

BURMORUSSIDAE, A NEW FAMILY OF PARASITIC WASPS (INSECTA, HYMENOPTERA) FROM MID-CRETACEOUS BURMESE AMBER

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Abstract: A new genus and species, *Burmorussus mirabilis*, is described based on two specimens from the mid-Cretaceous Burmese amber, and considered to be a specialized parasitic wasp of wood-living hosts. The new taxon is characterized by an orussid-like ocellar crown, big eyes, antennae attached well above the clypeus, and antennal grooves or ventral transverse frontal carinae absent. Additionally, all legs carry a prominent lanceolate lobe on the third tarsomere. A similar structure is found, but organized differently, in Recent Orussidae and Stephanidae, serving as

part of a vibration analyser. Although sharing some characters with families Karatavidae, Orussidae and Paroryssidae, this new taxon cannot be assigned to any of these families. We propose a new monotypic family Burmorussidae and assign it to the superfamily Orussoidea. A phylogenetic analysis confirms the monophyly of Orussoidea, which occurs a sister group to Apocrita.

Key words: Orussoidea, Karatavitoidea, phylogeny, mid-Cretaceous, Burmese amber.

MID-CRETACEOUS (late Albian to early Cenomanian) amber from the Hukawng Valley in Myanmar is currently one of the richest sources of knowledge about insects and other segments of the non-marine biosphere of that period (Rasnitsyn 1996; Zherikhin & Ross 2000; Grimaldi *et al.* 2002; Ross *et al.* 2010; Rasnitsyn *et al.* 2016; Guo *et al.* 2017; Ross 2018). It is noteworthy that endemic families, including Aptenoperissidae, Bryopompilidae, Melittosphecidae, Myanmarinidae and Othniodellithidae (Poinar & Danforth 2006; Engel *et al.* 2016; Rodriguez *et al.* 2016; Guo *et al.* 2017; Rasnitsyn *et al.* 2017), comprise a particularly impressive proportion of Hymenoptera in the Burmese amber. In this report, we describe one more endemic wasp from this source.

The new family Burmorussidae described herein shares characters with the extinct Mesozoic families Karatavidae (Rasnitsyn 1963, 1969; Rasnitsyn *et al.* 2006; Rasnitsyn & Zhang 2010) and Paroryssidae (Martynov 1925; Rasnitsyn 1963, 1968), and extant Orussidae recorded since the Cretaceous (Rasnitsyn 1977; Basibuyuk *et al.*

2000; Vilhelmsen 2004; Vilhelmsen & Zimmermann 2014). Families Orussidae and Paroryssidae are grouped into the superfamily Orussoidea, which forms a sister group to the Apocrita (Ronquist *et al.* 1999, 2012; Vilhelmsen *et al.* 2001, 2008, 2010; Rasnitsyn & Zhang 2010; Heraty *et al.* 2011; Sharkey *et al.* 2012; Peters *et al.* 2017). Jurassic Karatavidae is the only family within the superfamily Karatavitoidea and displays numerous plesiomorphic characters; this points to its ancestral position with respect to Orussoidea and Apocrita (Rasnitsyn & Zhang 2010). Rasnitsyn & Zhang (2010) proposed an infraorder, Orussomorpha, for Karatavitoidea and Orussoidea, but this taxon is paraphyletic. The new fossil described herein from the mid-Cretaceous Burmese amber represents a major addition to the above diversity.

MATERIAL AND METHOD

Here, we describe two specimens collected from the amber mines sited in the Hukawng Valley of Kachin

Province, Myanmar (for locality details see Li *et al.* 2018). The age of Burmese amber is still debated. The rock containing the Burmese amber has been radiometrically dated at 98.79 ± 0.62 myr (Shi *et al.* 2012). The amber displays clear traces of re-deposition and could therefore be older than the enclosing rocks (Ross *et al.* 2010). However, the most recent research by Smith & Ross (2018) contradicts this hypothesis and suggests an early Cenomanian age for the amber. Here, we will not discuss this problem and refer to it informally as mid-Cretaceous.

The specimens described herein are registered and deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS; specimen prefix NIGP). The material was studied under a Nikon SMZ-10 R stereoscopic microscope and a Nikon Optiphot compound microscope with magnifications up to $800\times$ at the State Key Laboratory of Palaeobiology and Stratigraphy, NIGPAS, and using Leica M165C stereomicroscope with a Leica DFC 420 camera at the A.A. Borissiak Paleontological Institute, Russian Academy of Sciences, in Moscow. In most instances, incident and transmitted lighting were employed simultaneously. Helicon Focus Pro $\times 64$ was used to stack photos for better depth of field. The line drawings were prepared based on photographs using image-editing software (CorelDraw X7 and Adobe Photoshop CS6).

Cladistic analysis was performed with PAUP 4.0a software (Swofford 2003). Our data matrix is drawn from the character sets of Ronquist *et al.* (1999), Vilhelmsen (2003), Vilhelmsen *et al.* (2010), Rasnitsyn & Zhang (2010), Vilhelmsen & Zimmermann (2014) with corrections and additions, and is available in Zhang *et al.* (2020). All characters were considered with equal weight; 13 characters were ordered and 44 were unordered (for details, see Zhang *et al.* 2020). Multistate characters were interpreted as polymorphism. The cladogram was rooted using Xyelidae as outgroup. A branch-and-bound search was employed to find all most parsimonious trees. To evaluate the reliability of retained tree we used bootstrap analysis (500 replicates) with full heuristic search, keeping up to 1000 most parsimonious trees at every replicate (starting seed = 1310, the time when analysis was started).

Wing venation nomenclature follows Rasnitsyn (1969). The number before the vein name refers to the abscissa number (Fig. 1B).

SYSTEMATIC PALAEOLOGY

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Order HYMENOPTERA Linnaeus, 1758
Superfamily ORUSSOIDEA Newman, 1834

Families included. Orussidae Newman, 1834, Paroryssidae Martynov, 1925, Burmorussidae fam. nov.

Diagnosis. Forewing with Sc absent; costal area wider than C; 1-Rs proclined; 3r-m absent; 2m-cu absent or nebulous; a1-a2 present; A2+3 before a1-a2 usually not developed or nebulous, when present, forming an anal loop. Hindwing with 3r-m lost, cell 2+3r-m open; jugal lobe present. Halves of the first abdominal tergum fused to form entire plate (propodeum). Propodeum and metapostnotum not fused with metapleura laterally. Abdominal segment 2 cylindrical or slightly depressed, wider than long, without waist. Larva carnivorous (known only for extant Orussidae; the shape of ovipositor in Paroryssidae and the presence of tibial vibration sensors in Burmorussidae suggest a carnivorous larval diet for these fossil families as well).

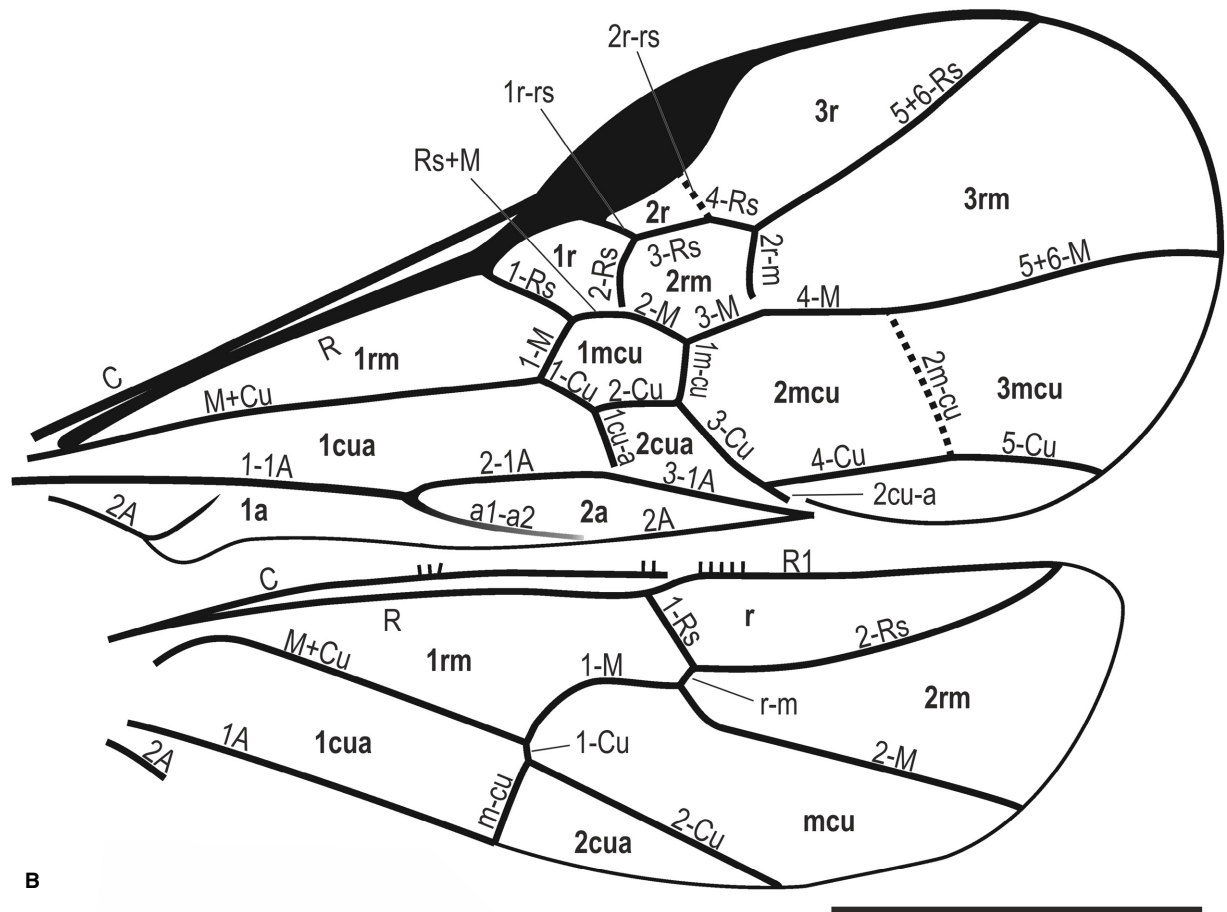
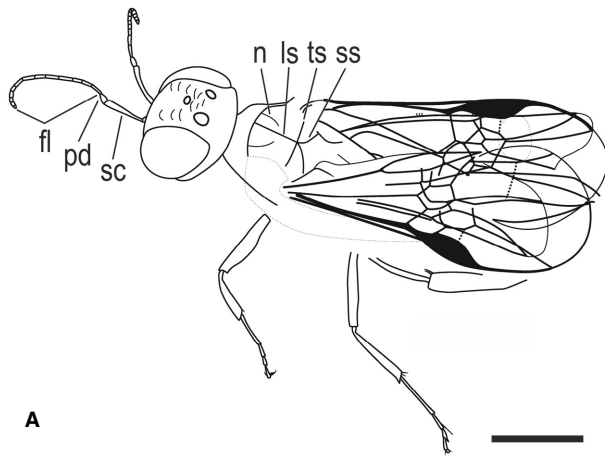
Comparison. Orussoidea resembles Karatavitoidea Rasnitsyn, 1963 in having the fore wing with Sc absent, 1-Rs proclined, the hind wing with the jugal lobe present, and the 1st abdominal segment with both halves of tergite fused, modified into the propodeum but not fused completely with the metapleura. It differs from Karatavitoidea in absence of 3r-m in the fore wing and absence of 1m-cu in the hind wing. It also differs from Siricina in the structure of 1st abdominal segment (both halves of tergite fused, modified into the propodeum but not fused completely with the metapleura), carnivorous larval diet; from Apocrita (= Vespina excluding Orussoidea and Karatavitoidea) in the absence of true wasp waist, presence of A2+3 in the fore wing (except Kuafuidae) and in the presence of jugal lobe in hind wing (from the majority of Apocrita).

Family BURMORUSSIDAE nov.

LSID. urn:lsid:zoobank.org:act:8122239D-A1FF-4FF5-9905-6AC354C8CE6A

Type genus. *Burmorussus* gen. nov.

FIG. 1. *Burmorussus mirabilis* gen. et sp. nov., holotype NIGP167698, mid-Cretaceous, Burmese amber. A, interpretative drawing (sc, scape; pd, pedicel; fl, flagellum; n, notauli; ls, longitudinal sulcus; ts, transverse sulcus; ss, scuto-scutellar sulcus). B, reconstruction of wings with vein names (regular) and cell names (bold), nebulous veins shown by dotted lines. C–E, photos of the specimen from various aspects. All scale bars represent 0.5 mm. Colour online.



Genera included. Only the type genus.

Diagnosis. Head with crown of paired backward-pointing teeth around median ocellus (ocellar corona) with ventralmost coronal teeth well below the ocellus, ventral unpaired tooth absent. Eyes large, occupying the major part of head surface. Antennae with 12 flagellomeres, attached high above clypeus, at midheight of eye. No ventral transverse frontal carina and antennal grooves developed. Mandibular tips meeting anteriorly of labrum. Mesonotum with longitudinal, transverse, scuto-scutellar sulci and notauli developed; admedial and adlateral lines invisible possibly because of rough mesonotal sculptures. Middle and hind coxae separated by elongated postepisternum. Fore wing with crossveins 1r-rs, 2r-rs, 2r-m, 1m-cu, 2m-cu, 1cu-a, 2cu-a and a1-a2 developed, 3r-m lost; 1r-rs shorter than 2r-rs; 2A well developed beyond a1-a2 and partly spectralized basad of a1-a2; 3A absent; wing fixation apparatus (cenchri + rough area within anal loop) not developed. Hind wing with cell r enclosed; crossveins 1r-m and cu-a present, 2r-m and m-cu lost. 1st abdominal segment flat dorsally, with halves of tergite fused, differing in shape and surface sculpture from subsequent segments, forming a kind of propodeum, not fused laterally with metapleura; articulation between 1st and 2nd abdominal segments (propodeum and 1st metasomal) flexible, waist between 1st and 2nd segments wide in upper view and not deep in side view.

Comparison. The new family differs from Orussidae and Paroryssidae in having antennae with 12 flagellomeres attached high above the clypeus, the elongated postepisterna separating the middle and hind coxae, the wing fixation apparatus absent, fore wing with 1r-rs, 2r-rs and 2m-cu present. A more detailed morphological and phylogenetic analyses of Burmorussidae in comparison with other taxa is provided in the Discussion below.

Genus BURMORUSSUS nov.

LSID. urn:lsid:zoobank.org:act:4BB9C96B-47F6-45C7-B8CD-DA346E0CFFC5

Derivation of name. From Burma (former name of Myanmar) and genus *Orussus* Latreille, 1796.

Type species. *Burmorussus mirabilis* sp. nov.

Species included. Type species only.

Diagnosis. As for family, by monotypy.

Burmorussus mirabilis sp. nov.

Figures 1, 2

LSID. urn:lsid:zoobank.org:act:27C5F4EB-16C6-4450-8FFE-8D58E8A59B34

Derivation of name. From Latin *mirabilis*, amazing.

Material. Holotype NIGP167698, paratype NIGP169597.

Description. Male. Head and thorax shining, mesoscutellum, antennae, legs, wing veins and abdomen brown, wing membrane not coloured. Head as wide as high, roughly dotted; eyes large with height equal to *c.* 0.7× head height; ocelli ovate with lateral ones slightly wider than median one, distance between ocelli equal to *c.* 2× lateral ocellus width; ocellar corona consisting of 5–6 pairs of teeth, with upper teeth overlapping and forming irregular transverse sculpture between lateral ocelli. Antenna with scape long and robust, 4.0× as long as wide and 0.4× as long as eye height, and *c.* 0.2 of antennal length; pedicel short, conical, 1.6× as long as wide, 0.28× as long as scape; flagellum filiform with 1st flagellomere 2.0× as long as pedicel and 5.2× as long as wide, 2nd 0.6× as long as 1st, following ones gradually decreasing in length but not in width, apical one 2.0× as long as wide, rounded apically. Mandibles with three teeth: one obtuse tooth on upper edge of mandible and two sharp teeth on tip. Thorax roughly dotted, with irregular transverse sculpture. Mesonotum with transverse suture deep; longitudinal and scuto-scutellar sulci dotted; notauli weak, converging, vanishing in the middle of mesonotum, reaching neither each other nor longitudinal suture nor transverse suture. Fore coxae with long lobes medial of trochanters. Tarsi 5-segmented with 4th tarsomere very short; 3rd one apically with lanceolate ventral apophysis. Hind tibia swollen (*c.* 4× as wide as 1st tarsomere), and slightly narrowed toward apex; fore and mid tibiae not swollen (2–3× as wide as 1st tarsomere). Middle tarsomere 2 with long seta reaching tip of apophysis of tarsomere 3. Fore wing with costal area narrow basally, gradually widened distally, 3× as wide as C at the widest point (near furcation of R and Rs); pterostigma completely sclerotized, with rounded posterior edge, 3.2× as long as wide; C overlapping base of pterostigma, costal flexion line oblique; 1-Rs 1.4× as long as 1-M; Rs+M short, 0.4× as long as 1-Rs; 2-Rs 2.0× as long as 1r-rs; 4-Rs 0.6× as long as 3-Rs; 1r-rs oblique, joining pterostigma at its 0.25 length; 2r-rs nebulous, vertical, 1.4× as long as 1r-rs, joining pterostigma at its 0.6 length; cell 1r 1.6× as long as wide, 2r 2.1× as long as wide, 3r 3.8× as long as wide; 2-M 1.9× as long as Rs+M; 3-M as long as 2-M; distal ends of Rs and M significantly diverging; cell 2rm 1.2× as long as wide; 1r-m bent towards wing base; 2r-m displaced basad; 2m-cu nebulous; 2-Cu 1.5× as long as 1-Cu; cell 1mcu 1.5× as long as wide; 2-1A 1.6× as long as 3-1A; cell 2a 4.8× as long as wide; 2-Rs, 1r-m, 1cu-a and 2cu-a each with one bulla in its lower part; 1A not developed beyond 2a cell; 2A spectralized between anal loop and a1-a2. Hind wing with basal hamulus absent, three median and seven distal hamuli present; cell r 4.4× as long as wide; 1-Rs

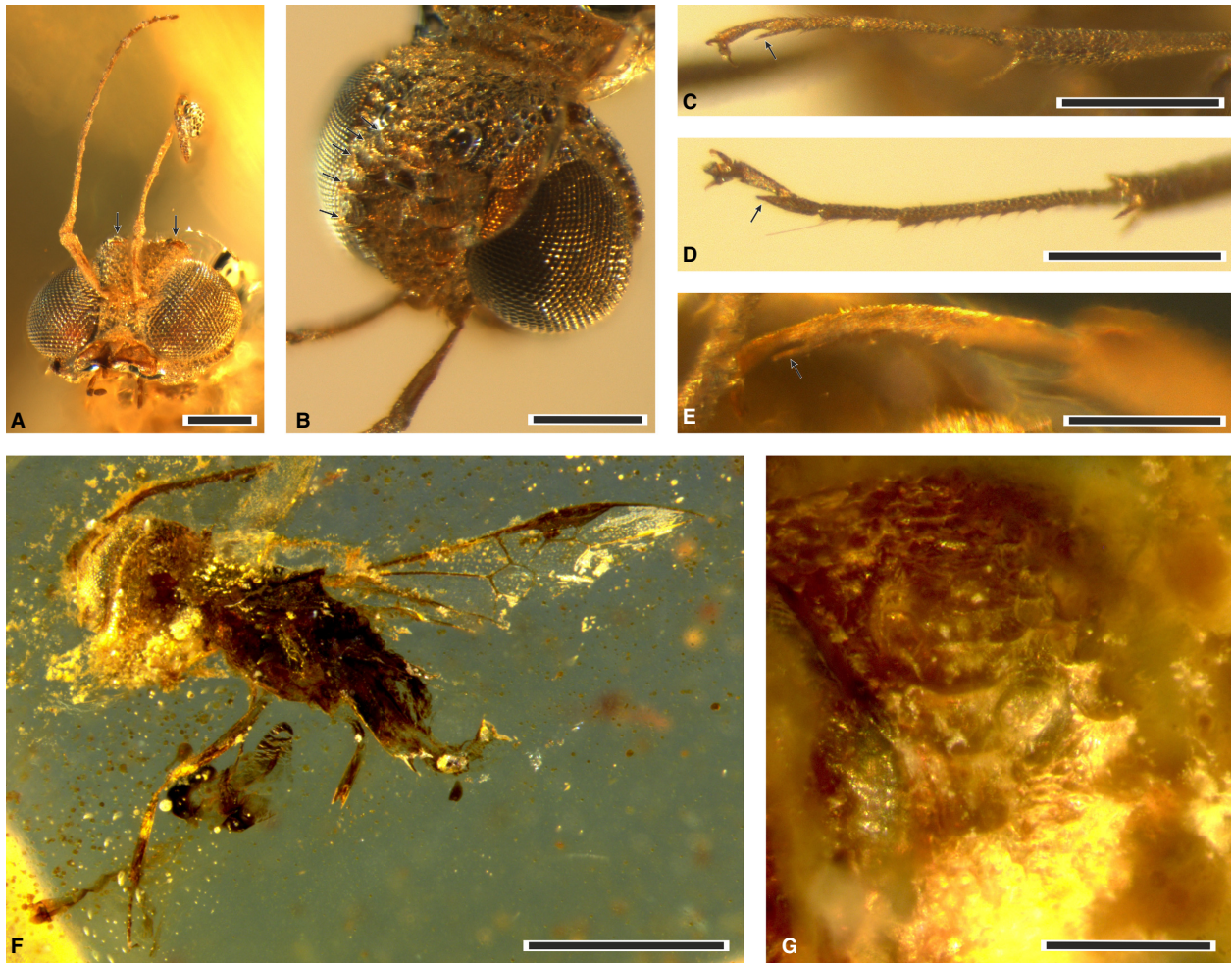


FIG. 2. *Burmorussus mirabilis* gen. et sp. nov., mid-Cretaceous, Burmese amber. A–E, holotype NIGP167698: A, head, frontal view, with teeth of ocellar corona shown by arrows; B, head, top view, with teeth of ocellar corona shown by arrows; C–E, fore, mid and hind-tarsi respectively, with lanceolate lobe on 3rd tarsomeres shown by an arrow, 4th tarsomere very short in all legs and hardly distinguishable from 5th one. F–G, specimen NIGP169597: F, general view; G, head sculpture. Scale bars represent: 0.2 mm (A–E, G); 1.0 mm (F). Colour online.

4.2× as long as 1r-m; 1-M bent anteriorly; distal part of M gently curved backwards; 1-Cu c. 0.2× as long as cu-a; a short stab of 2A running along wing posterior margin. 1st abdominal segment (propodeum) coarsely dotted, subsequent segments slightly rugged. Measurements: body length 2.5 mm, head height 0.68 mm, width 0.66 mm, eye height 0.43 mm, antennal length 1.2 mm, thorax length 0.7 mm, abdominal length 1.4 mm; fore wing length 1.8 mm, width 0.73 mm; hind wing length 1.5 mm, width 0.36 mm.

Remarks. By the structure of ocellar corona and the preserved venation, specimen NIGP169597 (Fig. 2F, G) is undoubtedly assigned to Burmorussidae. However, the specimen is too poorly preserved to add much to the description. It almost has the same size as the holotype of *B. mirabilis* judging from its fore wing 2.1 mm in length, but its gender is unknown due to its abdomen

missing. Here we preliminary assign this specimen to *B. mirabilis*.

PHYLOGENETIC ANALYSIS

The results of our phylogenetic analysis returned a single maximal parsimonious tree (Fig. 3) length 183 steps, CI = 0.4645, HI = 0.5519, RI = 0.7358, RC = 0.3418. The bootstrap supports for branches retained in the analysis are shown on Figure 3.

The goal of our analysis is in the positioning *Burmorussus* within the system of Hymenoptera. Our results do not necessarily show the true relationships within Symphytan taxa (bootstrap supports 17–29% for the symphytan clades). Clade Orussoidea plus Apocrita forms a good

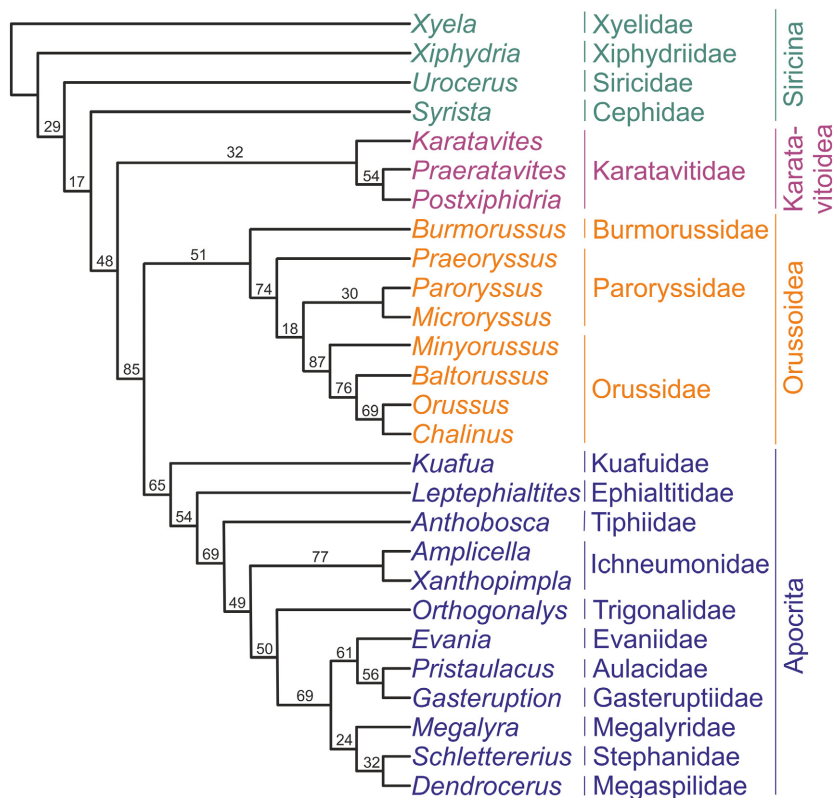


FIG. 3. The most parsimonious tree showing the relationships of general groups of basal Vespina. Bootstrap support is shown above the branches. Colour online.

monophyletic group (bootstrap support 85%). Karatavitoidea becomes a sister-group to Orussoidea + Apocrita, but with lower bootstrap support (48%). Orussoidea, including Orussidae, Paroryssidae and Burmorussidae, form a monophyletic group (but with bootstrap support of just 51%), sister to Apocrita *s. str.* Within Orussoidea, three groups are distinguishable. Orussidae, including fossil genera Minyorussus and Baltorussus, are strongly supported as being monophyletic (87% bootstrap support). On the other hand, Paroryssidae are evidently paraphyletic to Orussidae (bootstrap support for the clade including Praeoryssus + Paroryssus + Microryssus is just 20%). However, the clade including Paroryssidae + Orussidae is better supported (74% bootstrap value). Burmorussidae is placed as sister group to Paroryssidae + Orussidae, but only 50% of bootstrap replicates place Burmorussidae within Orussoidea. Another 23% of replicates places Burmorussidae within Apocrita *s. str.*, and 9% return the monophyly of the clade Burmorussidae + Orussidae (Orussoidea excluding Paroryssidae). Other groupings including Burmorussidae have bootstrap support less than 5%. Based on the results of the bootstrap analysis we can propose two hypotheses on the placement of Burmorussidae within Hymenoptera: within Orussoidea as a sister group to Paroryssidae + Orussidae or outside Orussoidea, as a sister group to Vespina and Paroryssidae + Orussidae (trichotomy).

The first hypothesis has much more solid support and seems more preferable.

Rasnitsyn & Zhang's (2010) Orussomorpha, including Karatavitidae, Orussidae and Paroryssidae, is demonstrably paraphyletic and is abandoned; this group is here referred to as basal Vespina.

The key character changes are shown in Figure 4. The most remarkable features of Burmorussidae in comparison with other hymenopteran families are discussed below.

DISCUSSION

The crown of backward-pointing teeth around the median ocellus (ocellar corona) is a remarkable feature specific to the families Orussidae and Stephanidae (char. 1). In Orussidae the ocellar corona consists of two rows of quite numerous teeth (usually three to six pairs) which are usually widened but not very big (char. 2). In Stephanidae it is differently organized with less numerous teeth (usually five), including an unpaired one below the median ocellus. The teeth are comparatively big, conical, and usually form a regular pentagon around the median ocellus. The ocellar corona is an adaptation for insects living inside wood. The teeth cut into the wood and anchor the head inside the boring gallery. It helps the insect to chew through the wood (Vilhelmsen & Turrissi 2011).

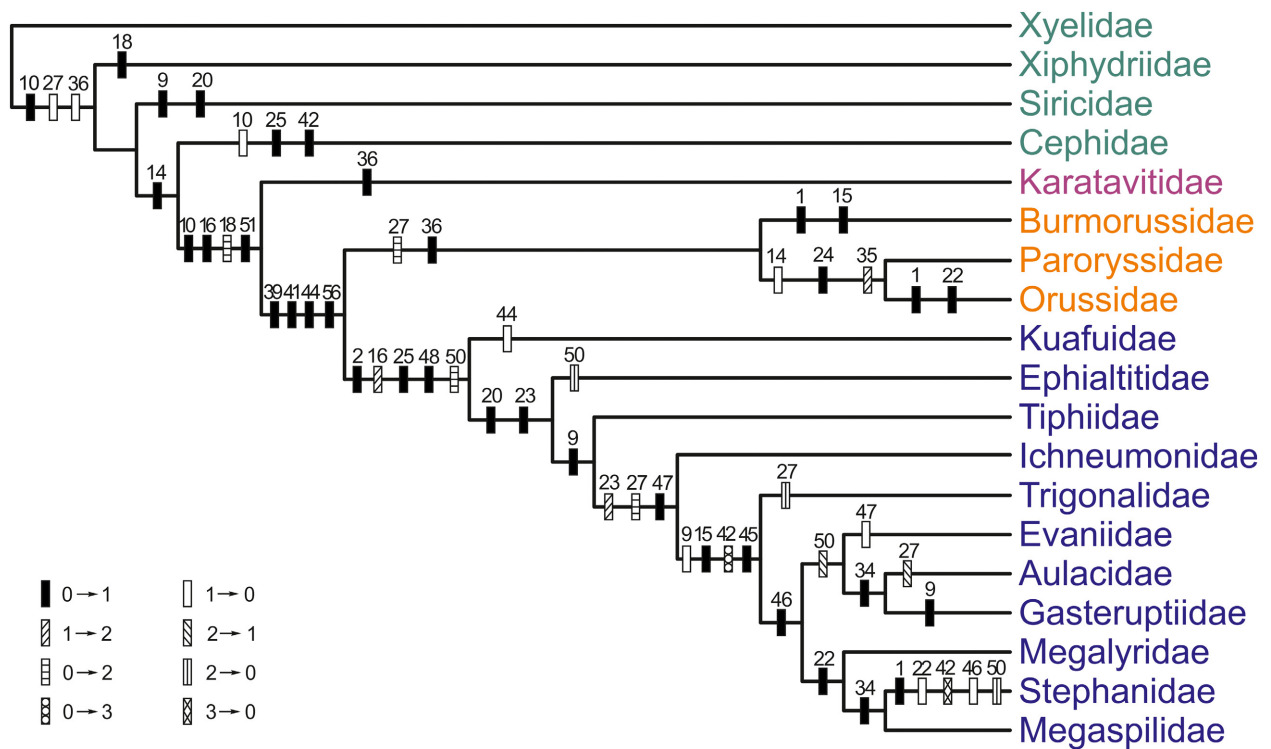


FIG. 4. The most parsimonious tree showing the relationships of general families of Hymenoptera. Character state changes are indicated. Colour online.

There are different structures serving for anchoring the body inside the boring hole in different groups of wood-living hymenopterans. Apart from the ocellar corona, the anchoring structures include transverse ridges on the notum and sometimes in other parts of the body (Ichneumonidae, Rhyssinae; Sepulcidae, Trematothoracinae; Vilhelmsen & Turrisi 2011; Kopylov & Rasnitsyn 2017), the dorsal spike ('horn') on the last abdominal tergite and transverse ridges on femora (Siricidae) or the pointed last abdominal tergite (Xiphydriidae) and parascobal crests (Pteromalidae, Leptofoeninae; Krogmann & Burks 2009). The same character sometimes occurs in unrelated groups: notal ridges in Trematothoracinae (Sepulcidae), Syntexinae (Anaxyelidae), Baissinae (Gasteruptionidae), Rhyssinae (Ichneumonidae) and Leptofoeninae (Pteromalidae) or head sculptures in Orussidae, Stephanidae, *Dodifoenus* (Pteromalidae), *Andrenelia* (Andreneliidae; Rasnitsyn & Martínez-Delclòs 2000).

Vilhelmsen & Turrisi (2011) supposed that the presence of an ocellar corona might have evolved in the common ancestor of Orussoidea and Apocrita, subsequently becoming lost in derived groups. But the structure of corona strongly differs in Orussidae and Stephanidae, and our cladogram shows that the ocellar corona was acquired independently in Orussidae and Stephanidae. Moreover, karatavitids (the immediate sister group of Orussoidea and Apocrita) have no teeth on head (at least we cannot

observe them on impressions). In Burmorussidae the structure of ocellar corona is very close to that in Orussidae. However, the corona is absent from Paroryssidae, the sister group to the Orussidae (Fig. 3).

The presence of an ocellar corona in *Burmorussus* indicates a wood-living lifestyle, which can also be confirmed by the coarsely sculptured body, the shape of mandibles (the mandibular tips protruding forwards over the labrum, which is an adaptation for chewing wood; Vilhelmsen & Turrisi 2011) and the subgenal vibration sensory organ which is supposed to be present in this genus (see below). The interesting peculiarity of the ocellar corona in *Burmorussus* is the position of the ventralmost teeth, which are located well below the median ocellus. In Orussidae, this character varies but the basalmost genera (*Baltorussus*, *Orussonia*, *Orussella*) have the ventralmost teeth at the level of or above the median ocellus; thus this character state is treated as plesiomorphic for Orussidae (Vilhelmsen 2003; Vilhelmsen & Zimmermann 2014).

Large eyes (more than 0.6 of head height) are not common among extant families of basal Vespina. The families Orussidae, Paroryssidae, Stephanidae, Megalynidae, Trigonalidae, Evaniidae, as well as crown siricines Siricidae and Xiphydriidae, usually have rather small eyes (less than 0.5 of head height), and only Gasteruptionidae and some Aulacidae break this rule. However, in the most basal Mesozoic Vespina lineages (Karatavidae, Ephialtitidae and

Kuafuidae) eyes are large, and positioned just above the mandibles. *Burmorussus* also has large eyes, resembling more closely Karatavitidae than Orussidae or Paroryssidae and points to this being the primitive condition for Orussoidea also (Fig. 3). The size of the eyes apparently changed a few times during the early evolution of Vespina.

The antennae of *Burmorussus* are unusual among basal Vespina in that they are attached high above the clypeus at the level of mid-height of the eye (char. 4). A lower position of antennae (at the level of the lower edge of eye) is characteristic for Xiphydriidae, Orussidae, Kuafuidae, most Stephanioidea and Evanioidea. The position of the antennae is generally unclear among Karatavitidae and Paroryssidae because they are known only from impression fossils where the position of antennal socket is almost impossible to locate precisely. However, this character can be determined in some karatavids: *Praeratavites daohugou*, *Praeparyssites orientalis*, *Postxiphydria daohugouensis*, *P. ningchengensis* (Rasnitsyn *et al.* 2006; Rasnitsyn & Zhang 2010) and one paroryssid: *Microryssus minus* (Rasnitsyn 1968); all their antennae are attached low.

Antennal grooves are lacking in *Burmorussus*. Running downward or upward of antennal bases, these grooves are used for protecting fragile antennae while moving through boring galleries. The structure is common in many wood-living hymenopteran groups, such as Siricidae, Orussidae, Evanioidea and Megalynidae, but is absent from some other wood-living families (Xiphydriidae, Stephanidae) (Vilhelmsen & Turrissi 2011). In *Burmorussus* the scape is long and robust, slightly curved and ornately profiled. It fits neatly into a furrow formed by the prominent eye and raised frons with the ocellar corona. We suspect that in *Burmorussus* this furrow served the same purpose as an antennal groove.

A very long scape and a 12-segmented flagellum in *Burmorussus* make the antenna slightly geniculate. That number of flagellomeres (chars 5, 6, 7) is unique within basal Vespina (Orussomorpha *sensu* Rasnitsyn & Zhang (2010)). Males of Karatavitidae and Paroryssidae have more polymeric antennae (more than 20 flagellomeres in Karatavitidae and more than 14 in Paroryssidae). Orussidae, however, have fewer segments in their flagellum. Extant orussids have nine flagellomeres in males and eight in females. Fossil orussid males (Cretaceous *Minyorussus* Basibuyuk *et al.*, 2000 and Eocene *Baltorussus* Schedl, 2011) also have nine flagellomeres, while female *Mesorussus* Rasnitsyn, 1977 from the Upper Cretaceous have ten flagellomeres (Vilhelmsen 2004). The long scape of *Burmorussus* is also a remarkable feature. Extant orussids sometimes have long scapes, but never as long as in *Burmorussus*. The scape in karatavids and paroryssids is not enlarged.

All legs of *Burmorussus* have a prominent lanceolate lobe on the 3rd tarsomere (distal flange), formed with a

cuticular outgrowth and not bearing long setae. A similar structure is known from Orussidae and Stephanidae, and serves as a part of a vibration analyser (Vilhelmsen *et al.* 2001, 2008; Vilhelmsen & Turrissi 2011). This system is crucial for insects to search for hidden hosts. In Orussidae, fore tarsomeres 1–3 in females are fused into one big basitarsomere with a prominent soft tip which is addressed to the substrate when searching for hosts. It perceives vibrations and conducts them to the enlarged subgenal organ located inside the swollen fore tibia, and the subgenal organ containing several hundred sensory units subsequently transforms the vibrations into nerve impulses. The legs in males are not modified for vibration sensing in Orussidae: the fore tibiae are not swollen and the fore tarsus consists of five segments without a soft tip (Vilhelmsen *et al.* 2001). In Stephanidae, females have the vibration analyser in hind legs. Hind tarsomeres 1–3 in different species may be fused or not, and the ‘gramophone needle’ is formed by the distal flange of tarsomere 4. The subgenal organ is developed in hind legs (in females and males), while the distal flanges of tarsomere 4 is developed in all legs. In females the distal flanges usually bear dense brushes of setae, while in males they are usually bald (Vilhelmsen *et al.* 2008). In *Burmorussus* the vibration analyser differs from that in Orussidae and Stephanidae. The lanceolate lobe in all legs of *Burmorussus* resembles in shape the distal flange of Stephanidae and lacks long setae, which is natural to stephanid males. On the other hand, these flanges are formed with 3rd tarsomeres, while 4th tarsomeres are tiny and have no processes. The hind tibia of *Burmorussus* is swollen (4× as wide as the first tarsomere and 2× as wide as the mid tibia) and slightly narrowed apically, which would be odd if the body support is the only function of the tibia. Such an obvious disproportion between the tarsal and tibial widths is unlikely to have been caused by locomotion. It is apparent that an enlarged subgenal organ is present inside the hind leg. A swollen hind tibia can also be observed in some Paroryssidae (*Microryssus crassipes*, *M. robustus*) and its shape may also indicate a subgenal organ inside the hind tibia.

The antennae of female Orussidae are robust with the last flagellomeres transformed into strongly sclerotized ‘mallets’, which are used for producing sound waves inside wood. Therefore, the vibration reception system may function in two modes: as a ‘passive sonar’, registering sounds emitted by the host, or as an ‘active sonar’, registering reflected sound waves. The first mode allows the location of sounds emitted by hosts and the second mode allows the location of boring galleries inside the tree. The first mode is possibly used by stephanids while the second is characteristic for orussids (Vilhelmsen *et al.* 2001, 2008). The antennal ‘mallets’ and swollen tibiae are developed only in female orussids. Males keep apart from host-seeking activities and therefore their antennae and legs are not modified

for the vibration sense. Unfortunately, *Burmorussus* is only known from a male which has slender antennae with the rounded tip not modified for tapping. The method of host location of this wasp remains unknown until we find a female specimen of Burmorussidae.

The postepisternum of middle and hind thoracic segments forms a pair of elongate processes between the mesocoxae and metacoxae (char. 15) in *Burmorussus* (for a more detailed discussion of this character see: Rasnitsyn 1980; Johnson 1988; Rasnitsyn & Zhang 2010). Some Recent orussids (*Chalinus*) have an enlarged postepisternum, but it is never as long as in *Burmorussus*. Although an elongated postepisternum is characteristic for Evanioidea, Ceraphronoidea, Megalyridae, Trigonalidae and Stephanidae, these taxa are only distantly related to Orussoidea (Fig. 3) and our phylogenetic analysis suggests independent development of this character in *Burmorussus*.

The fore wing fixation apparatus in Hymenoptera consists of cenchri (paired rugged surfaces on the metanotum) and the rough area within a loop on 2A vein in the fore wing (char. 14). The structure is characteristic for all Siricina (except Cephidae) and basal Vespina (except *Karatavites*) and is lost in Apocrita (Rasnitsyn & Zhang 2010). *Burmorussus* losing the wing fixation apparatus is evidently a homoplasy with the other above-mentioned taxa.

Rasnitsyn (1969, 1980) proposed the hypothesis that Orussoidea ancestors have undergone a considerable size reduction at some point in their early evolutionary history. Vilhelmsen (2004) conducted a detailed study on size evolution of Orussoidea but did not succeed in decisively proving or refuting this hypothesis. *Burmorussus mirabilis* has a body length of 2.5 mm, being one of the tiniest representatives of 'Orussomorpha'. We realize that *Burmorussus* is not a direct ancestor but a sister group to Orussidae + Paroryssidae, so its tiny body size cannot prove the hypothesis positively. However, the small body size of the representative of the closest sister group can be regarded as an indirect proof of the size reduction hypothesis.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/859EA41A-0265-43F8-8DBF-158116E35CD6>.

The source data for the phylogenetic analysis, including the matrix and the characters set, is available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k98sf7m34>.

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REFERENCES

- BASIBUYUK, H. H., QUICKE, D. L. J. and RASNITSYN, A. P. 2000. A new genus of the Orussidae (Insecta: Hymenoptera) from Late Cretaceous New Jersey amber. 305–311. In GRIMALDI, D. A. (ed.) *Studies on fossils in amber, with particular reference to the cretaceous of New Jersey*. Backhuys Publishers.
- ENGEL, M. S., HUANG, D., ALQARNI, A. S. and CAI, C. 2016. A remarkable evanoid wasp in mid-Cretaceous amber from northern Myanmar (Hymenoptera: Evanioidea). *Cretaceous Research*, **60**, 121–127.
- GRIMALDI, D. A., ENGEL, M. S. and NASCIMBENE, P. C. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, **3361**, 1–71.
- GUO, M., XING, L., WANG, B., ZHANG, W., WANG, S., SHI, A. and BAI, M. 2017. A catalogue of Burmite inclusions. *Zoological Systematics*, **42**, 249–379.
- HERATY, J., RONQUIST, F., CARPENTER, J. M., HAWKS, D., SCHULMEISTER, S., DOWLING, A. P., MURRAY, D., MUNRO, J., WHEELER, W. C., SCHIFF, N. and SHARKEY, M. 2011. Evolution of the hymenopteran megadiapause. *Molecular Phylogenetics & Evolution*, **60**, 73–88.
- JOHNSON, N. F. 1988. Midcoxal articulations and the phylogeny of the order Hymenoptera. *Annals of the Entomological Society of America*, **81**, 870–881.
- KOPYLOV, D. S. and RASNITSYN, A. P. 2017. New sepulcids (Hymenoptera: Sepulcidae) from the Lower Cretaceous of Asia: II. Ghilarellinae and Trematothoracinae. *Paleontological Journal*, **51**, 291–303.
- KROGMANN, L. and BURKS, R. A. 2009. *Doddifoenus wallacei*, a new giant parasitoid wasp of the subfamily Leptofoeninae (Chalcidoidea: Pteromalidae), with a description of its mesosomal skeletal anatomy and a molecular characterization. *Zootaxa*, **2194**, 21–36.
- LATREILLE, P. A. 1796. *Précis des caractères génériques des insectes, disposés dans un ordre naturel*, Prévôt, Paris, 238 pp. <https://doi.org/10.5962/bhl.title.58411>
- LI, L., SHIH, C., RASNITSYN, A. P., LI, D. and REN, D. 2018. A new wasp of Myanmarinidae (Hymenoptera: Stephanidae) from the mid-Cretaceous Myanmar amber. *Cretaceous Research*, **86**, 33–40.
- LINNAEUS, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum*

- Characteribus, Differentiis, Synonymis, Locis. Editio 10. Vol. 1*, Laurentius Salvius, Stockholm, 824 pp.
- MARTYNOV, A. V. 1925. To the knowledge of fossil insects from Jurassic beds in Turkestan. *Bulletin de l'Academie des Sciences de l'URSS*, **19**, 753–762.
- NEWMAN, E. 1834. Attempted division of British insects into natural orders. *Entomologists Magazine*, **2**, 379–431.
- PETERS, R. S., KROGMANN, L., MAYER, C., DONATH, A., GUNKEL, S., MEUSEMANN, K., KOZLOV, A., PODSIADLOWSKI, L., PETERSEN, M., LANFEAR, R., DIEZ, P. A., HERATY, J., KJER, K. M., KLOPFSTEIN, S., MEIER, R., POLIDORI, C., SCHMITT, T., LIU, S., ZHOU, X., WAPPLER, T., RUST, J., MISOF, B. and NIEHUIS, O. 2017. Evolutionary history of the Hymenoptera. *Current Biology*, **27**, 1013–1018.
- POINAR, G. O. Jr and DANFORTH, B. N. 2006. A fossil bee from Early Cretaceous Burmese amber. *Science*, **314**, 614.
- RASNITSYN, A. P. 1963. Late Jurassic Hymenoptera of Karatau. *Paleontological Journal*, **1**, 86–93. [in Russian]
- 1968. Novye mezozoiskie pilil'schiki [New Mesozoic sawflies (Hymenoptera, Symphyta)]. 190–236. In ROHDENDORF, B. B. (ed.) *Yurskiye nasekomye Karatau [Jurassic insects of Karatau]*. Nauka, Moscow.
- 1969. Proiskhozhdenie i evoliutsiia nizshikh pereponchatokrylykh [Origin and evolution of the lower Hymenoptera]. Proceedings of the Paleontological Institute of the USSR Academy of Sciences, **123**. Nauka, Moscow, 196 pp.
- 1977. Novye pereponchatokrylye iz iury i mela Azii [New Hymenoptera from the Jurassic and Cretaceous of Asia]. *Paleontological Journal*, **11**, 349–357.
- 1980. Proiskhozhdenie i evoliutsiia pereponchatokrylykh nasekomykh [The origin and evolution of Hymenoptera]. Proceedings of the Paleontological Institute of the USSR Academy of Sciences, **174**. Nauka, Moscow, 192 pp.
- 1996. Burmese amber at the Natural History Museum. *Inclusion/Wrosteck*, **23**, 19–21.
- and MARTÍNEZ-DELCLÒS, X. 2000. Wasps (Insecta: Vespida = Hymenoptera) from the Early Cretaceous of Spain. *Acta Geológica Hispánica*, **35**, 65–95.
- and ZHANG, H. 2010. Early evolution of Apocrita (Insecta, Hymenoptera) as indicated by new findings in the Middle Jurassic of Daohugou, Northeast China. *Acta Geologica Sinica – English Edition*, **84**, 834–873.
- ANSORGE, J. and ZHANG, H. 2006. Ancestry of the orussoid wasps, with description of three new genera and species of Karatavitidae (Hymenoptera = Vespida: Karatavitoidea stat. nov.) *Insect Systematics & Evolution*, **37**, 179–190.
- BASHKUEV, A. S., KOPYLOV, D. S., LUKASHEVICH, E. D., PONOMARENKO, A. G., POPOV, Y. A., RASNITSYN, D. A., RYZHKOVA, O. V., SIDORCHUK, E. A., SUKATSHEVA, I. D. and 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.
- POINAR, G. and BROWN, A. E. 2017. Bizarre wingless parasitic wasp from mid-Cretaceous Burmese amber (Hymenoptera, Ceraphronoidea, Aptenoperissidae fam. nov.) *Cretaceous Research*, **69**, 113–118.
- RODRIGUEZ, J., WAICHERT, C., VON DOHLEN, C. D., POINAR, G. O. JR and ANPIT, J. P. 2016. Eocene and not Cretaceous origin of spider wasps (Pompilidae): fossil evidence from amber. *Acta Palaeontologica Polonica*, **61**, 89–96.
- RONQUIST, F., RASNITSYN, A., ROY, A., ERICSSON, K. and LINDGREN, M. 1999. Phylogeny of the Hymenoptera: a cladistic reanalysis of Rasnitsyn's (1988) data. *Zoologica Scripta*, **28**, 13–50.
- KLOPFSTEIN, S., VILHELMSSEN, L., SCHULMEISTER, S., MURRAY, D. L. and RASNITSYN, A. P. 2012. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Systematic Biology*, **61**, 973–999.
- ROSS, A. J. 2018. Burmese (Myanmar) amber taxa, on-line checklist v.2017.4. https://www.nms.ac.uk/media/1156076/burmese-amber-taxa-v2017_4.pdf
- MELLISH, C., YORK, P. and CRIGHTON, B. 2010. Burmese amber. 208–235. In PENNEY, D. (ed.) *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press.
- SCHEDL, W. 2011. Eine Orussidae aus dem baltischen Bernstein (Hymenoptera: Symphyta). *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen*, **63**, 33–36.
- SHARKEY, M. J., CARPENTER, J. M., VILHELMSSEN, L., HERATY, J., LILJEBLAD, J., DOWLING, A. P. G., SCHULMEISTER, S., MURRAY, D., DEANS, A. R., RONQUIST, F., KROGMANN, L. and WHEELER, W. C. 2012. Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics*, **28**, 80–112.
- SHI, G., GRIMALDI, D. A., HARLOW, G. E., WANG, J., WANG, J., YANG, M., LEI, W., LI, Q. and LI, X. 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research*, **37**, 155–163.
- SMITH, R. D. A. and ROSS, A. J. 2018. Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resin-producing forests to brackish waters, and the age of the amber. *Earth & Environmental Science Transactions of the Royal Society of Edinburgh*, **107**, 239–247.
- SWOFFORD, D. L. 2003. *PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4*. Sinauer Associates, Sunderland, MA.
- VILHELMSSEN, L. 2003. Phylogeny and classification of the Orussidae (Insecta: Hymenoptera), a basal parasitic wasp taxon. *Zoological Journal of the Linnean Society*, **139**, 337–418.
- 2004. The old wasp and the tree: fossils, phylogeny and biogeography in the Orussidae (Insecta, Hymenoptera). *Biological Journal of the Linnean Society*, **82**, 139–160.
- and TURRISI, G. F. 2011. Per arborem ad astra: morphological adaptations to exploiting the woody habitat in the early evolution of Hymenoptera. *Arthropod Structure & Development*, **40**, 2–20.
- and ZIMMERMANN, D. 2014. *Baltorussus* total makeover: rejuvenation and sex change in an ancient parasitoid wasp lineage. *PLoS One*, **9**, e98412.
- ISIDORO, N., ROMANI, R., BASIBUYUK, H. H. and QUICKE, D. L. J. 2001. Host location and oviposition in a basal group of parasitic wasps: the subgenual organ,

- ovipositor apparatus and associated structures in the Orussidae (Hymenoptera, Insecta). *Zoomorphology*, **121**, 63–84.
- TURRISI, G. F. and BEUTEL, R. G. 2008. Distal leg morphology, subgenual organs and host detection in Stephaniidae (Insecta, Hymenoptera). *Journal of Natural History*, **42**, 1649–1663.
- MIKÓ, I. and KROGMANN, L. 2010. Beyond the wasp-waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). *Zoological Journal of the Linnean Society*, **159**, 22–194.
- ZHANG, Q., KOPYLOV, D. S., RASNITSYN, A. P., ZHENG, Y. and ZHANG, H. 2020. Data from: Burmorussidae, a new family of parasitic wasps (Insecta, Hymenoptera) from mid-Cretaceous Burmese amber. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.k98sf7m34>
- ZHERIKHIN, V. V. and ROSS, A. J. 2000. A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum, London*, **56**, 3–10.