

Phylogeny of Evanioidea (Hymenoptera, Apocrita), with descriptions of new Mesozoic species from China and Myanmar

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Abstract. The phylogeny of the superfamily Evanioidea is presented using morphology and DNA sequence data of selected extant and fossil genera by employing two phylogenetic methods, maximum parsimony and Bayesian inference. Based on our new results, the monophyly of Evanioidea is corroborated. Evanioidea, Anomopterellidae, Othniodellithidae, Andreneliidae and Evaniidae are monophyletic families, while Praeaulacidae, Aulacidae, Baissidae and Gasteruptiidae are paraphyletic families. In addition, four new genera (*Sinuevania* **gen.n.**, *Curtevania* **gen.n.**, *Exilaulacus* **gen.n.**, *Heterobaissa* **gen.n.**) with five new species (*Sinuevania mira* **sp.n.**, *Curtevania enervia* **sp.n.**, *Exilaulacus loculatus* **sp.n.**, *Exilaulacus latus* **sp.n.**, *Heterobaissa apetiola* **sp.n.**), and five additionally new species (*Newjersevania longa* **sp.n.**, *Newjersevania brevis* **sp.n.**, *Cretevania tenuis* **sp.n.**, *Cretevania venae* **sp.n.**, *Praeaulacus rectus* **sp.n.**) and one new combination [*Cretevania mitis* (Li, Shih & Ren, 2014a) **comb.n.**] are described based on well-preserved fossils from the Middle Jurassic Jiulongshan Formation in Inner Mongolia, China, the Early Cretaceous Yixian Formation in Liaoning, and mid-Cretaceous amber from Myanmar. This study documents the diversification of one major lineage of the mid-Mesozoic parasitoid revolution that dramatically changed food-web relationships in terrestrial ecosystems.

This published work has been registered in ZooBank, <http://zoobank.org/urn:lsid:zoobank.org:pub:CBC04ADA-0176-402D-9B43-E1B3CDA080E1>.

Introduction

The Hymenoptera traditionally have been divided into two suborders of Symphyta and Apocrita (Gauld & Bolton, 1988). Current studies suggested that there are three fundamental

clades, Unicalcarida (all Hymenoptera except Xyelidae, Tenthredinoidea and Pamphilioidea), Vespina (Orussidae + Apocrita) and Apocrita (Ronquist *et al.*, 1999; Schulmeister, 2003a, b; Vilhelmsen, 2006; Rasnitsyn & Zhang, 2010; Vilhelmsen *et al.*, 2010). Sharkey *et al.* (2012) first presented the higher-level phylogeny of extant Hymenoptera based on morphological and molecular data, which suggested that all superfamilies except vespoidea appear as monophyletic. Branstetter *et al.* (2017) proposed that ants are sister to bees and apoid wasps and that bees are specialized crabronid wasps from a densely sampled phylogeny of Aculeata using UCE phylogenomic data. Peters *et al.* (2017) inferred a time-calibrated and statistically

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solid phylogenetic tree of Hymenoptera from the analysis of phylogenomic data, and gave a new explanation of the origins and radiation of parasitoids, stinging wasps and bees. Moreover, based on careful evaluation of wasp waist morphologies from abundant fossils of northeastern China and phylogenetic results, palaeontologists now suspect that the early evolution of Apocrita might have originated from Karatavitidae of Orussoidea to Ephialtidae, then diversified into Stephanioidea and Evanioidea, and subsequently the remaining groups (Rasnitsyn & Zhang, 2010; Li *et al.*, 2015a). Alternatively, it was proposed that three different, derived lineages of narrow-waist wasps originating from Ephialtidae led to: (i) Kuafuidae, and then to remaining Apocrita of (ii) Stephanidae, and (iii) Evanioidea (Rasnitsyn & Zhang, 2010; Li *et al.*, 2015a).

The Evanioidea illustrate the diversification during the Jurassic and Cretaceous of a major parasitoid group that was part of the transformation of terrestrial food webs. Evanioidea are a small superfamily of parasitoid wasps that are characterized by two possible apomorphies. First, the metasoma is attached high on the propodeum (Goulet & Huber, 1993; Grimaldi & Engel, 2005). Second, all functional metasomal spiracles are lost except on the seventh segment (Goulet & Huber, 1993; Grimaldi & Engel, 2005). However, the loss in evanioids of functional metasomal spiracles 1–6 is a questionable autapomorphy, attributable to the observation that these spiracles are rudimentary and often difficult to determine if they are permanently closed or still functional. Generally, spiracles are large, distinctive structures, undoubtedly open in Siricina, Ichneumonomorpha and Vespomorpha. Otherwise, these spiracles can be small, either open or closed in Orussidae, Stephanidae, Evanioidea, Ceraphronomorpha and Proctotrupomorpha (Rasnitsyn & Zhang, 2010).

Fossil record of Evanioidea taxa

A review of Evanioidea taxonomy

For a long time, the superfamily Evanioidea was considered to include three extant families of Evaniidae, Gasteruptiidae and Aulacidae. However, Townes (1950) proposed that a transition existed between Gasteruptiidae and Aulacidae, and Aulacidae have been synonymized with Gasteruptiidae. Rasnitsyn accepted this view based on many Mesozoic fossils, which make it difficult to successfully delimit Gasteruptiidae and Aulacidae, even using the cladistic analysis proposed by Basibuyuk *et al.* (Rasnitsyn, 1980a, 1988, 2002, 2013; Basibuyuk *et al.*, 2002). In addition, rearing records indicate that evaniids develop as solitary predators whose larvae feed on cockroach eggs (Deans, 2005). However, aulacids are believed to be endoparasitoids on the wood-boring larvae of Xiphydriidae in Hymenoptera, and Buprestidae and Cerambycidae in Coleoptera (Hanson & Gauld, 1995; Jennings & Austin, 2004; Turrisi, 2011). Gasteruptiids are predator-inquilines that lay eggs inside the cells of solitary bees and wasps, nesting in the pith cylinders of plant stems and tunnels in wood, or alternatively in underground nests, with emergent larvae developing on

food stores or nest inhabitants (Jennings & Austin, 2004; Zhao *et al.*, 2012). Based on their living habits, Whitfield (1998) hypothesized a simple transition, from parasitoids colonizing wood-boring larval hosts to becoming ‘parasitoids’ of nest cells within plant stems instead of being parasitoids of cockroach egg cases. Such a transition was accompanied by the synapomorphies of the propleura forwardly extending beyond the pronotum and forming as a neck-like extension, the male antenna with 11 and a female with 12 antennomeres; and metasomal terga 1 and 2 fused into a long, gently tapering double segment. These three features are shared by Gasteruptiidae and Aulacidae, suggesting that these two groups have a closer relationship than with Evaniidae.

Evaniidae are a prominent, colourful and speciose family that are commonly called ‘ensign wasps’ or ‘hatchet wasps’ due to their short metasoma which is flag-shaped and attached to a long and thin petiole. These wasps also share the following additional characters: (i) deeply separated jugal lobes in the fore- and hindwings; (ii) loss of a tubular cross-vein on the distal portion of the forewings (except *Mesevania*); (iii) possession of the same number of antennal segments in males and females, although not necessarily demonstrated in some extinct genera; (iv) a head that is largely immovable and attached to the mesosoma on a short neck; and (v) an ovipositor that is usually short and thin (Fig. 1e, f). Currently, 20 extant genera with over 400 species are described, with an additional 16 extinct genera with 30 species from later Mesozoic and Paleogene deposits (Rasnitsyn, 1975, 1991; Jarzembowski, 1984; Rasnitsyn *et al.*, 1998, b; Basibuyuk *et al.*, 2000a, b, 2002; Zhang & Zhang, 2000; Nel *et al.*, 2002a, b; Cruickshank & Ko, 2003; Deans *et al.*, 2004; Engel, 2006; Zhang *et al.*, 2007; Peñalver *et al.*, 2010; Ghahari & Deans, 2010; Jennings *et al.*, 2012, 2013; Li *et al.*, 2014a).

Extant Gasteruptiidae are easily recognized parasitic hymenopterans because of their elongated ‘neck’ (the propleuron), the clavate metatibiae, and elongate and subclavate metasoma that are inserted very high (dorsad) on the propodeum (Fig. 1a, b) (Crosskey, 1951; Smith 2006). Presently about 500 extant species of Gasteruptiidae are divided into two subfamilies: Hyptiogastrinae with the two extant genera of *Hyptiogaster* Kieffer and *Pseudofoenus* Kieffer (Jennings & Austin, 1994, 1997a, b, 2002, 2005), and Gasteruptiinae with the four genera of *Gasteruption* Latreille, *Plutofoenus* Kieffer, *Trilobitofoenus* Macedo, and *Spinolafoenus* Macedo (Macedo, 2009). Nevertheless, only three extinct genera – *Kotujellites* Rasnitsyn, *Hyptiogastrites* Cockerell, and *Kotujisca* Rasnitsyn, from the Early Cretaceous – have been reported in Gasteruptiidae, all of which belong to Kotujellitinae (= Hyptiogastrinae) (Rasnitsyn, 2013).

Aulacidae, with a relatively slender body and long ovipositor, are mainly distinguished from Evaniidae and Gasteruptiidae by the presence of a forewing 2m-cu (Gauld & Bolton, 1988) and 3r-m (Konishi, 1990) veins, as well as the presence of a metapostnotum (Fig. 1c, d). This family comprises more than 221 extant species belonging to the two genera of *Aulacus* Jurine and *Pristaulacus* Kieffer (= *Panaulix* Benoit). Aulacid species are distributed in all zoogeographical regions, except Antarctica (Kieffer, 1912; Hedicke, 1939; Smith, 2001, 2005a, b, 2008; He *et al.*, 2002; Jennings *et al.*, 2004a, b, 2004c; Turrisi,

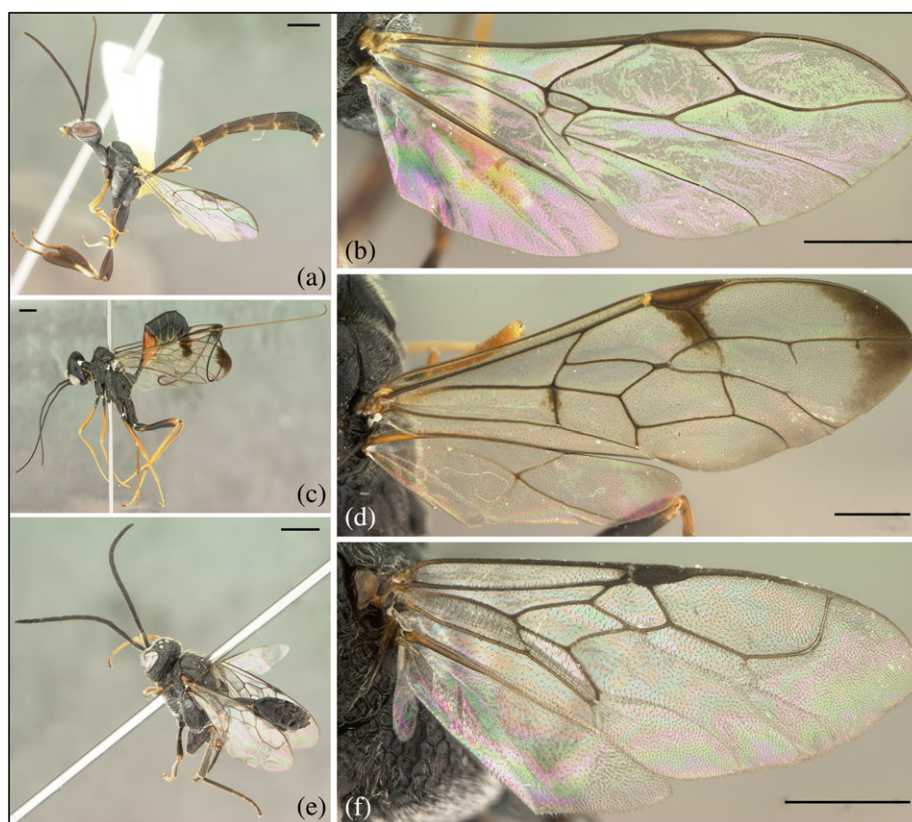


Fig. 1. Extant Evanioidea. (a, b) Gasteruptiidae; (c, d) Aulacidae; (e, f) Evaniidae. All specimens are housed in the National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. Scale bars = 1 mm. [Colour figure can be viewed at wileyonlinelibrary.com].

2004, 2005, Turrisi, 2006a, b, Turrisi, 2007; Jennings & Austin, 2006; Sun & Sheng, 2007a, b; Turrisi *et al.*, 2009, Turrisi, 2011; Smith & Vilela de Carvalho, 2010). Unfortunately, Aulacidae have a rare fossil record with only four genera of *Aulacus*, *Exilaulacus*, *Pristaulacus* and *Vectevania* represented, with ten species occurring from the Late Cretaceous to the Cenozoic (Appendix S1).

Recently, based on an analysis of data by Rasnitsyn (2013), it has been suggested that the Gasteruptiidae comprise four subfamilies: (i) Gasteruptiinae Kirby with about 500 species distributed globally (Crosskey, 1962; Rasnitsyn, 1991; Jennings & Austin, 2002; Macedo, 2011; Zhao *et al.*, 2012), consisting of two genera *Gasteruption* Latreille and *Hyptiogaster* Kieffer (= *Hyptiogastrini*); (ii) Bassinae Rasnitsyn have five genera (*Baissa* Rasnitsyn, *Manlaya* Rasnitsyn, *Humiryssus* Lin, *Mesepipolaea* Zhang & Rasnitsyn, and *Electrobaissa* Engel), all from the Cretaceous Period; (iii) Kotujellitinae Rasnitsyn, comprising three genera (*Kotujellites* Rasnitsyn, *Hyptiogastrites* Cockerell, and *Kotujisca* Rasnitsyn, from the Early Cretaceous); and (iv) Aulacinae Shuckard, consisting of more than 221 extant species belonging to genera *Aulacus* Jurine and *Pristaulacus* Kieffer (including the former *Panaulix* Benoit), all species of which are distributed in zoogeographic regions, except Antarctica (Kieffer, 1912; Hedicke, 1939; Smith, 2001, 2005a, b, 2008; He *et al.*, 2002; Turrisi, 2004, 2005, 2006a, b, 2007; Jennings *et al.*,

2004a, b, c; Jennings & Austin, 2006; Sun & Sheng, 2007a, b; Turrisi *et al.*, 2009; Smith & Vilela de Carvalho, 2010). In addition, the fossil genus *Vectevania* Cockerell is tentatively assigned to the subfamily of Aulacinae, from the uppermost Eocene of the Bembridge Marls of England (Rasnitsyn, 2013).

Several extinct families from the Mesozoic have been erected within Evanioidea, principally Praeaulacidae, Anomopterellidae, Baissidae, Cretevaniidae, Kotujellitidae, Andreneliidae and Othniodellithidae (Rasnitsyn, 1972, 1975; Rasnitsyn & Martínez-Delclòs, 2000; Engel *et al.*, 2016). Subsequently, two of these families, Baissidae and Kotujellitidae, were downgraded to subfamilies of Gasteruptiidae (Rasnitsyn, 1980a, b, 2013). In addition, Cretevaniidae and Andreneliidae were synonymized within Evaniidae (Basibuyuk *et al.*, 2002; Grimaldi & Engel, 2005). Nevertheless, Engel (2013) considers Baissidae as a separate family that is based on the six genera of *Baissa* Rasnitsyn, *Humiryssus* Lin, *Manlaya* Rasnitsyn, *Tillywhimia* Rasnitsyn & Jarzembowski, *Mesepipolaea* Zhang & Rasnitsyn and *Electrobaissa* Engel. These six genera possess an overall compact body form, a propleuron that does not extend forward to form a pronounced 'neck', metatibiae that are not clavate, and other distinctive features. Similarly, Rasnitsyn (2013) maintains Andreneliidae as a separate family because characters cited as putative synapomorphies for Andreneliidae and Evaniidae consist only of the first metasomal segment formed into a

petiole. The petiole is truly shared by all Evaniidae genera, and also appeared in other related taxa, such as *Nevania* of Praeaulacidae with their first and second segments formed as a long tubular petiole (Zhang & Rasnitsyn, 2007). Moreover, possession by *Andrenelia* of a distinctly elongated metasoma and a very long ovipositor are characters that apparently are reversed in Evaniidae, the latter of which are defined by an elongate head, a petiolate first metasomal segment with a stout, short gaster, and a short ovipositor.

Based on new, abundant fossil specimens from northeastern China and analyses of their phylogenetic placements, Anomopterellidae Rasnitsyn are restored as a valid family (Li *et al.*, 2013a). The Anomopterellidae differ from other families by having a forewing with eight enclosed cells, a 1-Rs much longer than the 1-M, 2r-m (lost), 3r-m (present), and 2m-cu (present) veins, the 2mcu wing cell as wide as 2+3r, 2A cells, the a_1 - a_2 vein absent, the first metasomal segment narrow basally, and a very short ovipositor. Currently, Anomopterellidae include three genera: *Anomopterella* Rasnitsyn, *Synaphopterella* Li, Rasnitsyn, Shih & Ren, and *Choristopterella* Li, Rasnitsyn, Shih & Ren.

Praeaulacidae are an extinct group characterized by complete forewing venation (except for some species of the subfamily Cretocleistogastrinae), a hindwing with at least the basal cell enclosed, retention of the medial mesonotal suture, and deployment of a long external ovipositor that historically has been considered ancestral to Evanioidea (Rasnitsyn, 1988). Presently, 20 extinct genera are allocated to three subfamilies: Cretocleistogastrinae Rasnitsyn, Praeaulacinae Rasnitsyn, and Nevaniinae Zhang & Rasnitsyn (Rasnitsyn, 1972, 1973, 1983; Jell & Duncan, 1986; Rasnitsyn, 1990a, b; Zhang & Rasnitsyn, 2007, 2008; Rasnitsyn & Zhang, 2010; Oberprieler *et al.*, 2012; Li *et al.*, 2013b, 2014b, 2015b; Li & Shih, 2014). All known Praeaulacidae from the Jurassic to the Cretaceous demonstrate distinct evolutionary trends toward overall miniaturization, venation reduction, pterostigma enlargement, and reduction of number of the antennal segments (Rasnitsyn, 1969, 1980a, b; Li *et al.*, 2013b, 2014b, 2015b; Li & Shih, 2014).

Othniodellithidae are a new family established in 2016 based on an amber specimen from Myanmar. This species can be easily placed within Evanioidea due to the elevated position of the attachment of the metasoma on the propodeum. Because the type specimen has massive, robust mandibles, elongate maxillary palpi, and prominent facial horn, it is readily identifiable among praeaulacid-like taxa. Engel and Huang consider it a separate family that differs from other Mesozoic Evanioidea (Engel *et al.*, 2016).

A review of published data on fossil Evanioidea

For this study, we reviewed and summarized all published data on fossil species of Evanioidea (Appendix S1). Our coverage extends from the latest Middle Jurassic at 165 Ma, the putative earliest record, to the end of the Miocene Epoch at 7 Ma. The described fossils of Evanioidea, summarized in Appendix S1, are based on several sources, principally Zhang & Rasnitsyn

(2008), Li *et al.* (2013a), and the EDNA fossil insect database (EDNA, 2015). These fossil Evanioidea comprise 59 genera and 171 species, including four new genera and ten new species described in this contribution.

The earliest record of Evanioidea are species of Anomopterellidae and Praeaulacidae, including 12 genera with 42 species, from the latest Middle Jurassic of the Jiulongshan Formation in China, dated to 165 Ma (Chen *et al.*, 2004; He *et al.*, 2004; Gao & Ren, 2006; Walker *et al.*, 2013). Recently, more complete fossils of these two families have been reported which display significant variation in body size, wing venation, shape of the first metasomal segment and antennal morphology (Zhang & Rasnitsyn, 2008; Rasnitsyn & Zhang, 2010; Li *et al.*, 2013a, b). However, fossils of other taxa of Evanioidea are still unknown from this time interval.

During the Cretaceous, the number of praeaulacids appeared to have declined sharply, with only seven documented genera of *Cretocleistogaster*, *Habraulacus*, *Miniwestratia*, *Nanowestratia*, *Praeaulacops*, *Praeaulacus* and *Westratia*. Significantly, no praeaulacids have been described after the Cretaceous. In addition, no species of Anomopterellidae have been reported after the Late Jurassic. In contrast to Anomopterellidae and Praeaulacidae, species of Evaniidae and Baissidae during the Cretaceous were relatively abundant, consisting of 13 genera with 33 species of Evaniidae and seven genera with 30 species of Baissidae. However, only one genus with two species of Aulacidae and five genera with five species of Gasteruptionidae have been reported from the Cretaceous. For the Cenozoic, only three genera, with eight species of Aulacidae and four genera with four species of Evaniidae, have been described and are currently known.

Materials and methods

Photography and repository of amber and compression fossils

All new fossils studied in this paper come from three later Mesozoic deposits in eastern Asia. The oldest material originates from compression deposits of the latest Middle Jurassic (late Callovian) Jiulongshan Formation at Daohugou, in Inner Mongolia, China. Fossils of intermediate age originate from compression deposits of the Early Cretaceous (late Barremian to earliest Aptian) Yixian Formation at Huangbanjigou, in Liaoning, China. The youngest fossils are amber specimens from deposits of earliest Cenomanian age in the Hukawng Valley of Kachin State, in northern Myanmar, approximately 100 km southwest of the Village of Tanai. All compression and amber specimens are deposited in the Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University (CNUB), in Beijing, China (Dong Ren, Curator). All specimens were examined and later photographed with a DFC500 digital camera (Leica, Wetzlar, Germany) attached to a Leica MZI65C dissecting microscope. The wing venation nomenclature used in this paper follows a modification of the system used by Rasnitsyn (1975).

The Jiulongshan Formation belongs to the well-recognized Yanliao Biota, which is known for yielding feathered dinosaurs,

mammals, conifers, and numerous insect taxa such as Coleoptera (Chang *et al.*, 2009), Trichoptera (Liu *et al.*, 2014), Lepidoptera (Zhang *et al.*, 2013), Grylloblattodea (Cui & Ren, 2013), Diptera (Shi *et al.*, 2015) and Hymenoptera (Li *et al.*, 2014b, 2015a), among others. Based on Ar-Ar and SHRIMP U-Pb dating, the Jiulongshan Formation corresponds to uppermost strata of the Middle Jurassic. Because of new calibrations of the Jurassic (Walker *et al.*, 2013), the age of this deposit has been considered as the latest Middle Jurassic (late Callovian), approximately 165–164 Ma (Walker *et al.*, 2013), just below the Middle Jurassic–Late Jurassic boundary.

The Yixian Formation belongs to the noted Jehol Biota, which has yielded abundant insect fossils, such as odonates (Li *et al.*, 2012), heteropterans (Yao *et al.*, 2013), mecopterans (Qiao *et al.*, 2012), neuropterans (Shi *et al.*, 2012a, b) and hymenopterans (Li *et al.*, 2014a; Wang *et al.*, 2013; Wang *et al.*, 2015a, b). The exact age of the Yixian Formation is still debated, and we tentatively consider the age as the Early Cretaceous (late Barremian–earliest Albian) (Wang *et al.*, 2005), which corresponds to an absolute age of about 125 Ma (Walker *et al.*, 2013).

Myanmar (Burmese) amber from the Hukawng Valley of Kachin State in northern Myanmar is significant for a few reasons. Recently, study of Myanmar amber has become more active because of well-preserved inclusions of diverse plants and animals (Zherikhin & Ross, 2000; Grimaldi *et al.*, 2002; Ross *et al.*, 2010; Boucot & Poinar, 2011; Labandeira, 2014). Based on palynological studies and ammonoid zonation within the surrounding rock units, as well as insect taxa preserved within the amber, recent age estimates have ranged from Albian to Cenomanian. Considering other factors, but especially radiometric dates obtained from the volcanic clasts present within the amber-bearing sediments, an age of earliest Cenomanian (98.79 ± 0.62 Ma) has recently been established for Myanmar amber (Cruickshank & Ko, 2003; Shi *et al.*, 2012a, b). This is the currently accepted date for Myanmar amber.

Taxon sampling

We sampled 66 terminal taxa that comprise 16 modern species and 50 fossil species, three of which were outgroup species. The extant genera that we sampled represented the three families of Evaniidae, Gasteruptiidae and Aulacidae of Evanioidea. The sampled genera were *Acanthinevania*, *Brachygaster*, *Decevania*, *Evania*, *Evaniscus*, *Hyptia*, *Micrevania*, *Prosevania*, *Semaemyia* and *Zeuxevania* in Evaniidae, *Gasteruption*, *Pseudofoenus* and *Hyptiogaster* in Gasteruptiidae, *Aulacus* and *Pristaulacus* in Aulacidae. Specimens of extant Evaniidae and Gasteruptiidae examined for this analysis are deposited in the collections of the Systematic Entomology Laboratory, Agriculture Research Service of the United States Department of Agriculture, and are housed at the Department of Entomology collections of the National Museum of Natural History, Smithsonian Institution, in Washington, D.C. The fossil genera represented eight families of Andreneliidae (*Andrenelia*), Anomopterellidae

(*Anomopterella*, *Choristopterella*, *Synaphopterella*), Aulacidae (*Aulacus*, *Exilaulacus*, *Pristaulacus*, *Vectevania*), Baissidae (*Baissa*, *Electrobaissa*, *Humiryssus*, *Heterobaissa*, *Manlaya*, *Mesepipolaea*), Evaniidae (*Botstvania*, *Cretevania*, *Curtevania*, *Eoevania*, *Eovernevania*, *Evaniella*, *Grimaldivania*, *Iberoevania*, *Lebanevania*, *Mesevania*, *Newjersevania*, *Praevania*, *Protoparevania*, *Procretevania*, *Sinuevania*, *Sorellevania*), Gasteruptiidae (*Hyptiogastrites*), Othniodellithidae (*Othniodelitha*) and Praeaulacidae (*Archaulacus*, *Aulacogastrius*, *Eosaulacus*, *Eonevania*, *Evaniops*, *Evanigaster*, *Gulgonga*, *Habraulacus*, *Nevania*, *Praeaulacinus*, *Praeaulacites*, *Praeaulacops*, *Praeaulacus*, *Praeaulacon*, *Sinaulacogastrius*, *Sinevania*). We excluded *Kotujisca* and *Kotujellites* of Gasteruptiidae, *Tillywhimia* of Baissidae, and *Cretoleistogaster*, *Miniwestratia*, *Nanowestratia* and *Westratia* of Praeaulacidae from the matrix due to their poor preservation, which consisted of sole fragmentary wings or distorted bodies. The outgroup taxa were selected based on previously published phylogenies of Hymenoptera (Rasnitsyn & Zhang, 2010; Sharkey *et al.*, 2012; Li *et al.*, 2015a), and on their putatively plesiomorphic wing venation and relatively broad propodeum-metasomal articulations. We chose *Orussus* of Orussidae, and *Acephalitia* and *Praeproapocritus* of Ephialtidae as outgroup taxa.

Morphological data

The morphological data were principally taken from earlier studies (Ronquist *et al.*, 1999; Jennings & Austin, 2000; Basi-buyuk *et al.*, 2002; Turrisi *et al.*, 2009; Peñalver *et al.*, 2010; Rasnitsyn & Zhang, 2010; Sharkey *et al.*, 2012; Li *et al.*, 2013a, b) and carefully checked, but some characters were excluded because they cannot be satisfactorily examined in fossil species. We also introduced additional, new characters that were well suited for examination in fossils. Eighty-one adult characters (Appendix S6: Figs 2, 3) were coded for the 63 ingroup and three outgroup taxa. All characters were treated as unordered and with equal weight. Inapplicable and unknown characters were coded with ‘–’ and ‘?’ respectively.

Molecular data

Molecular data for the extant taxa, consisting of eight species of Evaniidae, two species of Gasteruptiidae, and one species of Orussidae (Appendix S2), were downloaded from GenBank. Three gene fragments were used: cytochrome c oxidase subunit I (COI), 16S and 28S (Deans *et al.*, 2006; Sharkey *et al.*, 2012). Sequences were aligned using the CLUSTALX program, and genes were concatenated using MESQUITE (ver. 2.75; Maddison & Maddison, 2011), resulting in a final dataset that includes a total of 2296 aligned base pairs.

Phylogenetic methods

Because the DNA sequence data were only available from species of the extant families Evaniidae and Gasteruptiidae

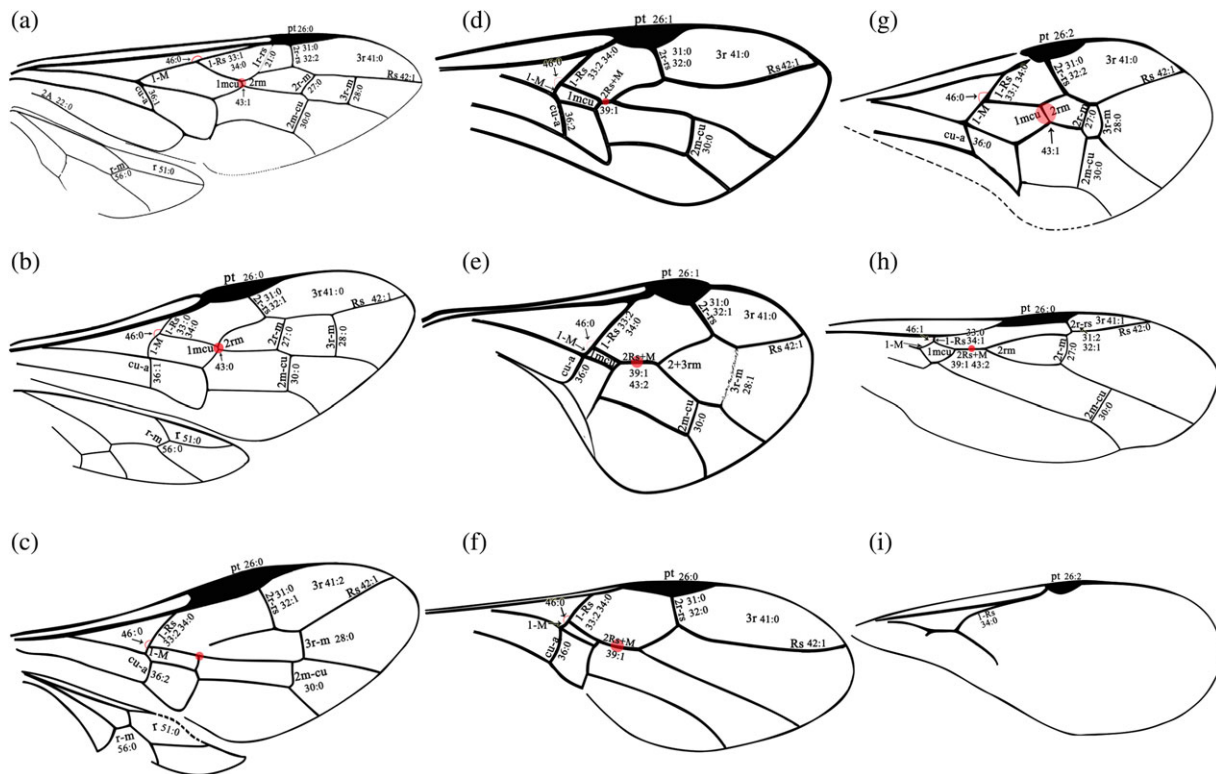


Fig. 2. Wings of Evanioidea. (a) Praeaulacidae (*Nevania*); (b) Praeaulacidae (*Praeaulacus*); (c) Anomopterellidae (*Anomopterella*); (d) Baissidae (*Heterobaissa*); (e) Aulacidae (*Exilaulacus*); (f) Gasteruptionidae (*Hyptiogastrites*); (g) Evaniidae (*Mesevania*); (h) Evaniidae (*Cretevania*); (i) Evaniidae (*Brachygaster*). Numbers refer to characters and states, Appendix S6. [Colour figure can be viewed at wileyonlinelibrary.com].

(~15.9 % of all ingroup terminals), it was difficult to resolve the phylogeny of Evanioidea based solely on molecular data or combined-evidence data. Consequently, we analysed our datasets as follows for easy comparison. First, to better explain the relationships among the families of Evanioidea, both maximum parsimony (MP) and Bayesian inference (BI) analyses were applied separately to the morphological dataset (Appendix S2) and the combined-evidence dataset (Appendix S3). Second, to evaluate the phylogenetic signal of the data and to construct a robust hypothesis of the relationships among the genera of Evanioidea, we employed a morphological dataset comprising 66 species (63 evanioids and three outgroups) based on 81 morphological characters (Appendix S3). All trees were rooted on *Orussus*.

Maximum parsimony analysis

Maximum parsimony analysis of the morphological dataset (Appendix S3) and the combined-evidence dataset (Appendix S4) were conducted with WINCLADA ver. 1.00.08 (Nixon, 2002) and NONA ver. 2.0 (Goloboff, 1993; Goloboff et al., 2003, 2008). Tree searches were performed using a heuristic search method consisting of the following options: set to hold 10 000 trees, T1000 replications, 100 starting tree replications, and a multiple TBR+TBR search strategy. Character coding was established by NEXUS DATA EDITOR 0.5.0 (Roderic, 2001), with all characters unordered and of equal weight.

Bayesian inference

Bayesian analyses of the morphological dataset (Appendix S3) and the combined-evidence dataset (Appendix S4) were performed in MRBAYES 3.2.3 (Ronquist & Huelsenbeck, 2003; Ronquist et al., 2012). For the combined-evidence dataset, two data partitions were used: one partition for molecular data with the best model selected by the software PARTITIONFINDER, and the other partition for morphological data with the Mk model (Lewis, 2001) and gamma distribution (Appendix S5). Two separate runs, each having unlinked partitions and four Bayesian Markov chain Monte Carlo (MCMC) chains (three heated and one cold) were run simultaneously for a total of 10 million generations, with sampling every 1000 generations and the first 25% discarded as burn-in. Stationarity was considered to be reached when the average standard deviation of split frequencies was below 0.01. A majority-rule consensus tree was computed with posterior probabilities for each node.

Results

Taxonomy

Hymenoptera Linnaeus, 1758
Apocrita Gerstaecker, 1867
Evanioidea Latreille, 1802

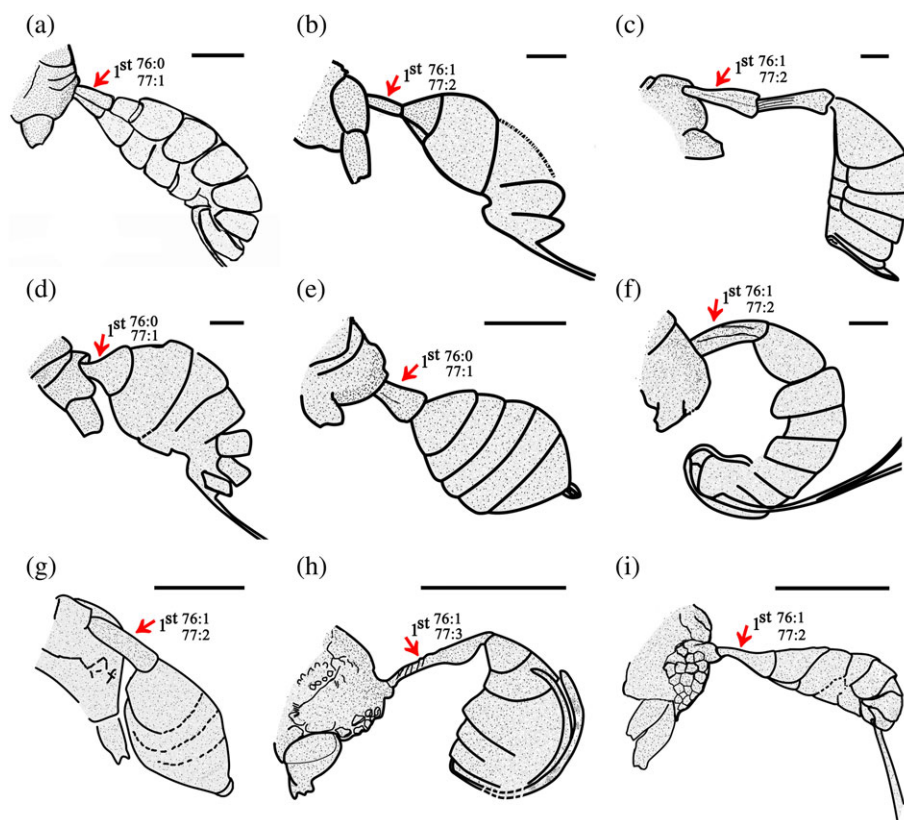


Fig. 3. First metasomal segment of Evanioidea. (a) Praeaulacidae (*Praeaulacon*); (b) Praeaulacidae (*Evaniops*); (c) Praeaulacidae (*Nevania*); (d) Praeaulacidae (*Praeaulacites*); (e) Anomopterellidae (*Anomopterella*); (f) Andreneliidae (*Andrenelia*); (g) Evaniidae (*Newjersevania*); (h) Evaniidae (*Eovernevania*); (i) Aulacidae (*Exilaulacus*); Numbers refer to characters and states, Appendix S6. [Colour figure can be viewed at wileyonlinelibrary.com].

Family Evaniidae Latreille, 1802

Sinuevania Li, Rasnitsyn & Ren gen.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:E80C2EDB-EF2C-4E1E-8DFE-6738EB20B11B>

Type species. *Sinuevania mira* Li, Rasnitsyn & Ren **sp.n.**

Etymology. The generic epithet is a combination of the Latin *sinus* -us (fourth declension), meaning 'bend', 'curve' or 'fold', which refers to the metasomal petiole of this wasp that is very long and curved; and *Evania*, a type genus name, often used as a suffix for generic names in Evaniidae. The gender is feminine.

Diagnosis. Small body size; antenna 13-segmented, long and clavate. Mesosoma stout, hind coxa long and stick-like, thin. Metasoma with first segment long and bent upward. Forewing with Rs and M strongly angled at their junction, at about 140°, meeting R well before pterostigma base; 1-M distinctly longer than 1-Rs; 2r-rs nearly as long as 1-Rs, meeting distal pterostigma; cu-a distinctly postfurcal vein, A complete; 2r-m, 3r-m rudimentary.

Included species. Type species only.

Remarks. For comparison with other genera, see key below.

Sinuevania mira Li, Rasnitsyn & Ren **sp.n.**

(Figs 4, 5)

<http://zoobank.org/urn:lsid:zoobank.org:act:3F483B02-A92D-4835-A392-30189FCD0F85>

Etymology. The specific epithet is derived from the Latin adjective *mirus* -a -um (second declension), meaning 'wonderful', 'astonishing' or 'extraordinary', which refers to this wasp species possessing a rather spectacular clavate antenna with very long and thin basal flagellomeres.

Diagnosis. As for the genus.

Material examined. Holotype, CNU-HYM-MA-2014002, female, well preserved.

Locality and horizon. Hukawng Village, Kachin State, northern Myanmar; Late Cretaceous [early Cenomanian].

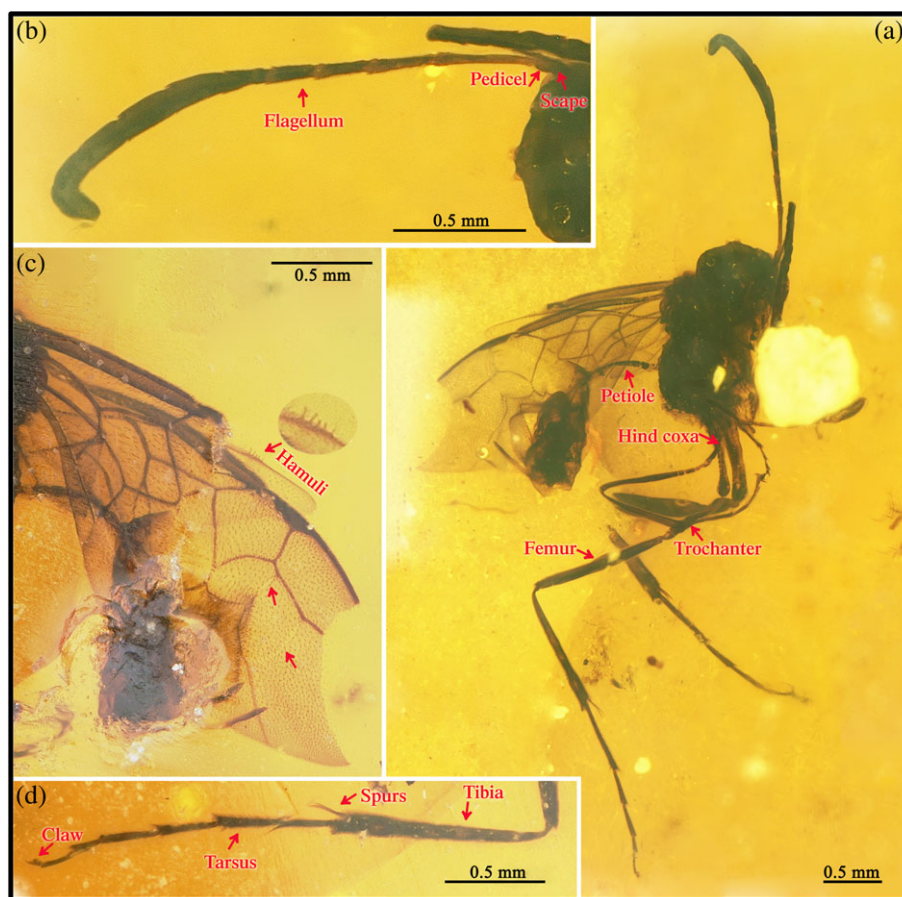


Fig. 4. *Sinuevania mira* gen. et sp.n. Holotype, CNU-HYM-MA-2014002. (a) Photograph of habitus; (b) antenna; (c) wings; (d) hind leg. [Colour figure can be viewed at wileyonlinelibrary.com].

Description. Female fully winged and of small body size (total body length approximately 2.8 mm). Integument of head, mesosoma and metasoma black; petiole, legs and ovipositor dark brown; wing veins light brown. Head rounded, 0.69×0.49 mm in lateral view, with relatively large compound eye. Antenna (1.62 mm) not obviously elbowed, articulated nearly the level of head mid-length; scape (0.14 mm) much longer than pedicel (0.03 mm), but nearly equal in width; 11 flagellar articles in total present, and first flagellar article longest and conspicuously thickened beyond middle, the length of flagellomeres from I to XI (in mm): 0.33, 0.24, 0.18, 0.16, 0.16, 0.17, 0.18, 0.12, 0.10, 0.10, 0.16, and from the sixth flagellomere, about $2\times$ as long as wide.

Mesosoma 0.64 mm high and 1.19 mm long, strongly sclerotized, compact and relatively high; pronotum without distinctly dorsal surface; propodeum long and arching from metasomal base toward hind coxa, areolate posteriorly. Legs much slender, strongly setose with conspicuous trochantellus and five tarsomeres; hind coxa (0.51 mm) almost stick-like, elongate (only slightly inflated basally), only somewhat shorter than head height, slightly longer than trochanter (0.46 mm); hind femur (1.11 mm) nearly as long as hind tibia (1.05 mm) with two spurs;

hind tarsomere length (mm): 0.60, 0.30, 0.28, 0.12, 0.17; pre-tarsal claws slender, arolium present. Metasoma deformed, narrow and elongate as preserved, about 1.56 mm long, with petiole long (0.53 mm) and thin, bended upward; valvifer 2 and sheath combined about 0.49 mm, exerted out of the end of metasoma.

Wings hyaline with abundant microtrichia. Forewing length about 2.28 mm, with venation relatively complete; pterostigma short and slightly broad; 1-M (0.36 mm) $2\times$ as long as 1-Rs (0.17 mm), and Rs and M angled about 140° at the junction of Rs and M; 1-Rs subvertical to Rs+M, meeting R before the base of pterostigma; 2r-rs (0.16 mm) nearly as long as 1-Rs, meeting pterostigma slightly behind the mid-length of it; 2-Rs long, distinctly curved, formed bracket-shape with 3r-m; 2r-m and 3r-m rudimentary; cu-a (0.17 mm) distinctly postfurcal, longer than 1Cu (0.12 mm); 2Cu (0.28 mm) slightly bent upward and nearly as long as 1m-cu (0.27 mm); cell 1mcu broad, nearly $2\times$ as long as wide; vein A complete, extending to the wing base. Hindwing without venation except Sc+R.

***Curtevania* Li, Rasnitsyn & Ren gen.n.**

<http://zoobank.org/urn:lsid:zoobank.org:act:DDA0F1CF-6101-4AA5-B93A-B4C842BA62BF>

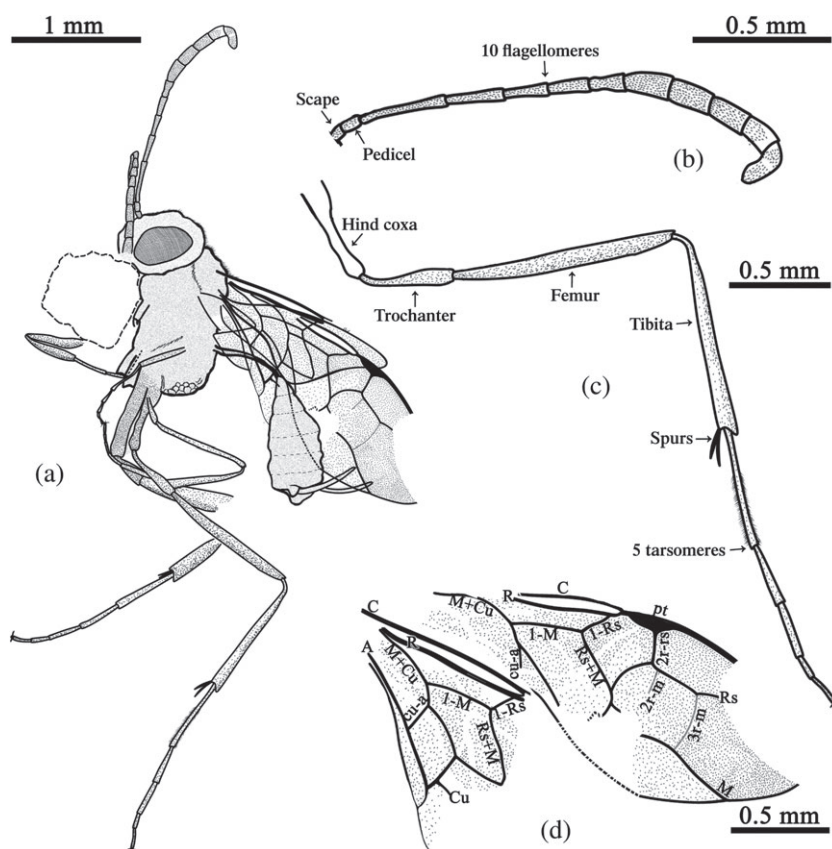


Fig. 5. *Sinuevania mira* gen. et sp.n. Holotype, CNU-HYM-MA-2014002. (a) Line drawing of habitus; (b) antenna; (c) hind leg; (d) wings.

Type species. *Curtevania enervia* Li, Rasnitsyn & Ren sp.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:41982F99-6A5F-432B-B552-07FFAA9C6ADE>

Etymology. The generic epithet is a combination of the Latin adjective *curtus* -a -um, (second declension), meaning 'short' or 'abbreviated', referring to the very shortened metasomal petiole of this wasp, and *Evania*, a type genus name, often used as a suffix for generic names in Evaniidae. The gender is feminine.

Etymology. The specific epithet is derived from the Latin adjective, *enervatus* -a, -um (second declension), meaning 'weakened' or 'powerless', and refers to the forewings with reduced venation.

Diagnosis. Small body size. Mesosoma stout, hind coxa normal. Male metasoma elongate, with first metasomal segment very short. Forewing with Rs and M nearly straight, meeting R well before pterostigma base; both 1-M and 2r-rs distinctly longer than 1-Rs. 2r-rs origin behind mid-length of pterostigma; 2Rs straight, vertical to 2r-rs, aligned with 1m-cu; 3Rs bent downward, 3r broad; no traces of 2r-m and 3r-m. Cu straight (not angular at 1m-cu). Cross-vein 1cu-a interstitial (well seen on Fig. 7a on reversed wing), 2cu-a lost, cell 2cua open distal.

Diagnosis. As for the genus.

Included species. Type species only.

Material examined. Holotype, CNU-HYM-MA-2014003, male, well preserved.

Remarks. For comparison with other genera, see key below.

Locality and horizon. Hukawng Village, Kachin State, northern Myanmar; Late Cretaceous (early Cenomanian).

Curtevania enervia Li, Rasnitsyn & Ren sp.n.
(Figs 6, 7)

Description. Male with small body size (total body length ~3.9 mm), dark brown to black, mesosoma and head obscured and microsculpture very difficult to observe. Head rounded, 1.12 × 0.96 mm in lateral view, narrower than mesosoma.

Mesosoma 1.76 mm high and 1.24 mm long, strongly sclerotized, compact and relatively high. Legs much slender, strongly setose with conspicuous trochantellus and five tarsomeres; hind

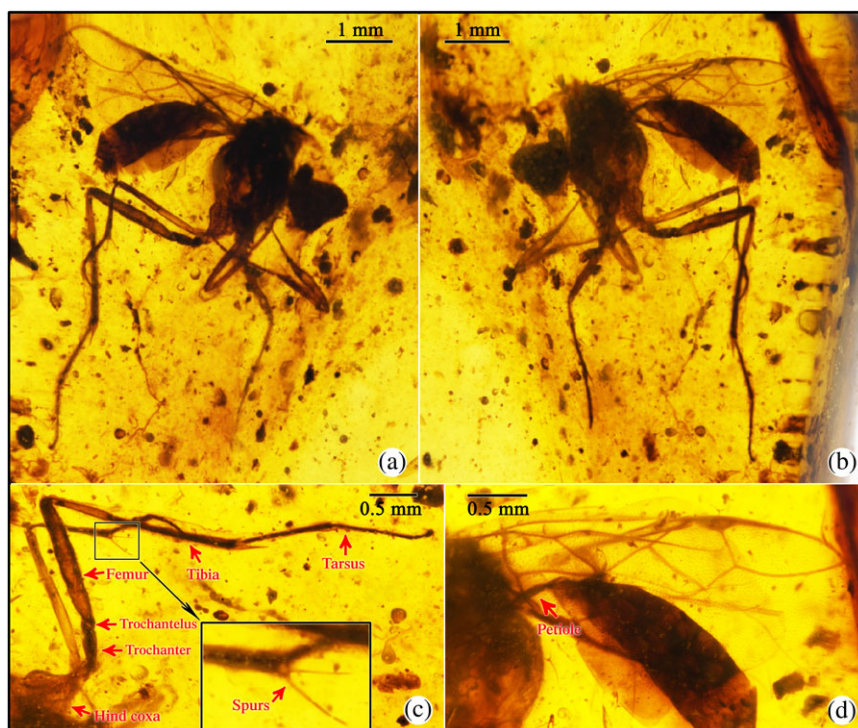


Fig. 6. *Curtevania enervia* gen. et sp.n. Holotype, CNU-HYM-MA-2014003. (a, b) Photograph of habitus; (c) hind leg; (d) metasoma. [Colour figure can be viewed at wileyonlinelibrary.com].

legs distinctly longer than fore- and midlegs; hind coxa (0.76 mm) broad, wider and longer than trochanter (0.41 mm); hind femur (1.45 mm) wider but shorter than hind tibia (2.01 mm), tibia with two spurs; five tarsomeres (in mm): I (0.52), II (0.48), III (0.15), IV (0.23), V (0.15); pretarsal claws slender, arolium present. Metasoma 2.19 mm long, with first metasomal segment formed as very short petiole (0.34 mm) and bending upward; remaining metasomal segments rather uniform in length, forming curved, elongate oval; hypopygium short, male genitalia elongate and narrow in side view.

Wings hyaline with abundant microtrichia, forewing length about 3.2 mm as preserved, with three enclosed cells, pterostigma short and slightly broad; 1-M (0.37 mm) 2.5× as long as 1-Rs (0.15 mm), and Rs and M nearly straight at the junction of Rs and M; 1-Rs inclined toward wing base, meeting R well before base of pterostigma; 2r-rs (0.32 mm) 2× as long as 1-Rs, meeting pterostigma slightly behind mid-length of it and nearly paralleled with Rs+M; 2-Rs straight, vertical to 2r-rs; both cell 1mcu and 1+2r very broad, nearly equal in length and width; 3Rs bent downward, 3r broad, 1.06 mm long and 0.41 mm wide and longer than 1+2r; free M very thin. Hindwing without venation except Sc+R.

Newjersevania Basibuyuk, Quicke & Rasnitsyn, 2000

Type species. *Newjersevania casei* Basibuyuk, Quicke & Rasnitsyn, 2000

Revised diagnosis. Small body size, < 5 mm. Antenna with 13 segments, slightly elbowed and not conspicuously thickened beyond middle. Forewing with 2r-m indistinct complete, or only as a very short anterior stub, or absent; free M indistinct basally, free Rs bending toward wing fore margin; Rs and M more or less straight; 1m-cu straight or slightly bent; vein 1cu-a interstitial or slightly postfurcal, 2cu-a conspicuously long. Metasoma moderately sized, shorter than mesosoma, spindle-shaped or rounded.

Species included. Type species, *N. nascimbenei* Basibuyuk, Quicke & Rasnitsyn, 2000, *N. longa* Li, Rasnitsyn & Ren **sp.n.** and *N. brevis* Li, Rasnitsyn & Ren **sp.n.**

Newjersevania longa Li, Rasnitsyn & Ren **sp.n.**

(Figs 8, 9)

<http://zoobank.org/urn:lsid:zoobank.org:act:657401EE-FD25-4E73-8152-CA56C063E252>

Etymology. The specific epithet is derived from the Latin adjective *longus* -a -um (second declension), meaning 'long', 'vast' and 'spacious' in both a temporal and spatial sense, referring to the forewing with 2r-rs vein that is longer than the 1-M vein.

Diagnosis. Forewing with 1-M nearly two times as long as 1-Rs; 2r-rs longer than 1-M; 1m-cu interstitial with 2-RS, slightly bent; cu-a interstitial.

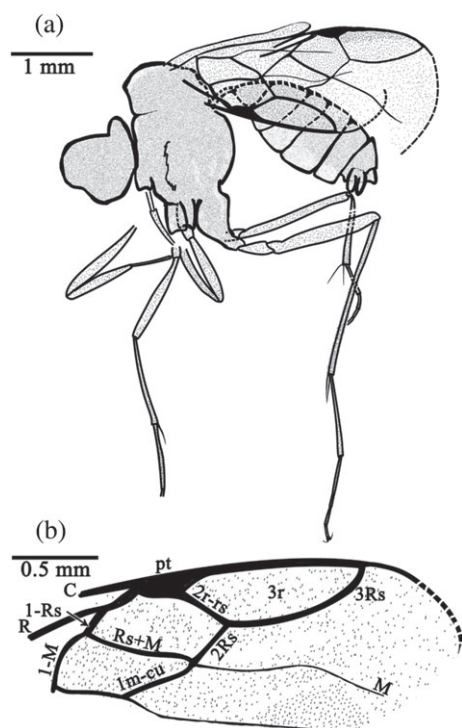


Fig. 7. *Curtevania enervia* gen. et sp.n. Holotype, CNU-HYM-MA-2014003. (a) Line drawing of habitus; (b) wings.

Type material. Holotype, CNU-HYM-MA-2014005, male, well-preserved.

Locality and horizon. Hukawng Village, Kachin State, Northern Myanmar; Late Cretaceous (early Cenomanian).

Description. Small evaniid, 2.48 mm long, dark brown to black (mesosoma and head obscured and structure very difficult to observe). Head transversely ovoid, 0.52×0.80 mm in lateral view, slightly wider than mesosoma. Antenna about 1.31 mm long, somewhat deformed, number of flagellomeres not precisely known.

Mesosoma 1.60 mm long and 0.74 mm high in lateral view. Legs apparently unsculptured, elongated, with five tarsomeres, pretarsal claws slender; arolium present. Hind legs longer and wider than fore- and midlegs; all legs with femur wider than tibia, and tarsomeres distinctly narrower than tibia. Within hind legs, tibia with one spur gradually swollen from basal to apical aspect; first tarsomere distinctly longer than others, five tarsomeres: I (0.52 mm), II (0.27 mm), III (0.13 mm), IV (0.10 mm), V (0.16 mm). Metasoma remaining segments oval, 0.94 mm long, 0.52 mm wide, first metasomal segment not clearly visible.

Wings hyaline with abundant microtrichia, forewing 2.28 mm long, 0.75 mm greatest width. Pterostigma dark brown, small with 0.26 mm long and 0.06 mm wide; 1-M (0.22 mm) twice as long as 1-Rs (0.09 mm), Rs and M angled about 150° at junction of Rs and M; 1-Rs inclined toward wing base, meeting R



Fig. 8. *Newjersevania longa* sp.n. Holotype, CNU-HYM-MA-2014005. (a) Photograph of habitus; (b) wings. [Colour figure can be viewed at wileyonlinelibrary.com].

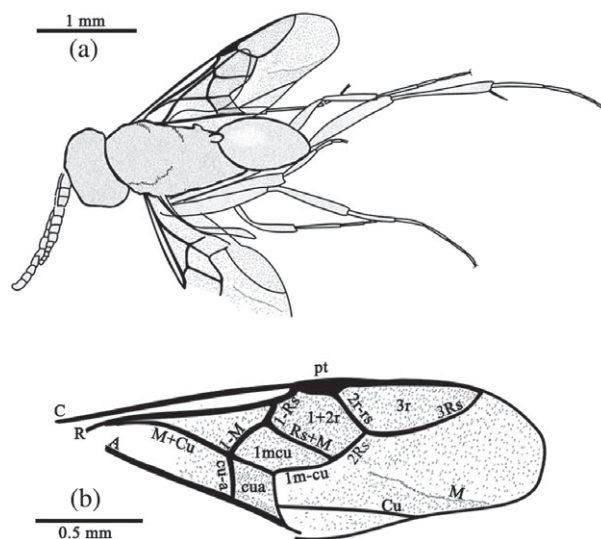


Fig. 9. *Newjersevania longa* sp.n. Holotype, CNU-HYM-MA-2014005. (a) Line drawing of habitus; (b) wings.

before the base of pterostigma; 2r-rs (0.24 mm) straight, slightly longer than 1-M, meeting pterostigma near its apex; cell 3r wide triangle, 0.64 mm long and 0.21 mm wide, slightly longer than cell 1+2r; 2Rs straight, vertical to 2r-rs, 3Rs bent downward; no traces of 2r-m and 3r-m, 1m-cu (0.27 mm) interstitial with 2-RS, slightly bent, longer than 1-M, cells 1m-cu and 1+2r nearly equal in length, but 1+2r slightly wider than 1m-cu; free M and Cu indistinct; 1cu-a interstitial, 2cu-a complete, both of them

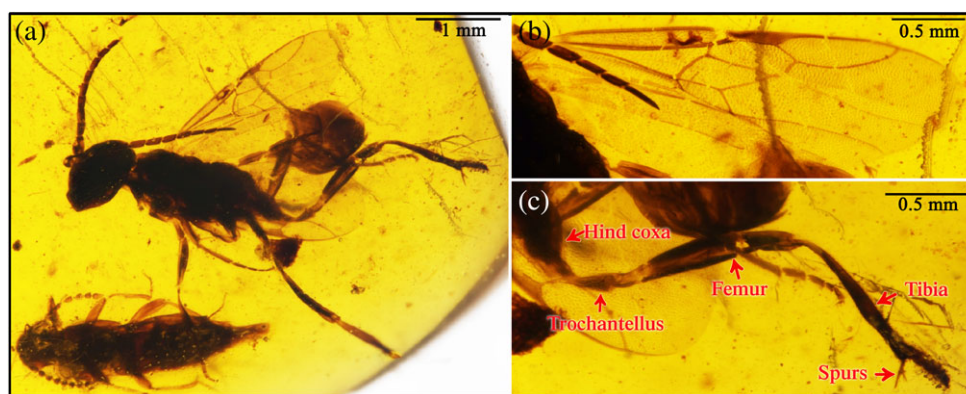


Fig. 10. *Newjersevania brevis* sp.n. Holotype, CNU-HYM-MA-2014006. (a) Photograph of habitus; (b) wings; (c) hind leg. [Colour figure can be viewed at wileyonlinelibrary.com].

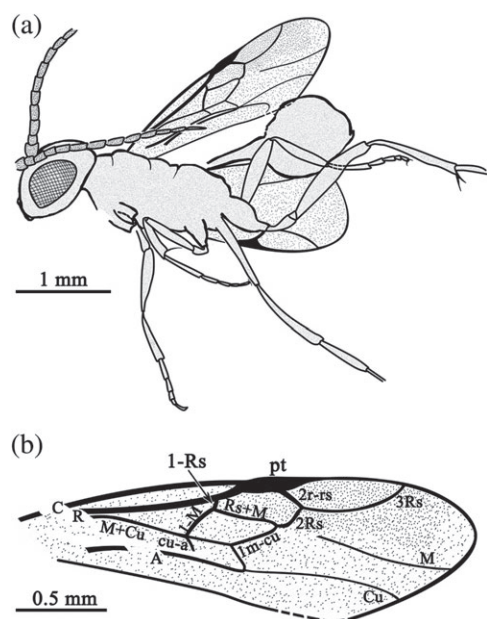


Fig. 11. *Newjersevania brevis* sp.n. Holotype, CNU-HYM-MA-2014006. (a) Photograph of habitus; (b) forewing.

reaching A; cell cua distinctly shorter than 1m-cu; A complete and extended to wing base. Hindwing 1.11 mm long and 0.35 mm wide, without veins other than R.

***Newjersevania brevis* Li, Rasnitsyn & Ren sp.n.**

(Figs 10, 11)

<http://zoobank.org/urn:lsid:zoobank.org:act:B8A0E4ED-3B2C-41DF-AEBC-8CD0DD97B4A0>

Etymology. The specific epithet is derived from the Latin adjective *brevis* -e (third declension) meaning 'short', 'shallow' or 'slight', and referring to the forewing with the 2r-rs vein that is shorter than the 1-M vein.

Diagnosis. Forewing with 1-M conspicuously longer than 1-Rs; 2r-rs shorter than 1-M; 1m-cu not reaching apex of RS+M, slightly bent; cu-a interstitial.

Type material. Holotype, CNU-HYM-MA-2014006, male, well-preserved.

Locality and horizon. Hukawng Village, Kachin State, northern Myanmar; Late Cretaceous (early Cenomanian).

Description. Small evaniid, 3.48 mm long; dark brown to black. Head transversely ovoid, 0.99×0.61 mm in lateral view, slightly wider than mesosoma; eyes large and ovoid, apparently without setae. Antenna about 2.08 mm long, with 11 flagellomeres, conspicuously narrowing towards apex, arising nearly the midpoint of eyes; scape wider than pedicel, both of them cylindrical.

Mesosoma slender, 1.54 mm long and 0.68 mm high in lateral view. Legs apparently unsculptured, with conspicuous trochantellus; hind legs longer and wider than fore- and midlegs; foreleg with femur wider than tibia; midleg with a strong apical spur; hind leg with broad coxa, 0.50 mm long and 0.29 mm wide, trochantellus distinctly narrower, hind femur slightly longer than tibia but distinctly wider than it, hind tibia with two spurs gradually thickened from basal to apical. First metasomal segment formed as petiole (0.68 mm), remaining segments rounded, 0.93 mm long, 0.86 mm wide.

Wings hyaline with abundant microtrichia; forewing 2.52 mm long, 1.61 mm greatest width. Pterostigma dark brown, elongate with 0.39 mm long and 0.09 mm wide; 1-M (0.22 mm) $4\times$ as long as 1-Rs (0.05 mm), and Rs and M angled about 165° at the junction of Rs and M; 1-Rs straight, meeting R before the base of pterostigma; 2r-rs (0.15 mm) straight, shorter than 1-M, meeting pterostigma behind its mid-length; 2Rs curved, vertical to 2r-rs at junction, 3Rs bent downward; cell 3r elongate oval, 0.66 mm long and 0.19 mm wide, distinctly longer than 1+2r; 1m-cu (0.27 mm) not reaching apex of RS+M, longer than 1-M, and cell 1m-cu and 1+2r nearly equal in width; free M and Cu

indistinct; 1cu-a interstitial, 2cu-a complete; cell cua distinctly narrower than 1mcu; A complete and extended to wing base.

Key to the known species of *Newjersevania* Basibuyuk, Quicke & Rasnitsyn, 2000

1. Forewing with 2r-m indistinct with tubular rudiments on both RS and M, free Rs and M reaching wing margin
..... *N. nascimbenei* Basibuyuk, Quicke & Rasnitsyn, 2000
– Forewing with 2r-m lost (rarely with rudiment on RS only) ..
..... 2
2. Forewing with pterostigma small, 2r-rs longer than 1-M
..... *N. longa* **sp.n.**
– Forewing with pterostigma relatively large, 2r-rs shorter than
1-M 3
3. Forewing with 1-Rs origin almost at the base of pterostigma,
2Rs straight, 3r more than twice as long as 1+2r
..... *N. casei* Basibuyuk, Quicke & Rasnitsyn, 2000
– Forewing with 1-Rs origin a distance more than 1-RS of the
base of pterostigma, 2Rs bent, 3r less than twice as long as 1+2r
..... *N. brevis* **sp.n.**

Cretevania Rasnitsyn, 1975

[*Procretevania*: Zhang & Zhang, 2000, p. 287 (type species, *P. pristine* Zhang & Zhang, 2000, NE China, Barremian, Lower Cretaceous); **syn.n.**]

[*Eovernevania*: Deans, Basibuyuk, Azar & Nel, 2004, p. 4 (type species, *E. cyrtocerca* Deans, 2004, Lebanese amber, Barremian, Lower Cretaceous); **syn.n.**]

[*Dabburatyus*: Kaddumi, 2005, p. 99 (type species, *D. extinctus* Kaddumi 2005, Jordan amber, Barremian, Lower Cretaceous); **syn.n.** (repeated in Kaddumi, 2007)].

Type species. *Cretevania minor* Rasnitsyn, 1975

Revised diagnosis. Head long, flattened posteriorly, adpressed to prothorax. Antenna short, elbowed, with 10 (*C. bechlyi*) or 11 flagellomeres (other species). Mesosoma practically as long as high, with notauli present (*C. bechlyi*) or absent (other species); with conspicuous areolate sculpturing, mainly in the propodeum. Fore- and midlegs long and thin; hind legs robust. Forewing without jugal lobes and with a wide costal cell; pterostigma narrow, short or long and nearly parallel-sided; cross-vein 2r-rs near pterostigma apex, short 1-Rs vein vertical or inclined towards forewing base; cross-veins r-m at least indicated by thickened or bent Rs or M; cell 1+2r not contacted with 1mcu, 2m-cu absent; 3r narrow and triangular; 1+2r longer than both 3r and basal cell. Hindwing with only costal vein present. Petiole elongate, tubular, thickened distally. Metasoma round or ovate in lateral aspect. Ovipositor long, exerted, and curved dorsally.

Comments. The genus *Cretevania* was established by Rasnitsyn (1975) on the basis of the type species *C. minor* and two

other species *C. major* and *C. minuta* from Late Cretaceous amber of Russia. Later, another two genera – *Procretevania* Zhang & Zhang, 2000, and *Eovernevania* Deans, 2004 – were described. Peñalver *et al.* (2010) proposed that *Procretevania* and *Eovernevania* are synonyms of *Cretevania* based on their impressive similarities in morphological characters and on a phylogenetic analysis (Peñalver *et al.*, 2010). Initially, we considered that the vast difference of body size among these three genera could not be ignored, because lengths of body and wings would be important characters to supplement the taxonomy (Li *et al.*, 2014a). However, the new species *C. tenuis* from the Myanmar amber is about 5 mm long and very close to *P. pristine*. The new material suggests that the apparently sharp body-size difference between *Procretevania* and the other two genera might be exaggerated taphonomically because small pieces of most Cretaceous amber favour preservation of small insects in contrast to those preserved in compression rocks. Therefore, we accept the proposal of *Procretevania* and *Eovernevania* as synonyms of *Cretevania*. We also add *Dabburatyus* Kaddumi 2005 (**syn.n.**) to the synonym list of *Cretevania*, because this genus shows all diagnostic characters of *Cretevania* (Kaddumi, 2005).

Species included. Type species and *C. major* Rasnitsyn, 1975 from Santonian amber of Yantardakh, northern Siberia; *C. minuta* Rasnitsyn, 1975 from Cenomanian of Agapa, North Siberia; *C. meridionalis* Rasnitsyn, 1991 from Aptian of Bon Tsagan in Mongolia; *C. concordia* Rasnitsyn, Jarzembowski & Ross, 1998 from Hauterivian of the Lower Weald Clay, southern England; *C. alcalai* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010, *C. alonsoi* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010, *C. montoyai* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010, *C. rubusensis* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 and *C. soplaensis* Pérez-de la Fuente, Peñalver & Ortega-Blanco, 2012, all from U. Aptian – L. Albian amber from northern Spain; *C. bechlyi* Jennings, Krogmann & Mew, 2013 and *C. tenuis* Li & Rasnitsyn **sp.n.**, from Cenomanian Myanmar amber; *C. cyrtocerca* (Deans, 2004) from Barremian Lebanese amber; *C. extincta* Kaddumi, 2005 (**comb.n.**) from Barremian Jordanian amber; *C. pristina* (Zhang & Zhang, 2000); *C. vesca* (Zhang, Rasnitsyn, Wang & Zhang, 2007); *C. exquisita* (Zhang, Rasnitsyn, Wang & Zhang, 2007); *C. mitis* (Li, Shih & Ren, 2014) **comb.n.**; and *C. venata* Li & Rasnitsyn **sp.n.**, all from Barremian Yixian Formation, NE China.

Key to the known species of *Cretevania* Rasnitsyn, 1975

1. Forewing with pterostigma short (2r-rs about as long as its distance to pterostigmal base), two r-m veins and 2m-cu absent 2
– Forewing with pterostigma long (2r-rs much shorter than its distance to pterostigmal base) 3
2. Forewing with 1-Rs subvertical to R, 1cu-a interstitial
..... *C. cyrtocerca* (Deans, 2004)
– Forewing with 1-Rs vertical to R, 1cu-a postfurcal
..... *C. tenuis* **sp.n.**

3. Forewing with 2m-cu present 4
 – Forewing with 2m-cu absent 5
4. Forewing with 2r-m, 2-Rs+M present
 *C. minor* Rasnitsyn, 1975
 – Forewing with 2r-m, 2-Rs+M absent *C. venata* sp.n.
5. Forewing with 2r-m indistinct, 2-Rs+M absent, 2rm triangle,
 nearly as wide as 1mcu
 *C. vesca* (Zhang, Rasnitsyn, Wang & Zhang, 2007)
 – Forewing with 2r-m entirely lost 6
6. Forewing with 1cu-a postfurcal 7
 – Forewing with 1cu-a interstitial or lost 9
7. Forewing with 1-Rs subvertical to R and Rs+M, 2r-rs long,
 marginal cell 3r nearly as long as 1+2r
 *C. mitis* (Li, Shih & Ren, 2014) **comb.n.**
 – Forewing with marginal cell 3r small triangle, about 1.5× as
 long as 1+2r 8
8. Forewing with cell cua broad, wider than 1mcu, free M
 geniculate distal of 2r-rs, 1-Rs vertical to R
 *C. montoyai* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010
 – Forewing with cell cua narrower than 1mcu, free M geniculate
 at the same level of 2r-rs, 1-Rs inclined towards wing base
 *C. alcalai* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010
9. Forewing with 1cu-a interstitial, nearly as long as 1-M, free
 M geniculate distal of 2r-rs, 1-Rs inclined towards pterostigma
 base *C. exquisita* (Zhang, Rasnitsyn, Wang & Zhang, 2007)
 – Forewing with 1cu-a entirely lost 10
10. Antennae short with 10 flagellomeres, mesosoma with
 notauli present
 *C. bechlyi* Jennings, Krogmann & Mew, 2013
 – Antennae short with 11 flagellomeres, mesosoma with notauli
 absent 11
11. Forewing with Cu between 1-M and 1m-cu not longer than
 1m-cu, 2r-m spectral, 2-Rs and 2-M straight, wing apex shape
 rounded
 .. *C. soplaensis* Perez-de la Fuente, Peñalver & Ortega-Blanco,
 2012.
 – Forewing with Cu between 1-M and 1m-cu not longer than
 1m-cu, 2r-m entirely lost 12
12. Forewing with 2-Rs+M present 13
 – Forewing with 2-Rs+M absent 18
13. Forewing with 2-Rs+M longer than 2r-rs 14
 – Forewing with 2-Rs+M shorter than 2r-rs 15
14. Forewing 1.1 mm long, with 1-Rs very short
 *C. minuta* Rasnitsyn, 1975
 – Forewing much longer (~2 mm or more)
 *C. major* Rasnitsyn, 1975
15. Forewing with M not geniculate opposite 2r-rs
 *C. meridionalis* Rasnitsyn, 1991
 – Forewing with M geniculate opposite 2r-rs 16
16. Forewing 2.3 mm long, with 1-Rs oblique to R, 3r cell short
 *C. alonsoi* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010
 – Forewing about 3 mm long, with 1-Rs vertical to R, cell 3r
 long 17
17. Forewing with 2-RS much longer than 3-RS
 *C. extincta* (Kaddumi, 2005)
 – Forewing with 2-RS as long as 3-RS *C. concordia* Rasnitsyn,
 Jarzembowski & Ross, 1988

18. Forewing 1.4 mm long, with cell 3r about as long as
 pterostigma *C. rubusensis* Peñalver, Ortega-Blanco, Nel &
 Delclòs, 2010
 – Forewing 3.3 mm long, cell 3r much longer than pterostigma
 *C. pristina* (Zhang & Zhang, 2000)

***Cretevania tenuis* Li, Rasnitsyn & Ren sp.n.**

(Figs 12, 13)

<http://zoobank.org/urn:lsid:zoobank.org:act:81627FD2-B887-464D-A6FD-B4FA9385591E>

Etymology. The specific epithet is derived from the Latin adjective *tenuis* -e (third declension), meaning ‘thin’, ‘fine’, ‘slight’ or ‘slender’, referring to the abdominal petiole of this wasp that is very narrow and longer than the mesosoma.

Diagnosis. Antenna with 11 flagellomeres, scape 3× as long as pedicel. First metasomal segment tubular, formed as a long petiole. Forewing with very short 1-Rs vertical to R; both 1-M and 2r-rs nearly straight, distinctly longer than 1-Rs; cu-a postfurcal vein.

Type material. Holotype, CNU-HYM-MA-2014007, well-preserved.

Locality and horizon. Hukawng Village, Kachin State, Northern Myanmar; Late Cretaceous (early Cenomanian).

Description. Small evaniid individual fully winged (sex unknown, total length 4.87 mm); dark brown to black in colour. Head large (1.18 × 1.01 mm in lateral view), nonsetose; eyes large and ovoidal, 0.82 × 0.61 mm, without setae; antenna inserted on middle between compound eyes, with 11 flagellomeres, about 2.06 mm long; scape about 3× as long as pedicel, ~0.24 mm long and 0.10 mm wide; pedicel very short, nearly as long as wide, not expanded apically; flagellomeres I–IV nearly equal in length and width, remaining segments slightly shorter and thickened than the first four segments.

Mesosoma near equal in length (1.35 mm) and high (1.34 mm); mesonotum and mesoscutellum ovoidal in lateral view. Legs apparently unsculptured, with conspicuous trochantellus and five tarsomeres; fore- and midlegs much more slender than hind legs, hind legs robust; hind legs with femur distinctly wider than tibia, tibia with one strong apical spur and some strong setae; pretarsal claws slender, arolium present. First metasomal segment formed as long petiole (1.07 mm), with tergum and sternum fused; second segment gradually thickened from base to apex, akin to a triangle in lateral view; third segment trapezoidal, nearly as long as second, but wider than it; the remaining three segments nearly equal in length and width.

Wings hyaline, with abundant microtrichia; forewing without jugal lobe, 2.03 mm long and 0.75 mm at greatest width (estimated); pterostigma dark brown and very small (0.23 mm long and 0.06 mm wide). Venation tubular, including 2M, 3M and free Cu, both of M and Cu extending to wing margin;

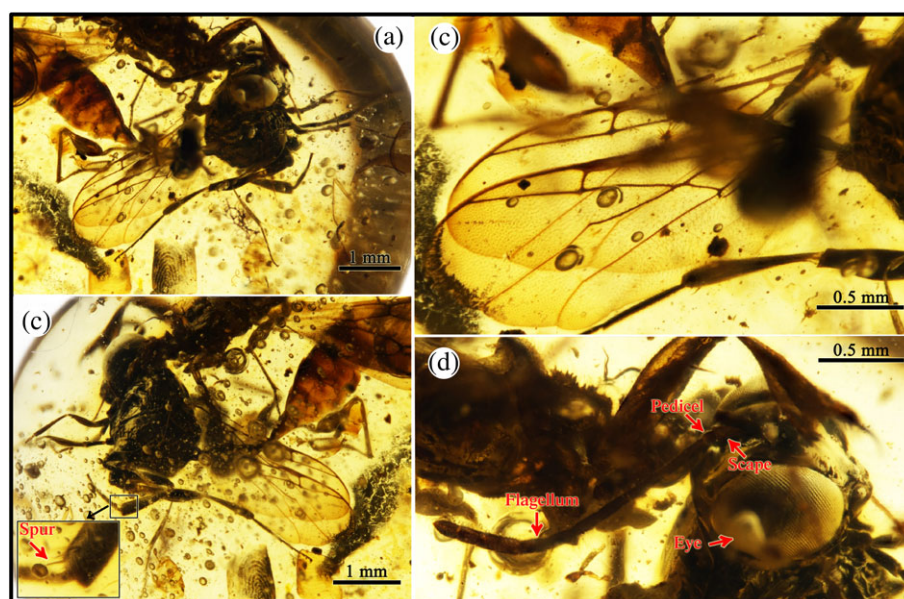


Fig. 12. *Cretevania tenuis* sp.n. Holotype, CNU-HYM-MA-2014007. (a, b) Photograph of habitus; (c) wings; (d) antenna. [Colour figure can be viewed at wileyonlinelibrary.com].

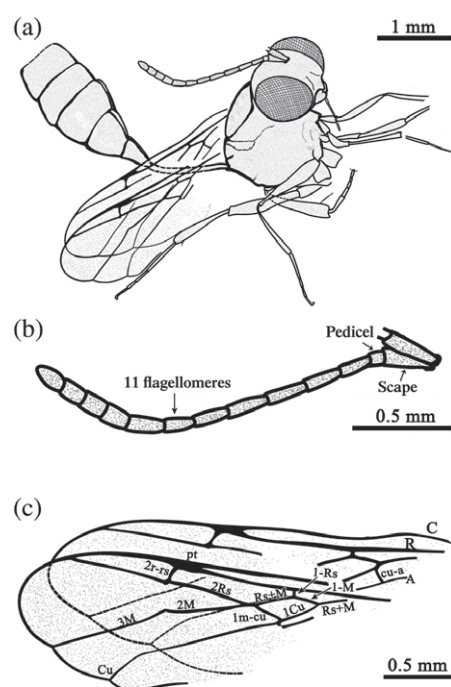


Fig. 13. *Cretevania tenuis* sp.n. Holotype, CNU-HYM-MA-2014007. (a) Line drawing of habitus; (b) antenna; (c) wings.

cross-vein 2r-rs nearly straight, originating from pterostigma apex; cross-vein 2rs-m not present (only a vestigial stub in the same position as 2r-rs); vein 1-Rs (0.05 mm) very short, vertical to R, keeping away from pterostigma base; vein 1-M (0.18 mm) nearly straight, about 4× as long as 1-Rs; vein Rs+M (0.28 mm)

longer than 1-M; Rs and M distinctly angled at the junction of Rs and M, about 102°; cu-a (0.11 mm) distinctly postfurcal, nearly as long as 2r-rs, reaching A completely; 1m-cu (0.20 mm) slightly longer than 1-M, cell 1mcu broad; cell 1+2r very narrow, nearly as wide as 3r; 1+2r (0.87 mm) distinctly longer than 3r (0.72 mm), 3r elongate triangle.

***Cretevania mitis* (Li, Shih & Ren, 2014) comb.n.**

(Fig. 14)

2014 *Procretevania mitis* Li, Shih & Ren, p. 49, fig. 1

New material. CNU-HYM-LB-2015001, collected near Huangbanjigou Village, Beipiao City, western Liaoning Province, China, of Early Cretaceous age. The new material is considered *P. mitis* Li, Shih & Ren, 2014, principally due to the following characters: forewing with 1-Rs inclined towards wing base, distinctly shorter than 1-M; 1-Rs and 1-M angled at junction of Rs+M (Y-shaped); pterostigma narrow, long, parallel-sided, meeting 2r-rs near its apex; 3r-m and 2m-cu absent. Metasoma rounded in lateral aspect, longer than mesosoma.

Description of new material. A female wasp in lateral view, body and forewing well preserved and veins clearly discernible. Body 6.02 mm long, mostly brown; head medium-sized, 0.82 mm long and 1.18 mm high, about 1.4× as high as long. Pronotum very short; mesonotum with scutum 3.7× as long as scutellum; metanotum short, nearly as long as scutellum, propodeum longer than metanotum. Metasoma with first segment not completely preserved; remaining segments oval. Ovipositor very thin, about 1.42 mm. Legs partly preserved; hind legs distinctly

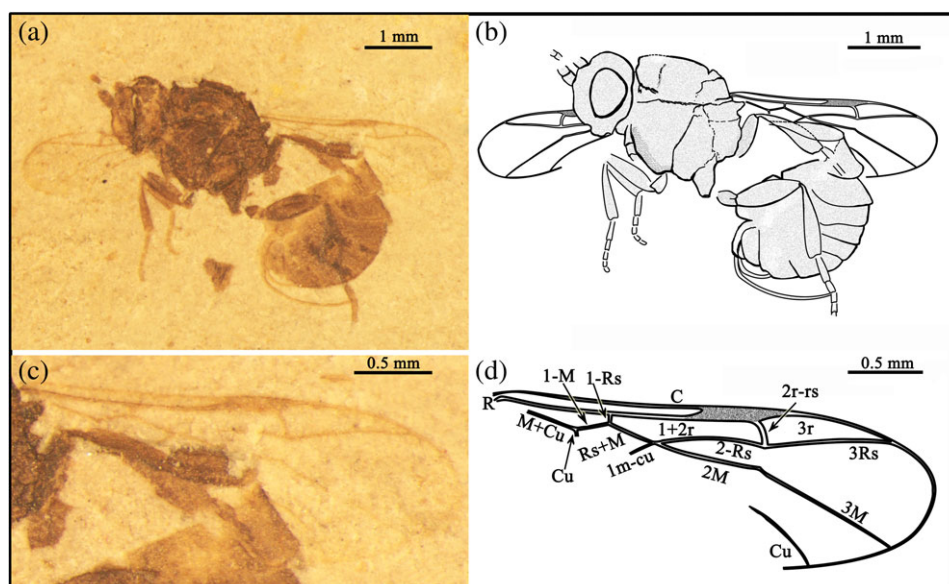


Fig. 14. *Cretevania mitis* (Li, Shih & Ren, 2014) **comb.n.** New material, CNU-HYM-LB-2015001. (a) Photograph of habitus; (b) Line drawing of habitus; (c) photograph of forewing; (d) Line drawing of forewing. [Colour figure can be viewed at wileyonlinelibrary.com].

thicker and longer than midleg, with coxa greatly expanded basally and narrowed apically, hind femur and tibia swollen, tibia sharply thickened from base to apical, with five tarsomeres and first segment much longer than others.

Forewing 3.07 mm long, with 1-M (0.23 mm) about 3× as long as 1-Rs (0.07 mm); pterostigma narrow, long, parallel-side, meeting 2r-rs at apex of pterostigma, pterostigmal base basad of midpoint of distance between 1-Rs base and 2r-rs; 2r-rs nearly 2× as long as pterostigmal width; 2Rs nearly 2.3× as long as Rs+M; cell 1+2r (1.04 mm) longer than 3r (0.86 mm); 3Rs slightly bent posteriorly a little beyond 2r-rs; 2M geniculate nearly the same level of 2r-rs, and 3M nearly straight; the end of free Cu bent.

***Cretevania venae* Li, Rasnitsyn & Ren sp.n.**

(Fig. 15)

<http://zoobank.org/urn:lsid:zoobank.org:act:D04DA356-920C-4A83-AA5F-94BCE9156290>

Etymology. The specific epithet is derived from the Latin noun *vena* -ae (first declension), meaning ‘vein’ or ‘blood vessel’, referring to the forewing with a 2m-cu vein present.

Diagnosis. Forewing with 2m-cu present, distal to 2r-rs; 1-Rs subvertical to R, shorter than 1-M; 1-Rs and 1-M angled (about 94°) at junction of Rs+M (Y-shaped); pterostigma narrow, long, parallel-sided, meeting 2r-rs near apex; 1cu-a postfurcal. Metasoma rounded in lateral aspect, longer than mesosoma.

Type material. Holotype, CNU-HYM-LB-2015002, well preserved except legs partly preserved.

Locality and horizon. Huangbanjigou Village, Beipiao City, western Liaoning Province, China; Early Cretaceous, from a radioisotopic date of 125 Ma, corresponding to late Barremian to early Aptian date (Walker *et al.*, 2013).

Description. Body 5.89 mm long, infusate with mesosoma partly dark. Head rounded, about 0.86 mm long and 0.75 mm high; with large oval compound eyes (0.70 mm long and 0.45 mm); antenna partly preserved, about nine segments discernible.

Mesosoma 1.64 mm long and 1.29 mm high, with mesonotum distinctly longer than metanotum; propodeum broad, with a long petiole attached high. Hind legs greatly thicker and longer than fore- and midlegs; midleg nearly equal in length and width to foreleg; hind coxa broad, thickened basally and narrowed apically; hind femur swollen from base to apex, with trochantellus distinguishable; hind tibia nearly as long as femur; tarsomeres five-segmented, first segment distinctly longer than any other segments. First metasomal segment formed as long petiole, about 0.5× as long as remaining segments combined, second segment triangular, remaining segments short, sickle-shaped in side view.

Forewing 2.39 mm long, with 1-M (0.13 mm) about 1.6× as long as 1-Rs (0.08 mm); pterostigma narrow, long, parallel-side, meeting 2r-rs at apex of pterostigma; pterostigmal base basad of midpoint of distance between 1-Rs base and 2r-rs; 2r-rs (0.16 mm) nearly 2× as long as pterostigmal width; 2Rs nearly 2× as long as Rs+M; cell 1+2r (0.88 mm) longer than 3r (0.67 mm); 3Rs slightly bent posteriorly, 3r elongate triangle, about 4× as long as wide; 2M geniculate nearly the same level of 2r-rs, and 3M short, 4M nearly straight; 1cu-a postfurcal, but only preserved a stub; 1m-cu nearly as long as 1-M, cell 1m-cu about 2.5× as long as wide; 2m-cu present well, distal of 2r-rs, 1.8× as long as 1m-cu; cell 2m-cu nearly as long as cell 1+2r.

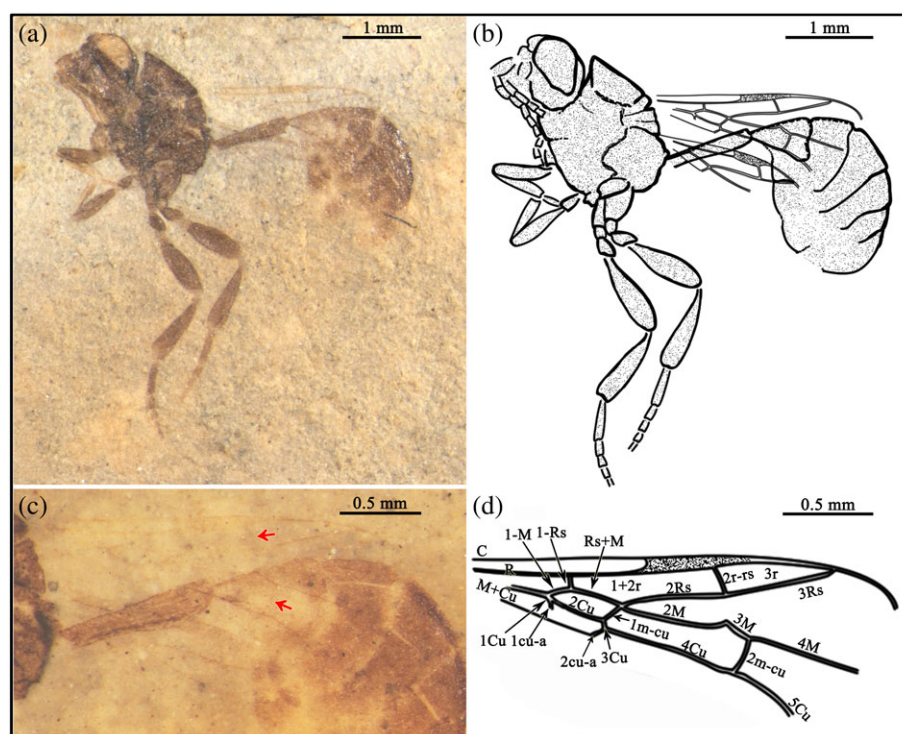


Fig. 15. *Cretevania venata* sp.n. Holotype, CNU-HYM-LB-2015002. (a) Photograph of habitus; (b) Line drawing of habitus; (c) photograph of forewing; (d) Line drawing of forewing. [Colour figure can be viewed at wileyonlinelibrary.com].

Key to fossil genera of Evaniidae

1. Forewing venation distinctly reduced (at most three closed cells including costal one) 2
 - Forewing venation more complete 3
2. Only C and R presented in forewing, all other veins absent *Hyptia* Illiger, 1807
 - Besides C and R, basal veins Rs and M, M+Cu present *Brachygaster* Leach, 1815
3. Forewing with 2r-m, 3r-m and 2m-cu all present 4
 - Forewing with 2r-m, 3r-m and 2m-cu alternatively presented or all of them absent 5
4. Forewing with 1cu-a distinctly postfurcal *Lebanevania* Basibuyuk & Rasnitsyn, 2002
 - Forewing with 1cu-a interstitial *Mesevania* Basibuyuk & Rasnitsyn, 2002
5. Forewing with Cu between 1-M and 1m-cu much shorter than 1-Rs, marginal cell wide triangular. Antenna elbowed, scape elongate, about as long as head *Sorellevania* Engel, 2006
 - Forewing with Cu between 1-M and 1m-cu not shorter than 1-Rs. Antenna not or slightly elbowed, scapes vary in length but all distinctly shorter than head length 6
6. Forewing with cell 1+2r elongate, longer than 3r and more than 2× as long as pterostigma length, 3r narrower triangular, nearly as wide as 1+2r *Cretevania* Rasnitsyn, 1975
 - Forewing with cell 1+2r shorter than 3r or nearly as long as it, 3r broad, more or less wider than 1+2r 7

7. Antenna with 15 or 16 segments, petiole short, pterostigma short, at most twice as long as wide, cu-a faintly postfurcal, 1A lost except basally *Bostvania* Rasnitsyn & Brothers, 2007
 - Antenna with 13 segments, petiole usually longer than its distance to mesoscutellum, pterostigma longer 8
8. Forewing with 1cu-a interstitial when preserved 9
 - Forewing with 1cu-a postfurcal when preserved 10
9. Forewing with 1-Rs distinctly shorter than 1-M, distalmost abscissa of Rs meeting anterior wing margin well before wing apex, 2r-m present *Eoevania* Nel, Waller, Hodebert & De Ploëg, 2002
 - Forewing with 1-Rs nearly as long as 1-M, 2r-m present but 3r-m absent, distalmost abscissa of Rs meeting anterior wing margin well before wing apex *Grimaldivania* Basibuyuk, Fitton & Rasnitsyn, 2000
10. Forewing with distalmost abscissa of Rs extending to wing apex, 1-Rs distinctly shorter than 1-M; 2r-rs short, nearly as long as 1-Rs, 3r large *Newjersevania* Basibuyuk, Quicke & Rasnitsyn, 2000
 - Forewing with distalmost abscissa of Rs meeting anterior wing margin well before wing apex 11
11. Forewing with 1-Rs nearly as long as 1-M, 2r-rs shorter than 1-Rs, antenna with 13 segments *Protoparevania* Deans, 2004
 - Forewing with 1-Rs distinctly shorter than 1-M 12
12. Forewing with 3r-m present, Rs and M not straight, angled at the junction of Rs+M 13

- Forewing with 3r-m absent, Rs and M nearly straight, 2r-rs longer than 1-Rs..... 14
13. First flagellomere elongate, distinctly narrower and longer than any other flagellomeres, legs much slender, distinctly longer than whole body length, petiole long and thin *Sinuevania* **gen.n.**
- First flagellomere short, columnar, faintly narrower than apical flagellomeres, petiole short and thick *Evaniella* Sawoniewicz & Kuprijanowicz, 2003
14. Petiole longer and thick, remaining metasomal segments shorter, ovate, legs thick with two tibia spurs *Iberoevania* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010
- Petiole shorter and thin, remaining metasomal segments elongate ovate, legs slender with two tibia spurs..... *Curtevania* **gen.n.**

Family Aulacidae Shuckard, 1841

Exilaulacus Li, Shih & Ren **gen.n.**

<http://zoobank.org/urn:lsid:zoobank.org:act:8ACDF005-57BD-461C-892D-24E3CA36FC35>

Type species. Exilaulacus oculatus Li, Shih & Ren **sp.n.**

Etymology. The generic epithet is combination of the Latin adjective *exilis* -e (third declension), meaning ‘thin’, ‘slender’ or ‘feeble’, and referring to the metasoma of this wasp having a very short waist, with first metasomal segment becoming narrow and tubular at its base; and *aulacus*, a type genus name, often used as a suffix for generic names in subfamily Baissinae and referring to an Early Cretaceous locality in central-southern Russia. The gender is masculine.

Diagnosis. Small body size, <3.5 mm. Occipital carina present. Antenna with scape longer than pedicel and 12 flagellar articles in male and female. Mesosoma very short and high. Pronotum medial aspect high, reaching dorsal level of mesoscutum; propleura short and not forming as a ‘neck’. Female hind coxa distinct with a transverse ovipositor guiding groove, on its inner surface marked below with a large tooth. Metasoma attached at propodeal hump close to metanotum, first metasomal segment tubular at the base; ovipositor long, surpassing the metasomal apex. Forewing with Rs and M smooth, sinuate or nearly straight, meeting R well before pterostigma base; 1-Rs longer than 1-M; 2r-rs inclined to wing apex or subvertical to pterostigma; 1Rs+M and 2Rs+M well preserved; 1cu-a interstitial or postfurcal, both 1cu-a and 2cu-a reaching A; 3r-m indistinct or leaving signs of its former position in slight angulation of Rs and M, 2m-cu; 2r-m traceless or lost; 2+3rm cell short and high, with RS between 2r-rs and 3r-m much shorter than adjacent vein sections.

Included species. Type species and *Exilaulacus latus* Li, Shih & Ren **sp.n.**

Remarks. Presently the subfamily Aulacinae have two definitive genera: *Pristaulacus* and *Aulacus*. *Pristaulacus* was characterized by the presence of an occipital carina, the presence of two or more distinctly tooth-like processes on the tarsal claws, and having an ovipositor-guiding groove on the hind coxa oriented transversely. By contrast, *Aulacus* lacks the occipital carina and has tarsal claws without tooth-like processes, although when the hind coxal groove is present, it is oriented longitudinally or obliquely (Turrisi *et al.*, 2009). In addition, Rasnitsyn (2013) tentatively placed an extinct genus, *Vectevania*, in Aulacinae, which have short propleuron, cell 1mcu inversely triangular, 2r-m spectral, 3r-m lost, 2m-cu tubular, metasomal segment 1 triangular whose fore part does not form a petiole. The new genus is assigned to the subfamily Aulacinae because it has a forewing with 2m-cu present, a propodeum with a metasomal attachment elevated, pyramidal and close to the metanotum, and a metasoma attenuate basally. However, *Vectevania* differs from other genera of this subfamily as follows: antennal segments are slender with 12 flagellar segments in the male; an occipital carina is present; the forewing has a very low 1mcu; the 2+3rm cell very short and high; the pronotum is high medially and reaches the dorsal level of the mesoscutum; the female hind coxa are distinct, with a transverse ovipositor guiding groove and its inner surface is marked below with a large tooth; and the metasoma is elongated, with first metasomal tergum delimited and formed with the sternum as a short petiole at the base of first metasomal segment.

Exilaulacus oculatus Li, Shih & Ren **sp.n.**

(Figs 16, 17)

<http://zoobank.org/urn:lsid:zoobank.org:act:08B2A9A5-AC24-4E9F-BE9B-853973358930>

Etymology. The specific epithet is derived from the Latin noun *oculatus* meaning a ‘small cell’ or ‘small chamber’, referring to the forewing with a very small 1mcu cell.

Diagnosis. Forewing with 1-Rs about 5× as long as 1-M; 1mcu very small; 1-Rs+M shorter than 2-Rs+M; 1cu-a interstitial, 2r-rs inclined to wing apex, slightly longer than pterostigma width; 3r-m indistinct, 2+3rm forming a small pentagon; 2m-cu tubular, based at 3r-m. Metasoma moderately elongate with first segment funnel-like; ovipositor long and exposed, about half length of the metasoma.

Type material. Holotype, CNU-HYM-MA-2014008, female.

Locality and horizon. Hukawng Village, Kachin State, northern Myanmar; Late Cretaceous (early Cenomanian).

Description. Total body length 3.17 mm; forewing length 2.17 mm; hindwing length 0.88 mm. Integument dark brown, wing membranes hyaline, clear, veins brown except pterostigma dark brown; setae widely scattered, minute and simple. Head 0.71 mm long and 0.83 mm high, slightly wider than mesosoma;

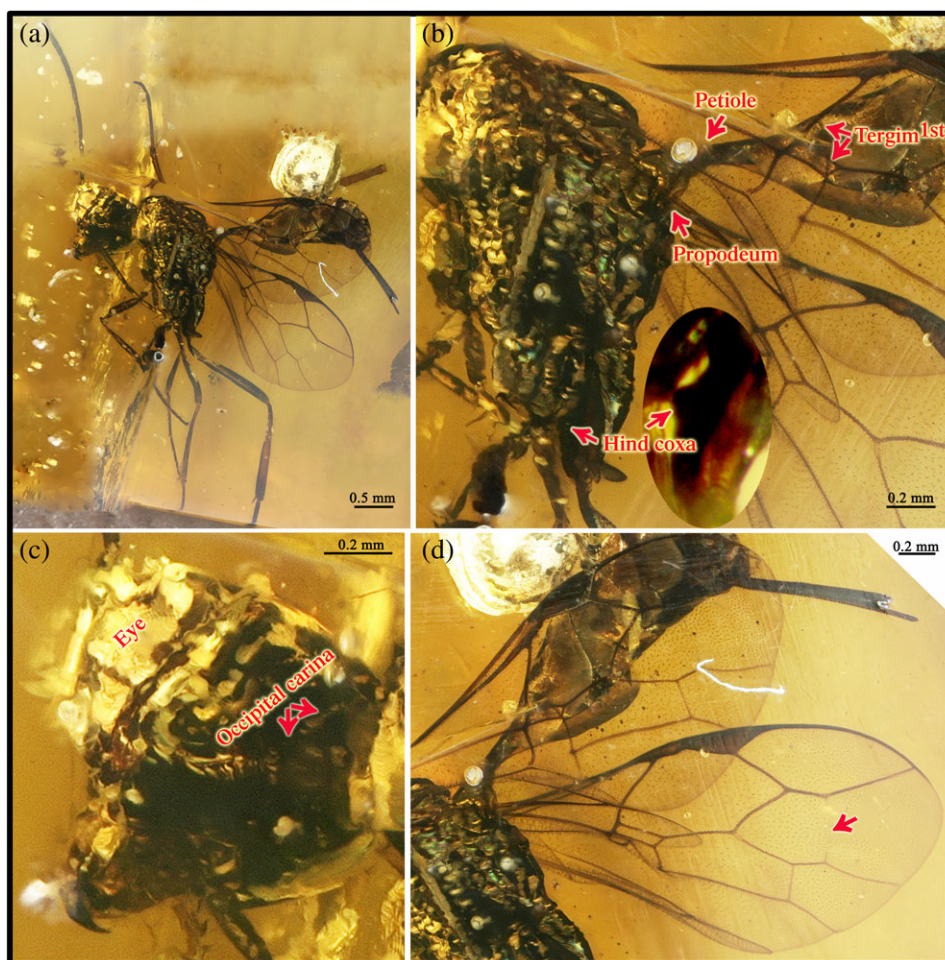


Fig. 16. *Exilaulacus loculatus* gen. et sp.n. Holotype, CNU-HYM-MA-2014008. (a) Photograph of habitus; (b) mesosoma and metasoma; (c) head; (d) wings. [Colour figure can be viewed at wileyonlinelibrary.com].

compound eyes prominent, oval in lateral shape, about 0.41 mm long and 0.47 mm high. Antenna (length 2.05 mm) filiform, with 12 flagellomeres; scape short, only slightly longer than wide, length 0.09 mm, pedicel shorter and narrower than scape; flagellomeres each longer than wide, first flagellomere as wide as pedicel, about 0.13 mm; flagellomeres II–VI nearly equal in length, remaining segments gradually shorter and wider except last segment, the last flagellomere segment sharply longer, about 4× as long as wide. Mandible short triangular, length 0.22 mm, base broad and tapering to apex, maxillary palpus partly preserved.

Mesosoma stout, about 0.93 mm long and 1.09 mm high; pronotum short, without distinct posterior dorsal surface; mesonotum with mesoscutum elevated above pronotum; pronotum posteriorly broad, anterior margin broadly rounded; metanotum greatly reduced; propodeum coarsely areolate throughout; articulation with metasoma high above metacoxal articulation. Legs slender, tibia not clavate; foreleg with coxa (0.20 mm), trochanter (0.15 mm), femur (0.53 mm), tibia (0.66 mm), five tarsomeres: I (0.41 mm), II (0.15 mm), III (0.11 mm),

IV (0.08 mm), V (0.11 mm); femur slightly wider than tibia; hind legs distinctly longer than fore and mid legs; hind coxa much broad and elongated; hind coxa (0.56 mm), trochanter (0.31 mm), femur (0.99 mm), tibia (1.21 mm). Metasoma elongate ovoid in shape, length 1.65 mm, first metasomal segment modified, petiolate at its base. Ovipositor 0.95 mm as preserved, well exposed from metasomal apex.

Forewing with pterostigma broad, 0.37 mm long and 0.16 mm wide; 1-Rs originating more proximad of pterostigmal base, separated by length about 0.11 mm, slightly longer than 1-M; 1-Rs and 1-M straight, 1-Rs (0.36 mm) 4.5× as long as 1-M (0.08 mm); 1cu-a nearly straight except for a small bend contacting A, confluent with 1-M; Rs+M noticeable, divided into a shorter abscissa 1Rs+M (0.18 mm) and a longer abscissa 2Rs+M (0.23 mm) by 1m-cu; 1m-cu (0.06 mm), slightly shorter than 1-M; 2Rs+M distinctly longer than 1m-cu; cell 1m-cu very small, nearly as long as cell cua, but distinctly narrower than it; 2m-cu cell relatively large, about 3× as long as 1m-cu; 2m-cu well preserved, slightly longer than 2Cu, nearly at the same level of 2r-rs; A complete, present proximad and distad 1cu-a, both

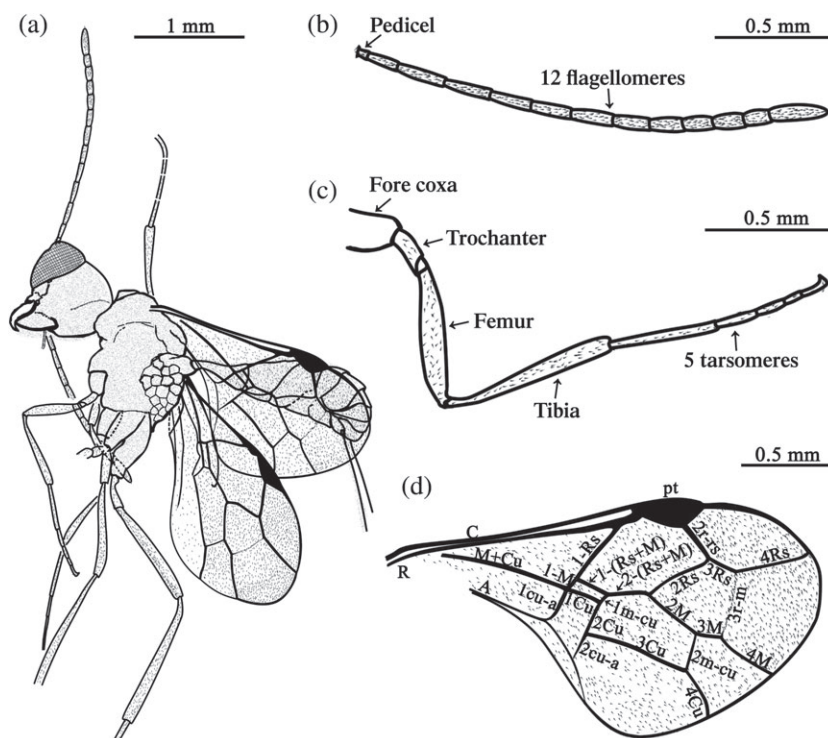


Fig. 17. *Exilaulacus loculatus* gen. et sp.n. Holotype, CNU-HYM-MA-2014008. (a) Line drawing of habitus; (b) antenna; (c) hind leg; (d) forewing.

1cu-a and 2cu-a reaching this vein; 2r-rs inclined at wing base, about 0.22 mm, slightly longer than pterostigma width; 2Rs and 4Rs slightly bent, 3Rs straight, cell 1+2r nearly as broad as 3r; 2M and 3M straight, cell 2+3rm short; 3r-m (0.34 mm) indistinctly present, slightly shorter than 1-Rs. Hindwing with venation greatly reduced, only wing outline discernible.

***Exilaulacus latus* Li, Shih & Ren sp.n.**

(Figs 18, 19)

<http://zoobank.org/urn:lsid:zoobank.org:act:73A94C22-CF5F-4505-AA6F-AA7307717285>

Etymology. The specific epithet is derived from the Latin word *latus* -a -um (second declension), meaning 'wide', 'broad' or 'full', referring to the forewing with a 1-Rs vein that is much longer than the 1-M vein and, in particular, the very broad 1+2r cell.

Diagnosis. Forewing with 1-Rs about 6× as long as 1-M, 1m-cu very narrow, 1-Rs+M much longer than 2-Rs+M; 1cu-a postfurcal vein; 2r-rs subvertical to pterostigma; 3r-m providing signs of its former position in slight angulation of Rs and M; 2m-cu tubular, based at 3r-m. Metasoma short ovate with first segment petiolate at the former part.

Type material. Holotype, CNU-HYM-MA-2014009, male.

Locality and horizon. Hukawng Village, Kachin State, northern Myanmar; Late Cretaceous [early Cenomanian].

Description. Total body length 2.36 mm, forewing length 1.66 mm as preserved. Integument dark brown, wing membranes hyaline, clear, veins brown except pterostigma dark brown; setae widely scattered, minute and simple. Head 0.59 mm long and 0.58 mm high, nearly as wide as mesosoma; compound eyes prominent, oval in lateral aspect, about 0.54 mm long and 0.39 mm high. Antenna (length 1.38 mm) filiform, with 12 flagellomeres; scape about 0.06 mm long, 0.04 mm wide, pedicel distinctly shorter and narrower than scape; flagellomere I much longer than pedicel, flagellomeres II–IV nearly equal in length and width, remaining segments gradually becoming shorter except last segment, last flagellomere segment sharply longer, about 4× as long as wide. Mandible short and triangulate in shape, length 0.14 mm, base broad and tapering to apex; maxillary palpus partly preserved.

Mesosoma stout, about 0.84 mm long and 0.63 mm high; mesonotum with mesoscutum elevated above; pronotal posterior broad; propodeum not very broad, articulation with metasoma high above metacoxal articulation. Legs slender; tibiae not clavate; hind legs longer and wider than fore- and midlegs; forelegs with coxae 0.22 mm long, femur 0.54 mm long and 0.13 mm wide, tibia distinctly narrower than femur, only 0.06 mm wide; tarsomeres partly preserved, narrower than tibia; hind coxa elongated, about 0.34 mm, femur 0.76 mm long and 0.14 mm wide, more than 5× as long as wide. Metasoma short ovoidal, length 0.88 mm, first metasomal segment modified, forming at the base a very narrow tubular structure, the petiole.

Forewing with pterostigma broad, 0.39 mm long by 0.13 mm wide; 1-Rs originating more proximad of pterostigmal

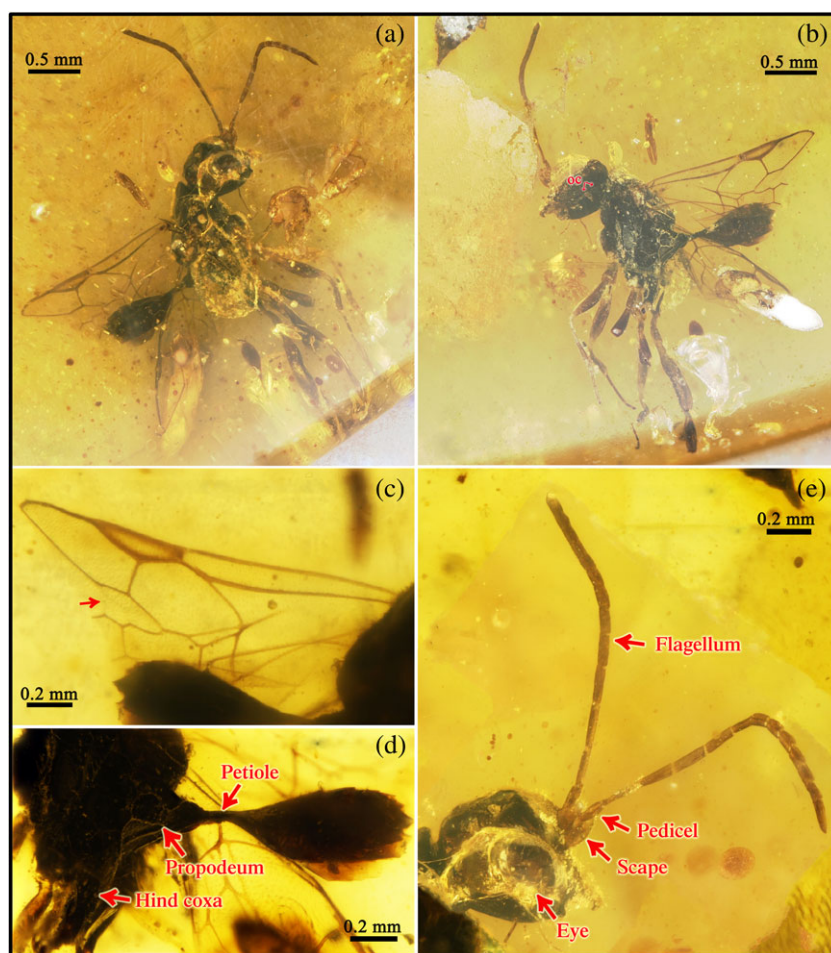


Fig. 18. *Exilaulacus latus* gen. et sp.n. Holotype, CNU-HYM-MA-2014009. (a–b) Photograph of habitus; (c) wing; (d) mesosoma and metasoma; (e) head. [Colour figure can be viewed at wileyonlinelibrary.com].

base, separated by length of about 0.12 mm; 1-Rs and 1-M straight, 1-Rs (0.17 mm) 5× as long as 1-M (0.03 mm); 1cu-a postfurcal, slightly curved vein; Rs+M well displayed, divided into longer abscissa 1Rs+M (0.24 mm) and shorter abscissa 2Rs+M (0.11 mm) by 1m-cu; 1m-cu (0.06 mm), nearly half of 2Rs+M; cell 1mcu narrower, about 3× as long as wide; 2m-cu present at the same level of 2r-rs, nearly as long as 2Rs+M; A complete, present proximad and distad 1cu-a, both 1cu-a and 2cu-a reaching it; 2r-rs slightly inclined at wing base, about 0.14 mm, nearly as long as pterostigma width; cell 1+2r distinctly broader than 3r; 2r-m and 3r-m absent, only geniculate in the same position of 2r-m and 3r-m.

Baissidae Rasnitsyn, 1975

Heterobaissa Li, Rasnitsyn & Ren gen.n.

<http://zoobank.org/urn:lsid:zoobank.org:act:1FD23E12-3660-45CF-94B1-F0C1A72A225A>

Type species. *Heterobaissa apetiola* Li, Rasnitsyn & Ren sp.n.

Etymology. The generic epithet is a combination of the classical Greek adjective, *heteros*, meaning ‘different’ or ‘deviating from’, referring to this wasp’s propleuron which forms a neck-like structure, but not the metasoma which is elongate and slender; and *baissa*, a type genus name, often used as a suffix for generic names in Baissinae and referring to an Early Cretaceous locality in central-southern Russia. The gender is feminine.

Diagnosis. Antenna thick, with more than 15 segments. Mesosoma with propleuron formed as a ‘neck’. Metasoma short but wide and coniform, with short ovipositor not extended beyond metasomal apex. Forewing with Rs & M straight, meeting R well before pterostigma base; 1-Rs about 3× as long as 1-M; 1cu-a postfurcal vein, completely reaching A; 1Rs+M longer, 2Rs+M shorter; 2m-cu present.

Included species. Type species only.

Remarks. The new genus is assigned to Baissidae because it bears a forewing with 2m-cu present, the propodeum with

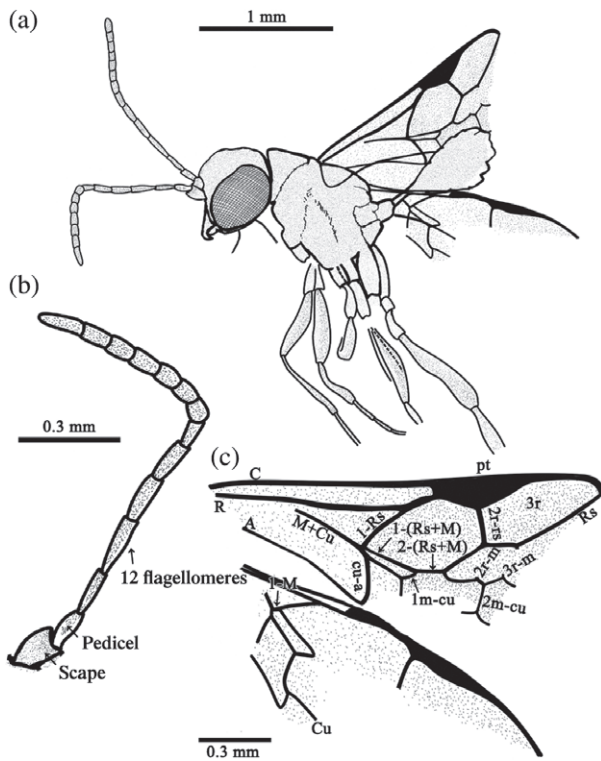


Fig. 19. *Exilaulacus latus* gen. et sp.n. Holotype, CNU-HYM-MA-2014009. (a) Line drawing of habitus; (b) antennae; (c) wings.

the metasomal attachment is not elevated and pyramidal, and the metasoma is not compressed. However, it differs from other genera of this subfamily in the following ways: the antennal segments are stout, the propleura obviously contributes to formation of the neck, both the 2r-m and 3r-m veins are absent, the metasoma is short yet wide and coniform, and the ovipositor is short and not exerted.

***Heterobaissa apetiola* Li, Rasnitsyn & Ren sp.n.**

(Fig. 20)

<http://zoobank.org/urn:lsid:zoobank.org:act:5FC5D916-F51A-4505-83DD-40DB0F085117>

Etymology. The specific epithet is derived from the Latin adjective *apetiulus* -a -um (second declension), a diminutive form, which means lacking a small 'stem', 'stalk' or 'foot' or 'without a petiole', referring to the metasoma of this wasp, which is conical and not petiolate with first metasomal segment and is wider than the other segments.

Diagnosis. As for the genus.

Type material. Holotype, CNU-HYM-LB-2015003, female.

Locality and horizon. Huangbanjigou Village, Beipiao City, western Liaoning Province, China; Early Cretaceous, from a

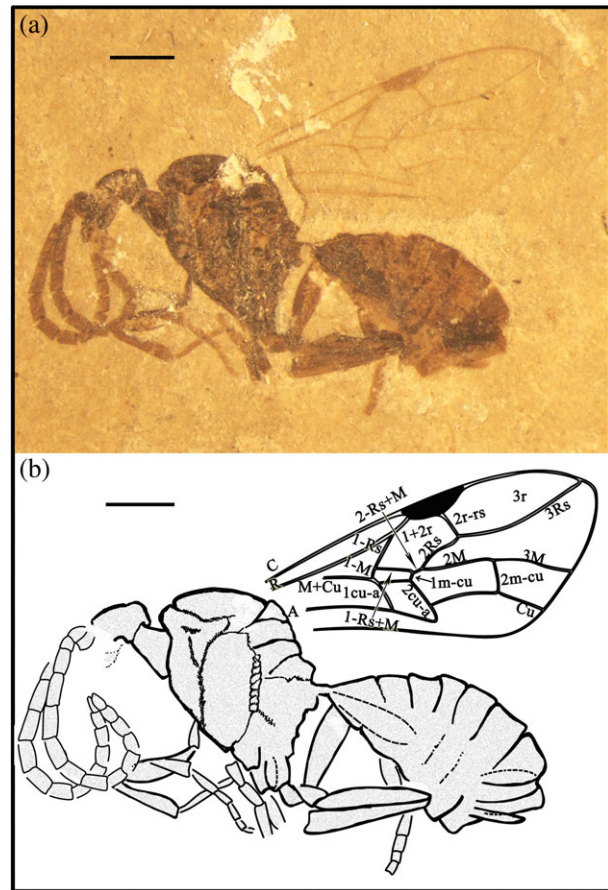


Fig. 20. *Heterobaissa apetiola* gen. et sp.n. Holotype, CNU-HYM-LB-2015003. (a) Photograph of habitus; (b) wing. [Colour figure can be viewed at wileyonlinelibrary.com.]

radioisotopic date of 125 Ma, corresponding to late Barremian to early Aptian date (Walker *et al.*, 2013).

Description. Total body length 6.99 mm; forewing length 4.82 mm, width 2.28 mm. Body dark brown, wing membranes hyaline, clear, veins brown except pterostigma dark brown. Head small with antennomere more than 15 thick segments as preserved.

Mesosoma stout, about 2.56 mm long and 1.96 mm high; propleuron formed as a 'neck', about 0.73 mm long; mesonotum broad, arched in lateral view; mesoscutellum nearly as long as metanotum; mesopleuron broad, contacting mid-coxa and metanotum, about 1.17 mm long and 1.37 mm high; propodeum coarsely curved along posterior border, articulation with metasoma high above metacoxal articulation. Legs partly preserved, hind legs longer than forelegs; hind coxa short, nearly as long as wide; hind femur with trochanter slightly longer than tibia, but nearly equal in width. Metasoma elongate ovoidal, length 3.63 mm, first metasomal segment narrower basally and thickens apically, remaining segments gradually wider than first. Ovipositor short, not extending to metasomal apex.

Praeaulacus Rasnitsyn, 1972

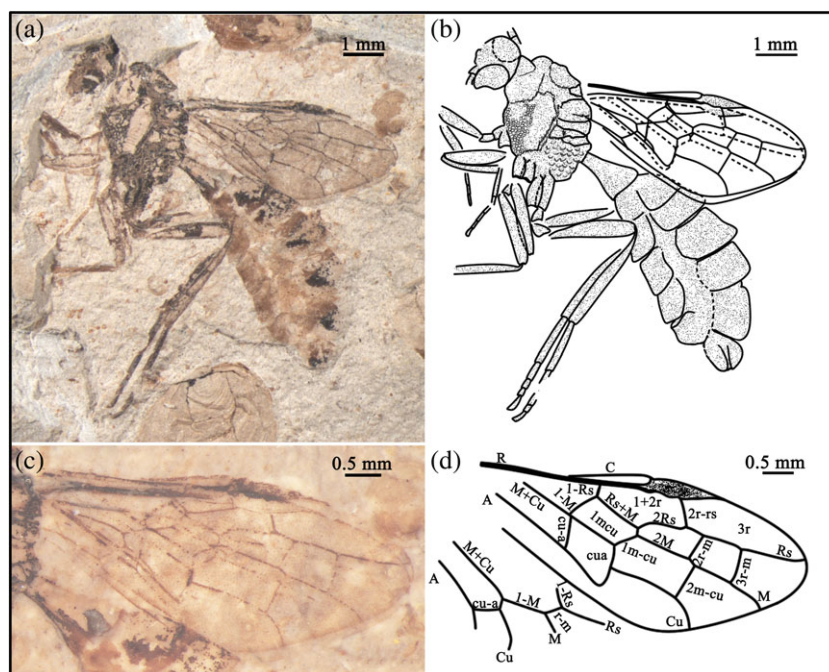
Revised diagnosis. Head not downwardly elongate. Forewing with 1-Rs shorter than wing distance to pterostigma, 1-Rs strongly inclined to wing base or subvertical to R; 2r-rs meeting Rs based of 2r-m or at the point where 2r-m meets Rs; 2r-rs shorter or longer than maximal width of 2rm; 3rm slightly shorter than 2rm; 2rm in contact with 1mcu by a short section of M; cu-a interstitial or slightly postfurcal. Hindwing with cu-a meeting Cu distad of M+Cu forking at an oblique angle.

Species included. The type species *P. cephalotus*, *P. cubocephalus*, *P. elegans*, *P. leptogaster*, *P. magnus*, *P. ventricosus* and *P. obscures* were established by Rasnitsyn (1972). *Praeaulacus patiens* and *P. sharteg* were established by Rasnitsyn (2008); *P. orientalis*, *P. daohugouensis*, *P. scabratus*, *P. exquisitus*, *P. sculptus*, *P. robustus* and *P. afflatus* were established by Zhang & Rasnitsyn (2008); *P. subrhombeus* and *P. tenellus* were established by Li, Shih & Ren (2014); and finally, *P. obtutus* was established by Li & Shih (2014), *P. byssinus* by Wang, Li and Shih (2015), and *P. rectus* **sp.n.**

(Fig. 21)

Etymology. The specific epithet is derived from the Latin word *rectus* -a -um (second declension), meaning 'straight', 'guided' or 'correct', referring to the forewing with a short, straight1-Rs vein that is vertical to the R vein.

Diagnosis. Forewing with 1-Rs subvertical to R, distinctly shorter than 1-M; Rs and M angled about 134° at the junction of Rs+M; cu-a faintly postfurcal vein, nearly straight. Hindwing with r-m long, nearly half the length of 1-M; cu-a contacting cu distinctly distal of M+Cu forking. First metasomal segment



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elongate-conical, and its apical width is more than 3× as wide as its basal width.

Type material. Holotype, CNU-HYM-NN-2015002, male.

Locality and horizon. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; latest Middle Jurassic, from a radioisotopic date of 165 Ma, corresponding to a latest Callovian date (Walker *et al.*, 2013).

Description. Total body length 9.67 mm; forewing length 5.35 mm; hindwing length 2.76 mm, as preserved. Body dark brown, wing membranes hyaline, clear, veins brown. Head small in size, about 1.03 mm long by 1.36 mm wide; compound eyes large and rounded, asymmetrically located on the two sides of head.

Mesosoma stout, about 2.75 mm long by 2.39 mm high; pronotum comparatively long but slightly narrower than head; mesonotum transversely ridged with notauli and parasidal suture; mesoscutum slightly shorter than mesonotum; metanotum distinctly reduced, nearly half the length of mesoscutum; metapostnotum medially slightly shorter than metanotum; mesopleura broad and coarsely areolate; propodeum not very broad compared with mesopleura, but still coarsely areolate; propodeal foramen much closer to metapostnotum than to hind coxa. Legs partly preserved; hind legs distinctly longer than fore- and midlegs and hind coxa much broader than fore- and midcoxa; hind femur distinctly wider and shorter than tibia, tibia slender with five tarsomeres; first segment of tarsomere distinctly longer than other segments, nearly as long as other segments combined. Metasoma distinctly longer than mesosoma, about 6.16 mm long; first metasomal segment elongate conical, and its apical width more than 3× as wide as its basal width; second and third segments nearly equal in length, but shorter than first segment; remaining segments slightly longer and wider than third segment; genitalia exposed, parameres discernible.

Forewing with pterostigma elongate, 1.05 mm long by 0.25 mm wide; 1-Rs originating more proximad of pterostigmal base, separated in length about 0.74 mm, slightly shorter than pterostigma; 1-Rs and 1-M strongly angulate at the junction of Rs+M, about 134°, 1-Rs (0.21 mm) subvertical to R, distinctly shorter than 1-M (0.53 mm); 2r-rs starting from the mid-length of pterostigma, about 2× as long as pterostigma width; 2r-m straight, distal 2r-rs, and cell 2rm longer than 3rm; 3r-m slightly bent, longer than 2r-m; 2m-cu straight, distal of 2r-m; cu-a faintly postfurcal vein, nearly straight; cell cua slightly wider than 1mcu, but nearly equal in length. Hindwing with venation complete, 1-Rs partly preserved; r-m straight, nearly half length of 1-M; cu-a contacting Cu distinctly distal of M+Cu forking; free Cu curved; both M+Cu and A extending to wing base.

Phylogeny

Parsimony analysis

The parsimony analysis of the morphological dataset (Appendix S3) yielded 360 most parsimonious trees, with the following

characteristics: tree length = 514, consistency index (CI) = 0.24, retention index (RI) = 0.68. When DNA sequence data for a select few ingroup and outgroup taxa were combined with the morphological scoring (Appendix S4), it returned 1424 most parsimonious trees, with tree length = 2332, increased CI = 0.64 and RI = 0.57. These consensus trees are shown in Fig. 22. Both the morphological data and the combined-evidence results show that the superfamily Evanioidea was recovered as a monophyletic clade. Within Evanioidea, Praeaulacidae comprise a paraphyletic grade at the base of the ingroups; Anomopterellidae are monophyletic. However, Aulacidae, Baissidae and Gasteruptiidae do not form a single clade, suggesting that Aulacidae and Baissidae should be downgraded to subfamilies within Gasteruptiidae, as proposed by Rasnitsyn in 2013, may be erroneous. Aulacidae as a monophyletic clade included the new amber genus *Exilaulacus* but excluded the *Vectevania*, which was temporarily placed into Aulacidae by Rasnitsyn (2013). *Hyptiogastrites* and *Manlaya* form a sister group and render the Gasteruptiidae and Baissidae as paraphyletic, which suggests that *Hyptiogastrites* should be transferred from Gasteruptiidae to Baissidae. Othniodellithidae are monophyletic at the base of Andreneliidae + Evaniidae; and Andreneliidae and Evaniidae are separately monophyletic and constitute a sister group.

Bayesian inference analysis

As previously mentioned, molecular data were only available for extant families, which are only ca. 15.9 % of all ingroup terminals. Therefore, it was difficult to resolve the phylogeny of Evanioidea based solely on molecular data or on combined-evidence data. Herein, we analysed our two datasets separately as shown in Fig. 23 for comparison. Both the morphological data and the combined-evidence data results show that the superfamily Evanioidea was recovered as a monophyletic entity, within Evanioidea, Praeaulacidae is paraphyletic at the base of the ingroups; *Hyptiogastrites* and *Manlaya* form a sister group that makes the Gasteruptiidae and Baissidae paraphyletic. The morphological and combined-evidence data are consistent with the results of MP analysis.

In summary, based on a comparison of the results from the MP and BI analyses as shown in Table 1, the following relationships can be easily observed among Evanioidea. First, the extinct family Praeaulacidae is paraphyletic at the base of the ingroups. Second, Anomopterellidae are monophyletic and sister group to the remaining families in a (((Aulacidae + Baissidae) + Gasteruptiidae) + Othniodellithidae) + (Andreneliidae + Evaniidae) relationship. Third, Aulacidae, Baissidae and Gasteruptiidae are paraphyletic groups. Fourth, the Othniodellithidae are monophyletic when considered more basal to Andreneliidae + Evaniidae. Fifth, Andreneliidae are the sister group of Evaniidae, and both lineages are monophyletic groups.

Discussion

Taxonomy and relationships among Evanioidea (Fig. 24)

Evanioidea are a monophyletic lineage supported by nine characters. This clade is corroborated by the results of Sharkey

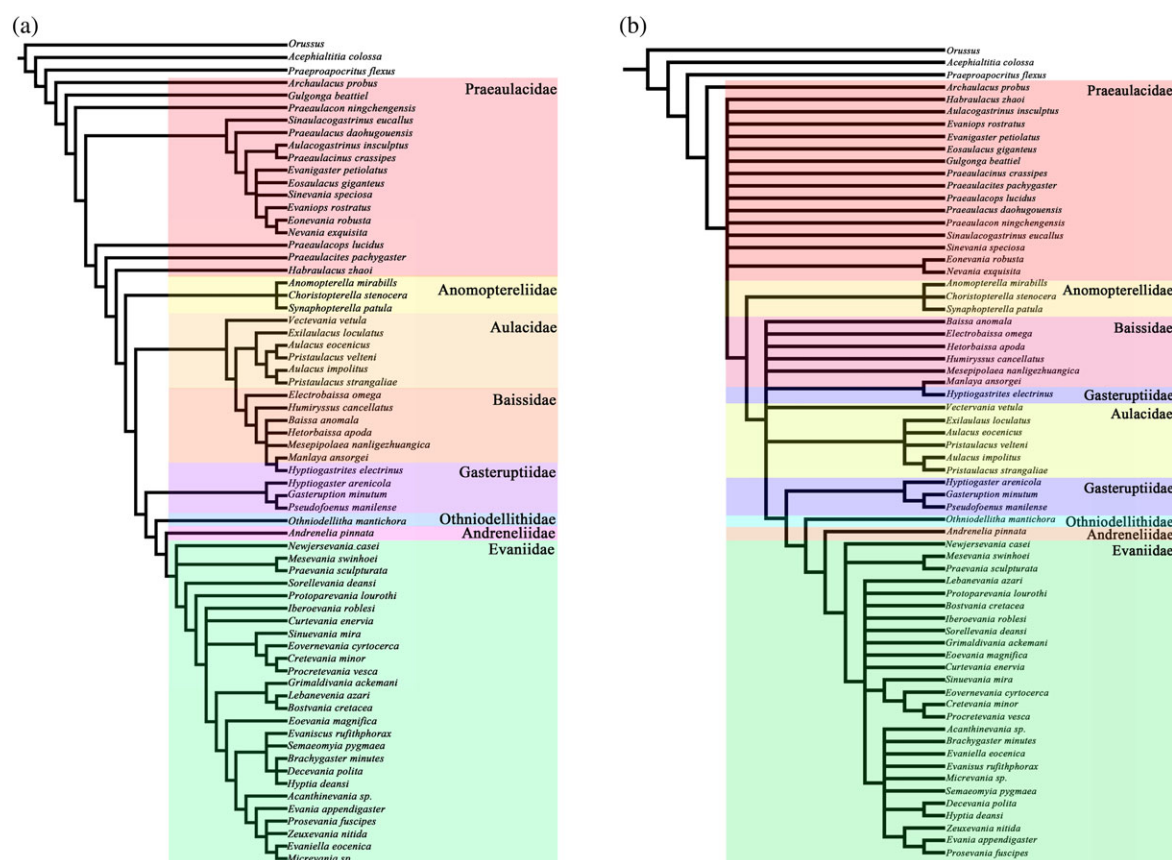


Fig. 22. Strict consensus trees recovered from parsimony analyses of: (a) morphological characters; (b) combined morphological characters and DNA sequence data. [Colour figure can be viewed at wileyonlinelibrary.com.]

et al. (2012). Praeaulacidae are a paraphyletic grouping of taxa occurring at the ingroup stem that represents a series of mostly small clades ancestral to Evaniioidea. Praeaulacidae also display some plesiomorphy characters, such as: (i) forewing cross-veins 2r-m, 3r-m and 2m-cu present; (ii), the appearance of forewing veins 2A and 1r-rs, which occurs in *Nevania exquisita* of Nevaniinae; (iii) the hindwing with an enclosed cell r, found in *Eosaulacus* and *Praeaulacus*; and (iv) cross-veins r-m, cu-a present, all of which are very similar to Ephialtitidae, which later defined Evaniioidea. Anomopterellidae are designated a monophyletic clade supported by five characters, and, along with Praeaulacidae, are the only Jurassic Apocrita which show the metasomal attachment in a high position, with all or at least most of the posterior propodeal face closed below the metasomal attachment. *Vectevania vetula* Cockerell has been very briefly described based only on the holotype collected in the latest Eocene Bembridge Marls in England. Cockerell (1922) initially ascribed this specimen to Evaniidae, which comprised the only family within the superfamily Evaniioidea at that time. Later, in 2013, Rasnitsyn temporarily attributed *Vectevania* to Aulacinae after a careful comparison of the morphological characters, even though this taxon assumed an intermediate taxonomic position between Baissinae and Aulacinae (Rasnitsyn, 2013). In our analyses, *Vectevania* forms a single clade that is a sister

group to Aulacidae + Baissidae. Potentially, it should be set up as a new family Vectevaniidae. The new Myanmar amber genus *Exilaulacus* is placed in a basal position to Aulacidae. *Hyptiogastrites*, formerly of the Gasteruptiidae sensu lato, is now the sister group of *Manlaya* within the newly erected Baissidae. These new-found relationships suggest that *Vectevania* should be separated from Aulacidae and probably occupies a more basal position than Aulacidae and Baissidae within Evaniioidea. As a result, *Hyptiogastrites* should be transferred from Gasteruptiidae to Baissidae. Consequently, our result supports establishment of Aulacidae, Baissidae and Gasteruptiidae as separate families of Evaniioidea. Othniellithidae is sister group to Andreneliidae + Evaniidae, and Evaniidae is a monophyletic group. Therefore, we generally consider that Evaniioidea, as currently constituted, comprise the nine families of Praeaulacidae, Anomopterellidae, Vectevaniidae, Aulacidae, Baissidae, Gasteruptiidae, Othniellithidae, Andreneliidae and Evaniidae.

The transformation and diversity of 'wasp waist' of Evaniioidea (Fig. 24)

Apocrita have a special structure in which its first abdominal segment has been incorporated into the thorax as the propodeum.

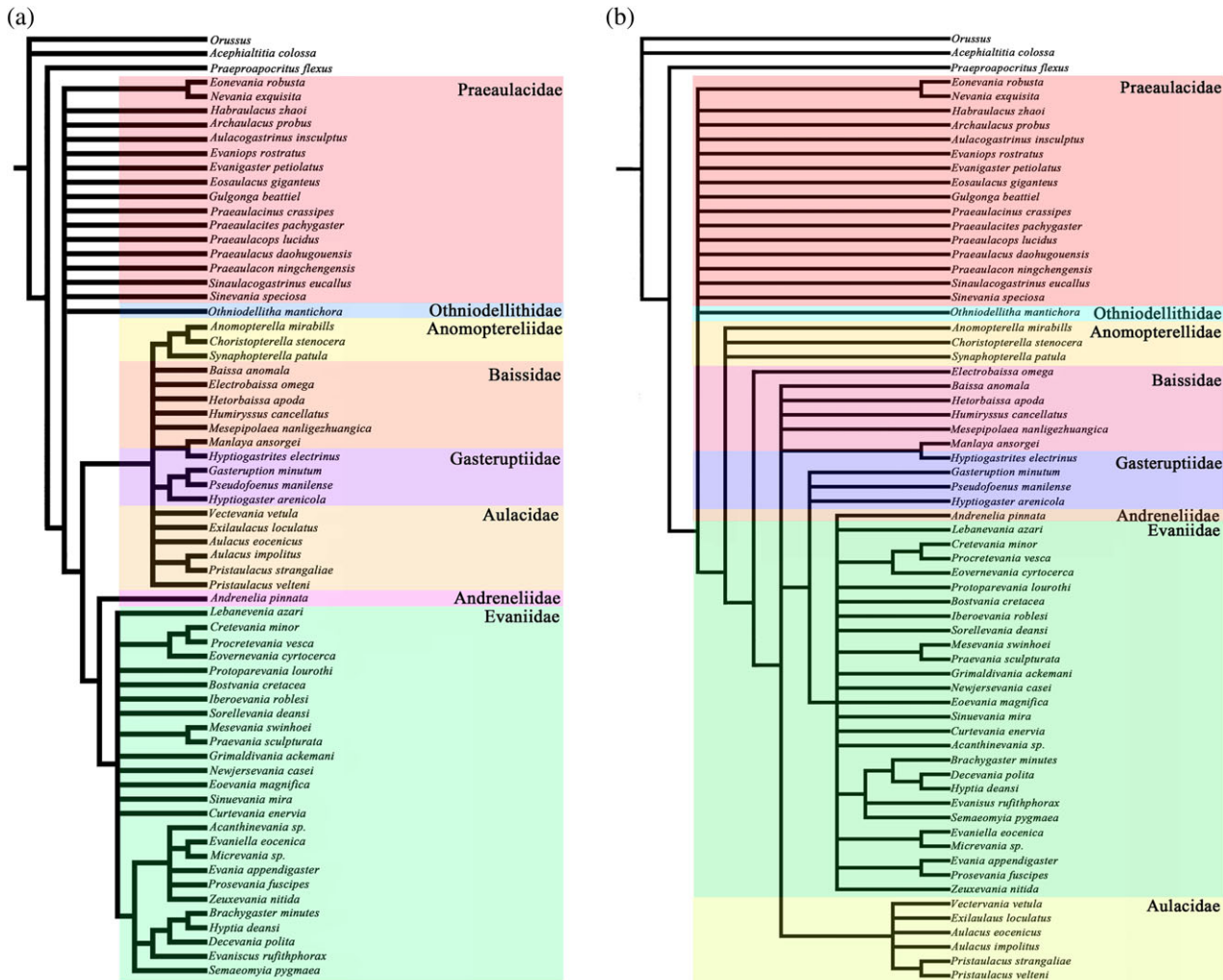


Fig. 23. Strict consensus trees recovered from Bayesian analyses of: (a) morphological characters; (b) combined morphological characters and DNA sequence data. [Colour figure can be viewed at wileyonlinelibrary.com.]

Table 1. Comparison of results from maximum parsimony (MP) analysis and Bayesian analyses.

Taxa	MP analysis		Bayesian analysis	
	Morphological data	Combined evidence	Morphological data	Combined evidence
Evanioidea	Monophyly	Monophyly	Monophyly	Monophyly
Praeaulacidae	Paraphyly	Paraphyly	Paraphyly	Paraphyly
Anomopterellidae	Monophyly	Monophyly	Monophyly	Paraphyly
Aulacidae	Paraphyly	Paraphyly	Paraphyly	Monophyly
Baissidae	Paraphyly	Paraphyly	Paraphyly	Paraphyly
Gasteruptiidae	Paraphyly	Paraphyly	Paraphyly	Paraphyly
Othniodellithidae	Monophyly	Monophyly	Paraphyly	Paraphyly
Andreneliidae	Monophyly	Monophyly	Monophyly	Paraphyly
Evaniidae	Monophyly	Monophyly	Monophyly	Paraphyly
Vetevaniidae	Monophyly	Paraphyly	Paraphyly	Paraphyly

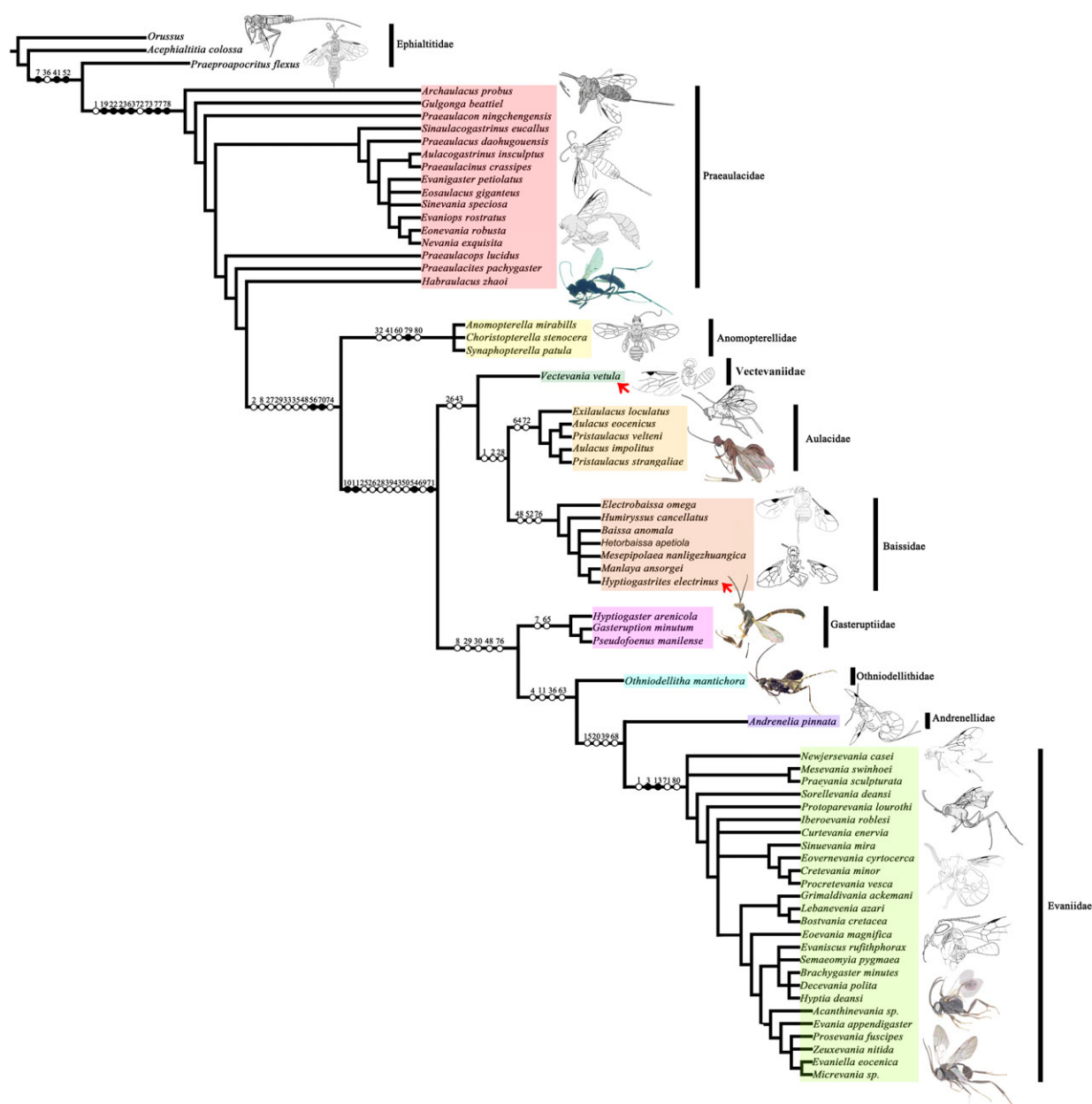


Fig. 24. Phylogeny of extant and extinct Evanioidea. Strict consensus tree recovered from parsimony analyses of morphological characters: 582 steps, consistency index = 0.21, retention index = 0.63; ●, nonhomoplastic changes; ○, homoplastic changes. [Colour figure can be viewed at wileyonlinelibrary.com].

The remaining abdomen, the metasoma, is connected to this hybrid region via a narrow propodeal–metasomal articulation forming the distinctive ‘wasp waist’, which serves an important function of providing maneuverability, flexibility and positioning for oviposition. In 2015, three separate evolutionary pathways were proposed for the transformation of the ‘wasp waist’ in three different derived lineages, leading from the apocritan Ephialtidae and ending in Evanioidea (Li *et al.*, 2015a, b). The third pathway in this proposal details a structural transformation from Ephialtidae to Evanioidea which consists of

a broad propodeum–metasoma articulation with closed hind coxae to form a relatively narrow propodeum–metasoma articulation some distance away from the hind coxae. As outlined in Fig. 24, the majority of species with the first metasomal segment that is broadly cone-shaped or cylindrical or a combined shape retain segment shapes similar to an elongated oval that occurs in Praeaulacidae. By contrast, the first metasomal segment forms a long or short tubular structure in several genera, such as *Evanioops*, *Nevania* and *Habraulacus*, the latter the only amber genus of Praeaulacidae.

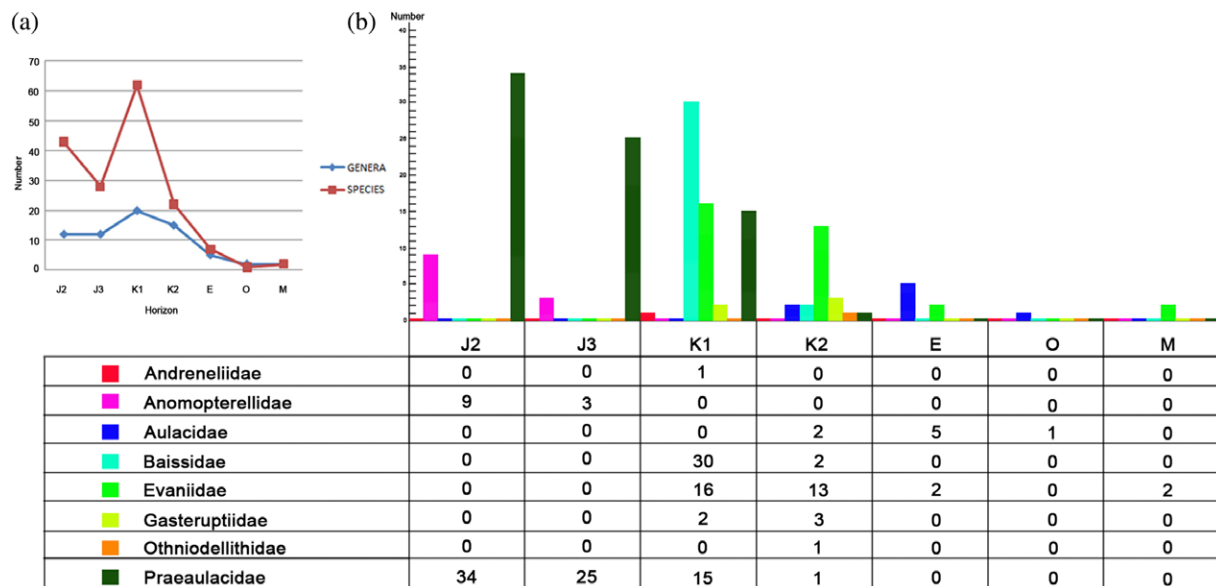


Fig. 25. Histograms of Evanioidea species and generic diversity during the mid-Mesozoic and Cenozoic. (a) Total number of genera and species of Evanioidea in the mid-Mesozoic and Cenozoic; (b) histogram showing the genus and species richness at the family level within the Evanioidea. [Colour figure can be viewed at wileyonlinelibrary.com].

In Anomopterellidae, the first metasomal segment forms as a very stable, short petiole, accompanied by changes such as its length:width ratio. This similarity in propodeal stability is also present in Aulacidae, in which the first metasomal segment is fused to a short petiole at the base, then becomes gradually swollen distally, and remains an elongated oval in its length:width ratio. Among the Baissidae, the first metasoma segment is not elongate, petiolate or tubular, and has a length/width ratio that is round or ovate. In Gasteruptiidae, the first metasoma segment is fused as a long petiole, resembling an elongated cylinder. The monobasic Othniodellithidae and Andreneliidae have the first metasomal segment as a simple structure, formed into either a short or long petiole. By contrast, in Evanidae, the first metasomal segment is formed into a long petiole, exemplified by the amber genus *Sinuevania* and many extant evanids, or alternatively a short petiole, such as *Lebanevania*. Based on the above descriptions, there is considerable diversity of the wasp waist among Praeaulacidae and Evanidae; by contrast, the remaining evanoid taxa retain morphological stability in this key adult structure.

Origin, early radiation and diversity of Evanioidea (Fig. 25)

The Evanioidea are a distinctive lineage of Apocrita within Hymenoptera that display the defining attribute of the metasoma attached high on the propodeum. Based on the histograms of fossil species and generic richness of Evanioidea (Fig. 25a), there is a relatively peak level of species and generic diversity in the Early Cretaceous at 125 Ma followed by a decrease in diversity into the Miocene 7 Ma. This diversity decrease trend represents a pattern that is rare for modern hymenopteran lineages. However,

the internal composition at species level of a family within Evanioidea shows even higher variability and more changes with time (Fig. 25b). The number of species of Anomopterellidae peaked in the Middle Jurassic and decreased during the Late Jurassic, after which no Anomopterellidae record has been reported. A similar pattern also occurs for Praeaulacidae, abundant during the Middle Jurassic and Late Jurassic, but decreasing considerably during the Late Cretaceous, followed by an absence of Praeaulacidae from the fossil record. In contrast, Baissidae were present extensively and reaching a peak during the Early Cretaceous, and presumably becoming extinct by the Cenozoic. Andreneliidae and Othniodellithidae are low-diverse clades that occurred solely during the Early Cretaceous and Late Cretaceous, respectively. The earliest known fossils of the extant Evanidae originated in the Early Cretaceous, and the overwhelming majority of species are recorded during the Cretaceous, but decreased considerably in the Cenozoic, perhaps representing a relict lineage. The remaining two extant families, Gasteruptiidae and Aulacidae, have their earliest occurrences, respectively, during the Early Cretaceous and Late Cretaceous, with the latter having an elevated spike in fossil occurrences during the Miocene. As we are aware, the diversity data of fossil taxa are affected by number and quality of fossil localities, effort and results of fossil excavation and the effects of taphonomy and fossilization processes. For example, smaller insects are more likely to be trapped by the resin and then fossilized into amber. On the other hand, very small insects are less likely to be preserved clearly on compression fossils. More importantly, the sparse records of amber and compression fossils may also result in sampling bias. Although these global trends are probably driven by occurrences from exceptional fossil deposits and relatively low, epoch-level diversities, these trendlines do

indicate that parasitoid taxa reached more elevated levels of genus and species-level diversity during the Middle Jurassic through Late Cretaceous and were followed by extinction at the end-Cretaceous ecological crisis, and a subsequent presence in the modern insect fauna at low diversity levels.

Recently, divergence-time estimation has played an important role in evolutionary biology. For example, the age or origin of the order Hymenoptera has been suggested to be 309 Ma, equivalent to the Middle Pennsylvanian, based on a combined-evidence analysis (Ronquist *et al.*, 2012). Notably, a node-dating analysis leads to a very similar result of 311 Ma, and accordingly the major radiation of basal Hymenoptera appeared in Permian. It is important to note that the proposed origin and timing of the early radiation time of Hymenoptera are considerably older than most previous estimates, which propose an origin during the Triassic and a radiation of most major lineages during the Jurassic (Grimaldi & Engel, 2005). Nevertheless, because the early fossil record of Hymenoptera is sparse, a gap of 74 Ma between the oldest fossils, *Triassoxyela foveolata* and *Leioxyela antique* at 235 Ma from the Middle Triassic–Late Triassic boundary interval, the origin of the order at 309 Ma seems at least possible (Rasnitsyn, 1964; Rasnitsyn & Quicke, 2002; Ronquist *et al.*, 2012).

A similar pattern also has been found for Evanioidea. Ronquist *et al.* (2012) estimated the stem-age and showed that the earliest divergence time of Evanioidea, based on combined-evidence dating, was in the Late Triassic at *c.* 221 Ma (Ronquist *et al.*, 2012), 43 Ma earlier than node dating based on the independent gamma rates model under BI, which provided a date of Early Jurassic at *c.* 178 Ma. These estimated ages can be compared with stem-age estimates of 214 Ma in Peters *et al.* (2017) and about 175 Ma in Branstetter *et al.* (2017), both based on node-dating. However, the hitherto earliest record of Evanioidea was reported for the two families of Praeaulacidae, exemplified by *Archaulacus* Li, Shih & Ren, *Aulacogastrinus* Rasnitsyn, *Eosaulacus* Zhang & Rasnitsyn, *Nevania* Zhang & Rasnitsyn, *Praeaulacus* Rasnitsyn, *Praeaulacon* Zhang & Rasnitsyn and *Sinaulacogastrinus* Zhang & Rasnitsyn, and Anomopterellidae, exemplified by *Anomopterella* Rasnitsyn and *Synaphopterella* Li, Rasnitsyn, Shih & Ren. These taxa all originated in the late Middle Jurassic at 165 Ma. The inferred times or origination and radiation of Hymenoptera, as well as the timing of these fossil occurrences, indicate that diversification within Evanioidea would have appeared no later than the Middle Jurassic, and in combination with the divergence time estimation of Ronquist *et al.* (2012), the origin age of Evanioidea may be pushed to the Early Jurassic, or possibly the Late Triassic.

Conclusions

Our investigation represents the first phylogenetic study of Evanioidea which includes most extinct and extant genera, and combines molecular and morphological data. The monophyly of Evanioidea is confirmed here and supported by a suite of morphological characters. The families Anomopterellidae, Othniodellithidae, Andreneliidae and Evaniidae are monophyletic,

while Praeaulacidae, Aulacidae, Baissidae and Gasteruptionidae are paraphyletic. *Vectevania* separated as a new family, Vectevaniidae, from Aulacidae and occupies a more basal position than Aulacidae and Baissidae within Evanioidea. The inferred times or origination and radiation of Hymenoptera, as well as the timing of these fossil occurrences, indicate that diversification within Evanioidea would have appeared no later than the Middle Jurassic, and in combination with the divergence time estimation of Ronquist *et al.* (2012), the origin age of Evanioidea may be pushed to the Early Jurassic, or possibly the Late Triassic. The present groups of evanioids are now a combination of extinct and extant lineages. Discovery and examination of more fossils from a variety of geological locations and periods, improving taxonomic coverage, and increasing molecular data will enable more complete analyses and probably lead to a more robust phylogenetic hypothesis.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. List of fossil species of Evanioidea of the world.

Appendix S2. List of recent taxa, specimens and GenBank accession numbers.

Appendix S3. Morphological data matrix, including 66 taxa.

Appendix S4. Total evidence data of 66 taxa.

Appendix S5. Total evidence of Evanioidea_MrBayes_Commands.

Appendix S6. Morphological characters coded in the phylogenetic analysis.

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The authors declare that there are no financial conflict interests (political, personal, religious, ideological, academic,

intellectual, commercial or any other), and no conflict interests in the manuscript.

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