised form

2 June 2018

Accepted in revised form 5 June 2018

Available online 7 June 2018

Keywords:

Hymenoptera

Aptenoperissidae

New species

Bizarre wasp

Mid-Cretaceous

Burmese amber

Isolated biota

Insular effect

ABSTRACT

Three new female wasps of the family Aptenoperissidae from the mid-Cretaceous Burmese amber are described as *Aptenoperissus magnifemoris* Rasnitsyn & Öhm-Kühnle, sp. nov., *A. etius* Rasnitsyn & Öhm-Kühnle, sp. nov., and *A. pusillus* Rasnitsyn & Öhm-Kühnle, sp. nov., assigned to the genus *Aptenoperissus* Rasnitsyn & Poinar, 2017. Features of the currently and previously described Aptenoperissidae indicate a high diversity of the group in the mid-Cretaceous fauna of Myanmar and suggest its possible insular nature; this is supported by the general characteristics of the fossil assemblage of Burmese amber.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

The family Aptenoperissidae was established based on the single female wingless parasitic wasp *Aptenoperissus burmanicus* Rasnitsyn & Poinar, 2017 from mid-Cretaceous Burmese amber (Rasnitsyn et al., 2017). Originally it was attributed to the superfamily Ceraphronoidea and subsequently re-attributed to the basal apocritan superfamily Stephanoidea based on features of males found in Burmese amber as well and described as three new species of *Aptenoperissus* Rasnitsyn & Poinar, 2017 (Zhang et al., 2018a). These features were the lack of wasp waist and a long and reclival crossvein 1-Rs. This attribution is further supported by combination of these features with incrassate hind legs and long parallel-sided cell 1mcu receiving a cu-a crossvein well after its base, as well as the short, needle-like ovipositors of the females, as is

characteristic of some species of the *Symphytopterus* Rasnitsyn 1975 (Ephialtitidae) show. The second female of this enigmatic and highly sexually dimorphic genus has been recently added to the above genus as a new species from Burmese amber (Zhang et al., 2018d). Now we report three further females belonging to the genus *Aptenoperissus* from the same source. Each of them represents a new species, a fact which additionally supports the impression of unexpected diversity of these unusual insects in the mid-Cretaceous fossil assemblage of the Burmese amber.

2. Material and methods

The fossil inclusions described herein were collected from the amber mines sited in the Hukawng Valley of Kachin Province, Myanmar (locality in Kania et al., 2015: Fig. 1). The rock yielding the amber at this site was dated to the late Albion of the Early Cretaceous (97–110 Ma) based on paleontological evidence (Cruikshank and Ko, 2003). A more recent study determined the

* Corresponding author.

E-mail address: alex.rasnitsyn@gmail.com (A.P. Rasnitsyn).

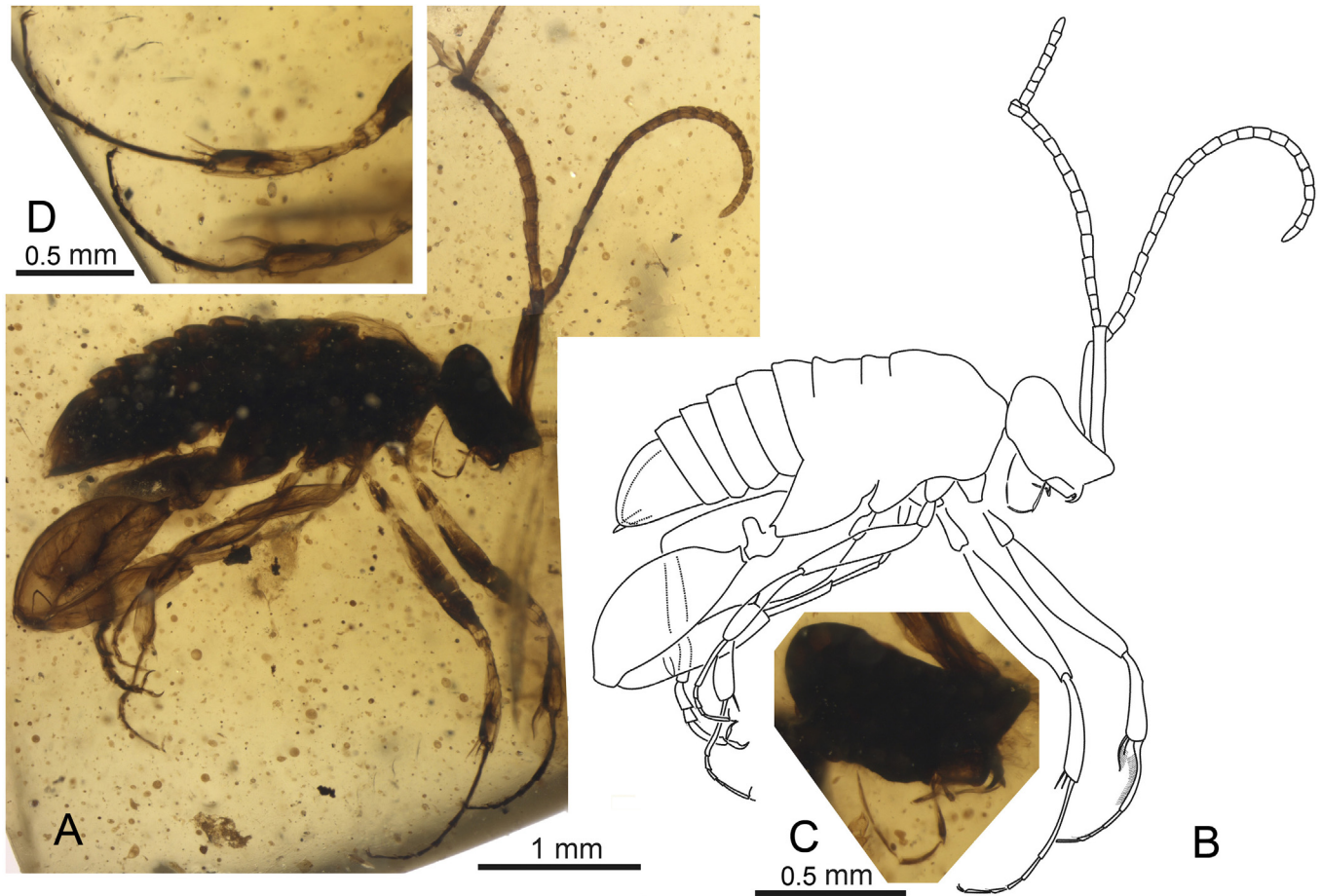


Fig. 1. *Apteroperissus magnifemoris* sp. nov., holotype PIN, no. 5620/1. A, B – lateral view, C – head, D – fore (below) and mid tibia and tarsus.

age of the rock to be 98.79 ± 0.62 Ma or at the Albian/Cenomanian boundary using U-Pb zircon dating (Shi et al., 2012). The date corresponds with the early Cenomanian, being the earliest Late Cretaceous. The amber displays clear traces of redeposition (Ross, 2015). Smith and Ross (2018) interpret the redeposition as co-sedimentary and so not affecting the above age identification as the earliest Late Cretaceous. And yet, based on that the above date is very close to the Albian–Cenomanian boundary (100.5 myr), we prefer to refer to the amber age carefully and informally as mid-Cretaceous.

The holotypes are deposited in the Öhm-Kühnle collection maintained permanently at the A.A. Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, coll. no. 5620. Observations and photographs were made with a Leica M165C stereomicroscope with a Leica DFC 420 camera. Line drawings were made with CorelDRAW software based on photographs. Helicon Focus Pro $\times 64$ was used to stack photos for better depth of field. All taxonomic acts established in the present work have been registered in ZooBank (see below), together with the electronic publication LSID: urn:lsid:zoobank.org:pub:C0CD1CF1-FF58-4B03-B55D-93095B523987.

3. Systematic palaeontology

Order: Hymenoptera Linnaeus, 1758
 Suborder: Vespina Laicharting, 1781
 Superfamily: Stephanoidea Leach, 1815
 Family: Apteroperissidae Rasnitsyn & Poinar, 2017

Genus *Apteroperissus* Rasnitsyn & Poinar, 2017

Apteroperissus magnifemoris Rasnitsyn & Öhm-Kühnle, sp. nov.
 LSID: urn:lsid:zoobank.org:act:BCEB7CCE-D3BC-411E-AF60-16C7677FBD9C
 Fig. 1.

Derivation of name. From Latin *magnifemoris*, with big femur.

Holotype. Female, PIN no. 5620/1; complete specimen with body integument somewhat degraded (black with surface sculpture practically invisible) and some body parts, particularly head, deformed.

Locality and Horizon. Hukawng Valley, Kachin State, Myanmar; lowermost Cenomanian or uppermost Albian, mid-Cretaceous.

Diagnosis. Female. Body length ca. 3 mm. Antenna 26-segmented. Scape as long as pedicel + 6 basal flagellar segments together. Pedicel as long as 1st flagellar segment. Metatrochanter with dorsal lobe. Fore femur much longer than thorax. Trochantelli lost. Tarsomeres with lower apices bearing elongate setae and no plantula. 4th tarsal segments not much shortened.

Description. Body black and appendages brown as preserved, with color depending on preservation of internal content, cuticle itself being pale brown where visible. Surface sculpture not discernible. Head distorted, much longer than high in side view, with no details visible including eye, with antenna attached to elevation(s) above mandibles (clypeus probably placed vertical to longitudinal head axis). Antenna with 26 segments, scape straight and parallel-sided as preserved, as long as pedicel + 6 basal flagellar segments together and thorax between head and propodeum, pedicel similar

to basal flagellomere, flagellomeres almost uniform, subcylindrical, less than twice as long as wide, basal and apical ones slightly shorter than others. Mandibles not big (as visible, 0.2 times as long as head), moderately wide, apparently parallel-sided, apex not visible. Maxillary palp with 4 long and thin segments visible (first of them somewhat thicker). Labial palp much shorter, with 3 elongate segments visible. Thorax (not mesosoma!) with no sutures discernible, about as long as high. Neck not visible. Propodeum and metasomal segments 1–5 distinct, similar in outline, often with weak subapical depression suggestive of possible transverse subapical pattern like in *A. zonalis* Zhang et al., 2018, with propodeum being shortest and 1st metasomal longest. Apical (7th) segment as long as high, with lower contour straight and upper convex. Hind trochanter with high dorsal lobe, trochantelli lost, fore femur thin, longer than thorax + propodeum, hind femur half as long as body without head, 2.5 times as long as wide. All tibiae shorter than respective femora, each with 2 pectinate spurs, longer spur bent, acute, most of basitarsus ventrally long-pectinate. Tarsi longer than tibiae, tarsomeres with following rate of dorsal length: fore 1: 0.32: 0.25: 0.17: 0.34; mid 1: 0.31: 0.20: 0.16: 0.33; hind 1: 0.36: 0.24: 0.12: 0.45, tarsomeres 1–4 with strong apical setae. Claws simple, moderately bent apically, with basal half straight and wide, angular at base of bent part and with several bristles there.

Measurements. total body length 3.1 mm; head length 0.8 mm, mesosoma length (excluding neck) 0.9 mm; metasoma length 1.7 mm; scape length 0.7 mm; flagellum length 2.5 mm; hind femur length 1.2 mm, width 0.5 mm; fore, mid and hind tibia length 0.95, 0.8 and 1.0 mm, respectively; fore, mid and hind tarsus length 0.95, 1.1 and 1.0 mm, respectively; metasoma length (excluding ovipositor) 1.75 mm.

Remarks. The present species differs from all female congeners in having long fore femur and, except for *A. burmanicus*, in big body size.

Aptenoperissus etius Rasnitsyn & Öhm-Kühnle, sp. nov.

LSID: urn:lsid:zoobank.org:act:9957236F-ACE2-4514-95B6-CBB4963BCF55

Fig. 2.

Derivation of name. After the movie character E.T. (= Extra-Terrestrial) that has an especially short body and long neck.

Holotype. Female, PIN no. 5620/2; complete specimen with some body parts not visible because of various inclusions (mainly plant debris) in amber, with some parts (particularly side and ventral aspects) hardly visible and with some body parts deformed (head distorted, antennae and legs partially compressed).

Locality and horizon. Hukawng Valley, Kachin State, Myanmar; lowermost Cenomanian or uppermost Albian, mid-Cretaceous.

Diagnosis. Female. Body length 2.1 mm. Antenna 20-segmented. Scape as long as pedicel + 7 basal flagellar segments together. Pedicel shorter than 1st flagellar segment. Metatrochanter with dorsal lobe. Fore femur not longer than thorax. Trochantelli lost. Tarsomeres with lower apices bearing elongate setae and no plantula. 4th tarsal segments not much shortened.

Description. Body and appendages dark brown, with yellow shine on most part of thoracic dorsum and rudimentary in some other places (possibly all or most of the insect was shiny before postburial deterioration), legs partially (mainly tarsi and femoral and tibial bases) more pale. No surface sculpture discernible. Head distorted, wide as preserved, somewhat impressed between eyes dorsally, with eyes moderately large, antennae attached mesally to low sublateral elevations above mandibles (clypeus probably placed vertically to longitudinal head axis). Antenna with 20 segments, scape slightly bent and almost parallel-sided, as long as pedicel + 7 basal flagellar segments together and as thorax between neck and propodeum, pedicel shorter than basal flagellomere, flagellomeres

almost uniform, slightly widened apically, less than twice as long as wide, basal and subapical ones slightly longer than wide. Thorax (not mesosoma!) with no sutures discernible, about as long as wide. Propodeum and metasomal segments 1–5 distinct, similar in outline except that propodeum about twice as long as these, with no subapical depression, but apparently with narrow apical translucent margin. Apical (7th) segment wider than long. Hind trochanter with high dorsal lobe, trochantelli lost, fore femur thin, about as long as thorax, hind femur about twice as long as wide. All tibiae shorter or (hind ones) as long as respective femora, each with 2 pectinate spurs, longer spur gently bent, acute, most of basitarsus long-pectinate ventrally. Tarsi longer than tibiae, tarsomeres with following rate of dorsal length: fore 1: 0.36: 0.21: 0.19: 0.36; mid 1: 0.35: 0.25: 0.15: 0.27; hind 1: 0.33: 0.26: 0.1: 0.57, tarsomeres 1–4 with strong apical setae. Claws simple, apically moderately bent, with basal half straight and wide, angular at base of bent part.

Measurements. total body length 2.1 mm; head width 0.6 mm, mesosoma length (excluding neck) 0.8 mm; metasoma length 0.8 mm; scape length 0.55 mm; flagellum length 1.55 mm; hind femur length 0.75 mm, width 0.35 mm; fore, mid and hind tibia length 0.45, 0.45 and 0.7 mm, respectively; fore, mid and hind tarsus length 0.63, 0.73 and 0.8 mm, respectively; metasoma length (excluding ovipositor) 0.8 mm.

Remarks. The species differs from its female congeners in having a 20-segmented antenna whilst having a large scape (longer than pedicel + basal 7 flagellomeres) and large eyes.

Aptenoperissus pusillus Rasnitsyn & Öhm-Kühnle, sp. nov.

LSID: urn:lsid:zoobank.org:act:2871DA9D-4D82-444A-AFFF-D245A86579E5

Fig. 3.

Derivation of name. From Latin *pusillus*, tiny.

Holotype. Female, PIN no. 5620/3; complete specimen badly covered with bubbles, so as much of the fossil is difficult or not at all visible.

Locality and horizon. Hukawng Valley, Kachin State, Myanmar; lowermost Cenomanian or uppermost Albian, mid-Cretaceous.

Diagnosis. Female. Body length 1.7 mm. Antenna 20-segmented. Scape shorter than pedicel + 3 basal flagellar segments together. Pedicel longer than 1st flagellar segment. Metatrochanter with dorsal lobe. Trochantelli lost. Fore femur as long as thorax + propodeum. Tarsomeres with lower apices bearing elongate setae and no plantula. 4th tarsal segments not much shortened.

Description. Body and appendages brown, with antenna, fore leg and mid and hind tarsi more pale. Integuments smooth where visible except thoracic dorsum at least partially apparently lineolate longitudinally and iridescent. Head big and apparently subspherical (part of contour obscured), with no detail visible except small round (or slightly oval) eye with comparatively big ommatidia (ca. 8–9 in vertical row) and narrow round occipital carina. Antenna with 20 segments, scape near straight, comparatively short and thick (shorter than pedicel + 3 basal flagellar segments together and than thorax between neck and propodeum), pedicel longer than basal flagellomere, flagellomeres apically widened, most are less than twice as long as wide, basal ones shortest, medial ones and apical segment longest. Neck short and wide, possibly quadrangular in section, sharply delimited from thorax. Thorax (not mesosoma!) with angular boundary between dorsal and lateral surface, with no discernible sutures, shorter than high. Propodeum and metasomal segments probably well separated (indicated as boundaries, but often just slightly, otherwise completely covered by bubbles), with their length shortening toward 6th metasomal one, with apical segment longest, triangular, slightly higher than long. Hind trochanter with dorsal lobe, trochantelli lost, fore femur

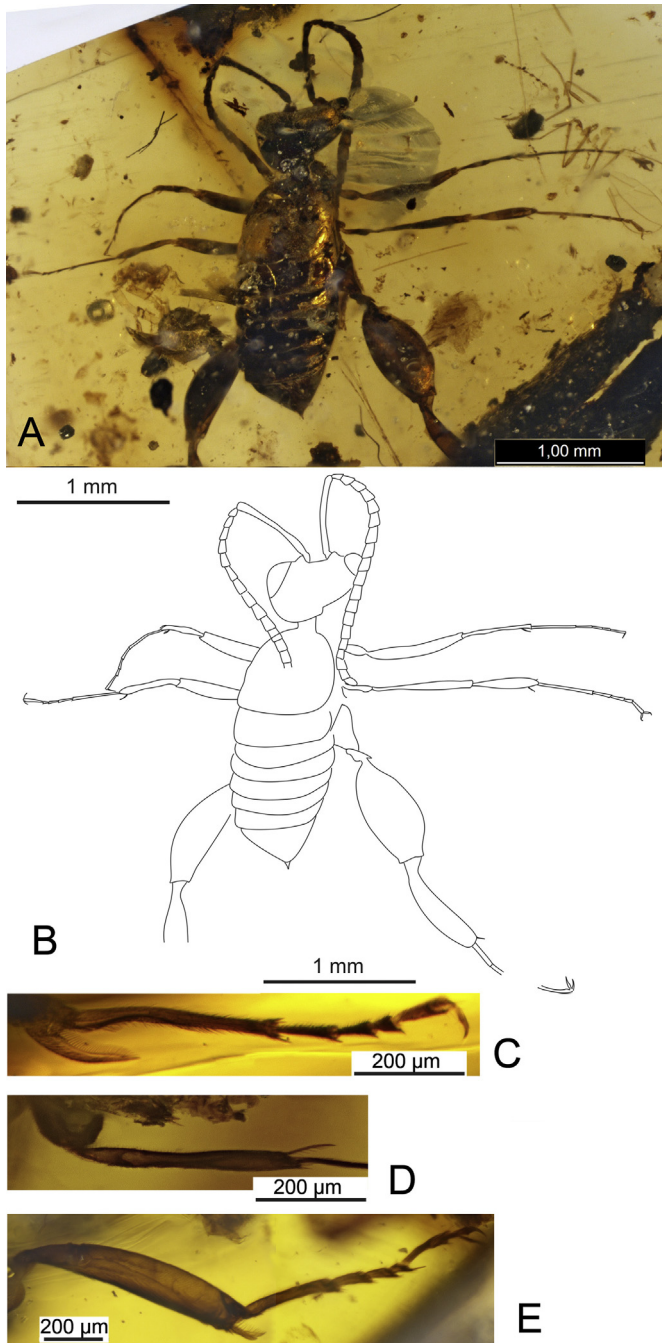


Fig. 2. *Aptenoperissus etius* sp. nov., holotype PIN, no. 5620/2. A, B – lateral view, C, E – fore, mid and hind tibia and tarsus.

not particularly thin, as long as thorax + propodeum, longer than its tibia. Longer fore tibial spur gently bent, acute, with comb of setae shortening apical, fore basitarsus with ventral comb almost until apex. Tarsi with following rate of dorsal tarsomere length: fore 1: 0.43: 0.30: 0.16: 0.50, hind 1: 0.35: 0.25: 0.16: 0.71, tarsomeres 1–4 with strong apical setae. Claws simple, apically moderately bent, transition between thicker basal and thinner apical halves apparently more smooth than in congeners.

Measurements. total body length 1.7 mm; head width about 0.5 mm, mesosoma length (excluding neck) 0.5 mm; metasoma length 0.9 mm; scape length 0.25 mm; flagellum length 1.4 mm; fore and hind tibia length 0.27 mm and 0.53 mm, respectively; fore

and hind tarsus length 0.47 mm and 0.6 mm, respectively; metasoma length (excluding ovipositor) 0.88 mm.

Remarks. The present species is the smallest among its congeners, but more significantly differs in its body proportions in having the relatively shortest scape and smallest eye (approximately one-fifth of head width) as compared to the other small congeners (*A. etius* and *A. zonalis*).

Key to the species of *Aptenoperissus*

1. Females 2
- Males 6
2. Fore femur longer than thorax + propodeum, flagellum 24-segmented, body length 3.1 mm*A. magnifemoris* sp. nov.
- Fore femur about as long as thorax 3
3. Body length 3.6 mm, flagellum 20-segmented, head transverse, eyes large*A. burmanicus* Rasnitsyn, Poinar, 2017
- Body length below 2.5 mm 4
4. Body length 1.7 mm, flagellum 18-segmented, scape shorter than pedicel + 3 basal flagellar segments together, head subspherical, eyes very small*A. pusillus* sp. nov.
- Body length 2.1–2.2 mm, eyes large, scape as long as pedicel + basal 5 flagellomeres 5
5. Scape as long as pedicel + basal 5 flagellomeres, pedicel longer than adjacent flagellomeres, flagellum 18-segmented or more, ...*A. zonalis* Zhang et al., 2018
- Scape as long as pedicel + basal 7 flagellomeres, pedicel shorter than adjacent flagellomeres, flagellum 18-segmented*A. etius* sp. nov.
6. Forewing length 2.2 mm, flagellum 20-segmented, hind tibial spur long pectinate*A. formosus* Zhang et al., 2018
- Forewing 3.5 mm or longer, flagellum more than 20-segmented, hind tibial spur at most short pectinate 7
7. Forewing length 3.5 mm, forewing with 2r-m crossvein present as stubs on RS and M*A. amabilis* Zhang et al., 2018
- Forewing length 4.7 mm, forewing with 2r-m totally lost*A. delicatus* Zhang et al., 2018

4. Discussion

The newly described aptenoperissid fossils considerably increase our knowledge concerning the diversity of these unusual wasps. Over-all, they are now known from nine specimens representing eight species (Fig. 4) found in eight amber pieces, each species in its own piece. Of these, five species are known as females only and three as males, however, the known males and females can in no case be assigned to a same species. This is caused by the deep sexual dimorphism and the varying feature combinations. Indeed, males of *A. formosus* Zhang et al., 2018 and *A. amabilis* Zhang et al., 2018 have a smaller body size and 20-segmented antenna, as do the females of *A. etius* sp. nov., *A. pusillus* sp. nov. and *A. zonalis* Zhang et al., 2018. In contrast, the male *A. delicatus* Zhang et al., 2018 is bigger and has a 26-segmented antenna, as the females *A. burmanicus* Rasnitsyn, Poinar, 2017 and *A. magnifemoris* sp. nov. However, we are aware of no specific feature which would allow to reliably assign a male of either *A. formosus* or *A. amabilis* to a female of either *A. etius*, *A. pusillus*, or *A. zonalis*. Equally, the male *A. delicatus* displays no specific similarity to either *A. burmanicus* or *A. magnifemoris*.

An additional reason to avoid association of sexes in *Aptenoperissus* other than based on serious evidence is that all eight species are known just from a single specimen each (except for *A. formosus* with the holotype and sole paratype syninclusion in one and the same piece of amber). This attests the genus as highly diverse with each its particular species being rare, with low probability of being found repeatedly. Therefore, it is not possible to

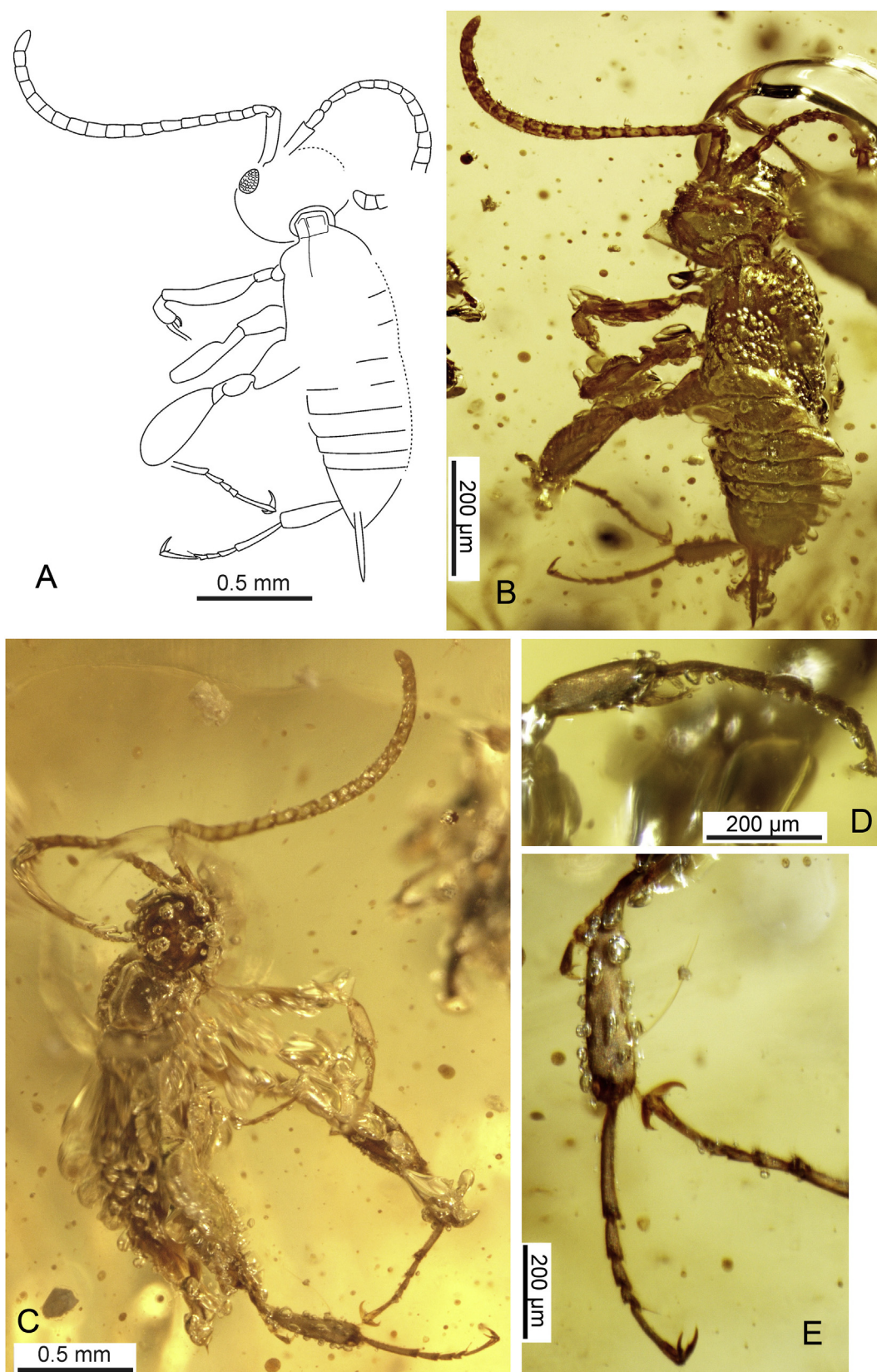


Fig. 3. *Aptenoperissus pusillus* sp. nov., holotype PIN, no. 5620/3. A, B – dorsolateral view, C – opposite lateral view, D – fore tibia and tarsus, E – hind tibia and tarsi.

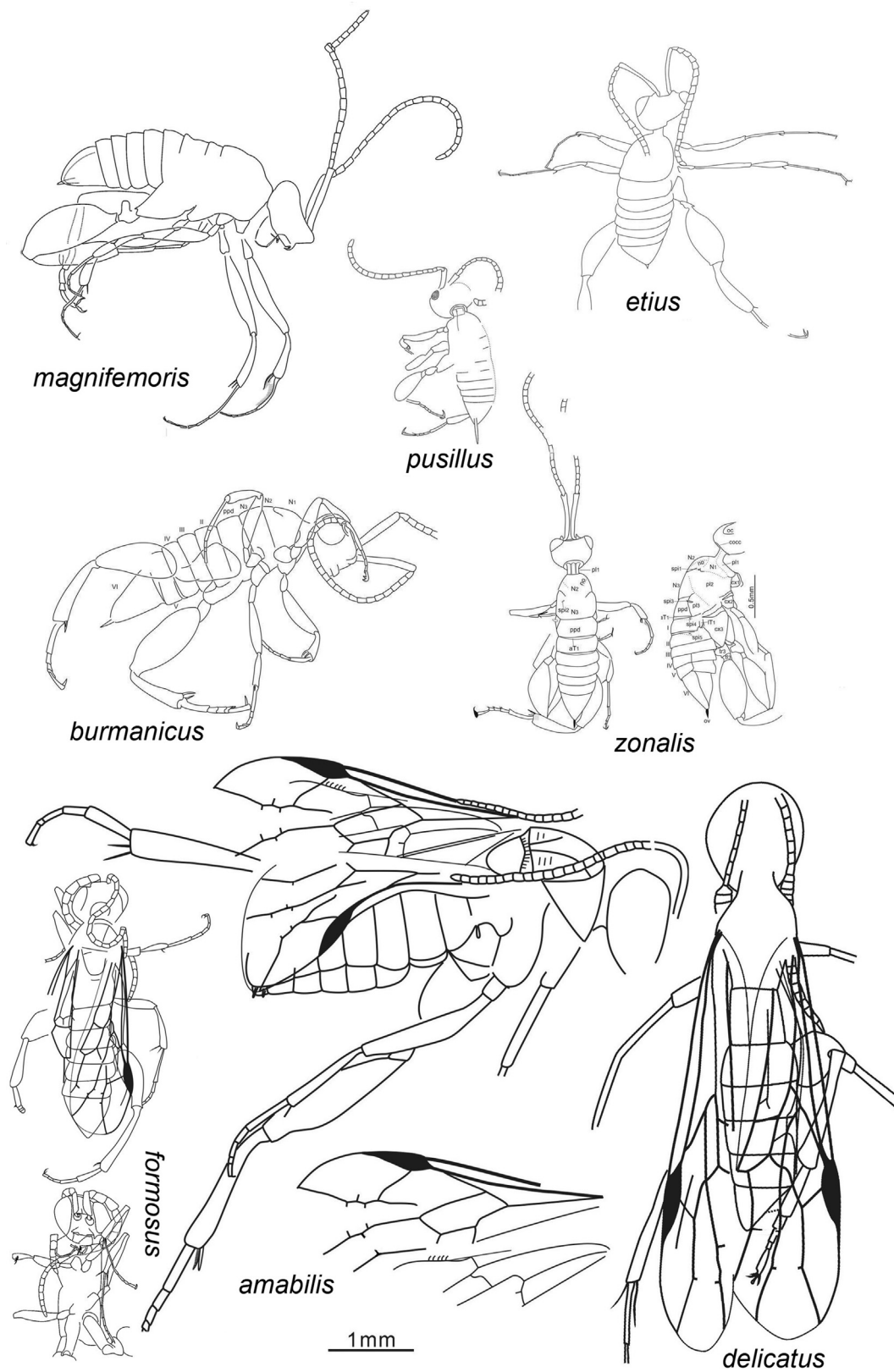


Fig. 4. All eight species of *Aptenoperissus* in scale for comparison.

seek conspecificity of males and females of *Aptenoperissus* unless undeniable evidence is presented.

The new species are attributed to the genus *Aptenoperissus* based on the diagnostic characters of the latter: body with no wasp waist, antenna geniculate and polymerous (>16 flagellomeres), fore tibia with two spurs, hind legs incrassate, females apterous and with nine externally visible segments (four mesosomal and five metasomal), with thorax (including propleurae) consolidated in a hard and almost sutureless box well separated from propodeum, males winged, with long and reclival crossvein 1-Rs and long, parallel-sided cell 1m-cu receiving cu-a crossvein well after its base.

The above stated inference about the high diversity of *Aptenoperissus* in the insect assemblage in Burmese amber allows to draw significant conclusions which are explained in the following. The genus known by now (Rasnitsyn et al., 2017; Zhang et al., 2018a; Zhang et al., 2018d; present paper) can be properly attested as an unusual, even grotesque form. The following features rarely or never occur in the entire order Hymenoptera, and decidedly never in combination:

- Antenna which is simultaneously polymerous (>16 segments) and geniculate (never recorded elsewhere in the order)
- Female thorax consolidated in a hard and almost sutureless box including all pro-, meso and metaterga and respective pleura, but not propodeum which is left clearly delimited (never recorded elsewhere in the order)
- Fore tibia with the second spur secondarily restored after loss by the common ancestor of Ucalcarida, the clade embracing Cephoidea, Siricoidea, Xiphydrioidea (if considered independent of Siricoidea), Orussoidea and Apocrita (otherwise recorded in the crown group Ceraphronoidea only)

The high species-level diversity and grotesque morphology do not exhaust the noteworthy features of *Aptenoperissus*. The genus and, hence, the whole family Aptenoperissidae is according to our current knowledge endemic to the Myanmar terrain in the mid-Cretaceous; its superfamily, the basal apocritan Stephanoidea, however was flourishing in the Jurassic (Rasnitsyn and Zhang, 2010). Therefore, we state the possibility that these very features could form an insularity syndrome, which is characteristic of taxa flourishing on isolated islands, minor continents and ancient lakes. Marsupialia and Monotremata in the Australian realm, dodo on Mauritius, fish and crustaceans in the Baikal and African rift lakes etc. represent popular examples of insularity. This hypothesis is further supported by the existence of other families only known from the Burmese amber assemblage (such possibly endemic families are more numerous there than in any other amber lagerstätte), in Hymenoptera (Zhang et al., 2018c) and beyond (Ross, 2018), with many of these taxa being quite bizarre. Other possibly endemic orders in the Burmese amber assemblage are for example orders Alienoptera (Bai et al., 2016, 2018) and Tarachoptera (Mey et al., 2017) and further the families Myanmarinidae (Li et al., 2018; Zhang et al., 2018b), Mysteromyiidae (Grimaldi, 2016), Oligidae (Vršanský and Wang, 2017), and Manipulatoridae (Vršanský and Bechly, 2015).

The above observations suggest the possibility of an insular nature of the mid-Cretaceous Burmese biota. This hypothesis contradicts paleogeographical inferences from paleotectonic research indicative of a collision of the Indo-China group of plates, including the West Burma plate, with Asia (via South and North China plates) before the end-Triassic (Lawver et al., 2003; Metcalfe, 2013); an alternative hypothesis is that the Central Burma plate collided with Sino-Burma by the mid-Cretaceous (Acharyya, 2010). A differing theory (Heine et al., 2004; Seton et al., 2012), based on marine magnetic anomalies and geological data, placed the collision of the

West Burma plate with the Proto-Southeast Asia mainland in the Late Cretaceous near 80 Ma (l.c., Plate 1e). This would imply the West Burma plate as an island isolated well and long (since more than 140 Ma; l.c., Plate 1b) by the inferred time of Burmese amber (around 100 Ma; see above). It is far beyond our expertise to judge and select a correct plate tectonics hypothesis. Yet we can see that the currently available paleontological information, as presented on hand, favors the inference that the Burmese amber fossil assemblage reflects a pre-collision rather than post-collision structure of the biota. The proposal by Poinar (2018) that the Burmese amber biota is simply of Gondwanan nature cannot be accepted until better grounded, because the Levantine ambers of unquestioned Gondwanan origin reveal a rather ordinary fauna more similar to that of Laurasia than to the Burmese fossil assemblage (see above).

5. Conclusion

Aptenoperissidae, with their eight species in a single genus, represent a bizarre, morphologically unique, sexually extremely dimorphic, species-rich group of unknown biology which is only known from and possibly endemic of mid-Cretaceous Burmese amber. These features lead us to the conclusion of a high likelihood of an insular nature of the Burmese amber fossil assemblage and therefore geographic isolation, which later might have been combined with a gradually increasing contact of biota with increasing proximity of the Sunda plate, before the actual plate collision. This contradicts several current theories about the tectonic history of northern Myanmar, however being congruent with the theory of Heine et al. (2004), placing the plate collision in the Late Cretaceous. We hope that further research will help to solve this puzzle.

Acknowledgements

The authors thank Dr Dmitry Shcherbakov (Paleontological Institute, Russian Academy of Science) for help with literature and for the useful discussion concerning a possible isolation of the Burmese amber biota. We offer our sincere gratitude to the anonymous reviewers for their comments. For APR, this research was supported by the Program of the Presidium of the Russian Academy of Sciences “Problems of the Origin of Life and Formation of the Biosphere”.

References

- Acharyya, S.K., 2010. Tectonic evolution of Indo-Burma range with special reference to Naga-Manipur Hills. *Memoir Geological Society of India* 75, 25–43.
- Bai, M., Beutel, R.G., Klass, K.-D., Zhang, W., Yang, X., Wipfler, B., 2016. †Alienoptera — A new insect order in the roach-mantodean twilight zone. *Gondwana Research* 39, 317–326.
- Bai, M., Beutel, R.G., Zhang, W.W., Wang, S., Hörnig, M., Gröhn, C., Yan, E., Yang, X.K., Wipfler, B., 2018. A new Cretaceous insect with a unique cephalo-thoracic scissor device. *Current Biology* 28, 438–443. <https://doi.org/10.1016/j.cub.2017.12.031>.
- 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.
- Grimaldi, D.A., 2016. Diverse orthorrhaphan flies (Insecta: Diptera: Brachycera) in amber from the Cretaceous of Myanmar: Brachycera in Cretaceous amber, Part VII. *Bulletin of the American Museum of Natural History* 408, 131 pp.
- Heine, C., Müller, R.D., Gaina, C., 2004. Reconstructing the lost eastern Tethys ocean basin: convergence history of the SE Asian margin and marine gateways. *Geophysical Monograph Series* 149, 37–54.
- Kania, I., Wang, B., Szewo, J., 2015. *Dicranoptycha* Osten Sacken, 1860 (Diptera, Limoniidae) from the earliest Upper Cretaceous Burmese amber. *Cretaceous Research* 52, 522–530.
- Lawver, L.A., Dalziel, I.W.D., Gahagan, L.M., Martin, K.M., Campbell, D.A., 2003. The PLATES 2003. Atlas of plate reconstructions (750 Ma to Present Day). PLATES progress report no. 280-0703. UTIG Technical Report 190, 97 pp.
- Li, L.F., Shih, C.K., Rasnitsyn, A.P., Li, D.Q., Ren, D., 2018. A new wasp of Myanmarinidae (Hymenoptera: Stephanoidea) from the mid-Cretaceous Myanmar amber. *Cretaceous Research* 86, 33–40.

- Metcalfe, I., 2013. Gondwana dispersion and Asian accretion: Tectonic and palaeogeographic evolution of eastern Tethys. *Journal of Asian Earth Sciences* 66, 1–33.
- Mey, W., Wichard, W., Müller, P., Wang, B., 2017. The blueprint of the Amphiesmenoptera – Tarachoptera, a new order of insects from Burmese amber (Insecta, Amphiesmenoptera). *Fossil Record* 20, 129–145.
- Poinar Jr., G.O., 2018. Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. *Historical Biology*. <https://doi.org/10.1080/08912963.2018.1446531>.
- Rasnitsyn, A.P., Zhang, H.C., 2010. Early evolution of Apocrita (Insecta, Hymenoptera) as indicated by new findings in the Middle Jurassic of Daohugou, North-east China. *Acta Geologica Sinica (English edition)* 84 (4), 834–873.
- Rasnitsyn, A.P., Poinar Jr., Brown, A.E., 2017. Bizzare wingless parasitic wasp from mid-Cretaceous Burmese amber (Hymenoptera, Ceraphronoidea, Aptenoperissidae fam. nov.). *Cretaceous Research* 69, 113–118.
- Ross, A., 2015. Insects in Burmese amber. *Entomologentagung Frankfurt/M. Programm und Abstracts* 72.
- Seton, M., Müller, R.D., Zahirovic, S., Gaina, C., Torsvik, T., Shepard, G., Talsma, A., Gurnis, M., Turner, M., Maus, S., et al., 2012. Global continental and ocean basin reconstructions since 200 Ma. *Earth-Science Review* 113, 212–270.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Wang, 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.
- Smith, R.D.A., Ross, A.J., 2018. Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resin-producing forests to brackish-marine waters, and the age of the amber. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 107 (2–3), 239–247.
- Vršanský, P., Bechly, B., 2015. New predatory cockroaches (Insecta: Blattaria: Manipulatoridae fam. n.) from the Upper Cretaceous Myanmar amber. *Geologica Carpathica* 66 (2), 133–138.
- Vršanský, P., Wang, B., 2017. A new cockroach, with bipectinate antennae, (Blattaria: Olidae fam. nov.) further highlights the differences between the Burmite and other faunas. *Biologia* 72 (11), 1327–1333.
- Zhang, Q., Rasnitsyn, A.P., Wang, B., Zhang, H.C., 2018a. New data about the enigmatic wasp from mid-Cretaceous Burmese amber (Hymenoptera, Stephanioidea, Aptenoperissidae). *Cretaceous Research* 84, 173–180.
- Zhang, Q., Rasnitsyn, A.P., Wang, B., Zhang, H., 2018b. Myanmarinidae, a new family of basal Apocrita (Hymenoptera: Stephanioidea) from mid-Cretaceous Burmese amber. *Cretaceous Research* 81, 86–92.
- Zhang, Q., Rasnitsyn, A.P., Wang, B., Zhang, H.C., 2018c. Hymenoptera in Burmese amber: new families and a review of the fauna. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* (in press).
- Zhang, Q., Rasnitsyn, A.P., Zhang, H.C., 2018d. New female *Aptenoperissus* from mid-Cretaceous Burmese amber. *Cretaceous Research* (in press).