

A review of the fossil Embolemidae (Hymenoptera: Chrysidoidea), with description of seven new species and history of the family

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ABSTRACT

The fossil Embolemidae (Hymenoptera: Chrysidoidea) are reviewed. Keys to the genera and species of this family are presented. Five new species of *Embolemus* are described from Cenomanian Kachin amber (Myanmar), namely: *Em. antiquus* sp. nov., *Em. burmensis* sp. nov., *Em. cretacicus* sp. nov., *Em. ohmkuhnlei* sp. nov. and *Em. zherikhini* sp. nov. They are the first *Embolemus* species recorded from Burmese amber. One new species of *Embolemopsis* from Barremian Wealden amber (UK), is described: *Ep. maryannae* sp. nov., the oldest known embolemid wasp and the first hymenopteran described from Wealden amber. The genus *Ponomarenkoa* is transferred from Dryinidae to Embolemidae. A new species of *Ponomarenkoa* (*P. burmensis* sp. nov.) is described from Cenomanian Kachin amber. The genera of Embolemidae are divided into three groups. The phylogenetic significance of the new species of Embolemidae and the history of the family are discussed. Nymphs of Cixiidae and Achilidae are recorded as hosts of Embolemidae. Possible hosts of fossil embolemids are discussed. For the first time, Achilidae (*Proteptera kaweckii*, from Baltic amber) are recorded as hosts of Dryinidae. *Proteptera kaweckii* is also recorded for the first time from Rovno amber.

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1. Introduction

The family Embolemidae (Hymenoptera: Chrysidoidea) includes 64 extant species worldwide (Olmi et al., 2020a) which are parasitoids of Hemiptera Auchenorrhyncha (Olmi et al., 2014c). The family comprises three extant genera (*Ampulicomorpha* Ashmead, 1893 (habitus in figs 1–4 in Olmi, 1996), *Embolemus* Westwood, 1833 (habitus in figs 5–8 in Olmi, 1996), and *Trogloembolemus* Olmi, Mita and Guglielmino, 2014a (habitus in figs 6–7 in Olmi et al., 2014b).

The distinction between *Ampulicomorpha* and *Embolemus* is controversial. Van Achterberg and Van Kats (2000) treat them as

synonyms, since the length and pigmentation of the veins enclosing the 2Cu cell (and mostly the posterior spurious vein near the anal vein (A)) may be variable (2Cu being either closed by strongly pigmented veins (in *Ampulicomorpha*) or open or partly closed by little pigmented veins (in *Embolemus*) and is the only character used to separate males of these two genera; the females are not a problem, because they are micropterous or brachypterous in *Embolemus* and macropterous in *Ampulicomorpha*). Olmi et al. (2014c) considered both genera valid, because they seem to be biologically separated, having different hosts and biology. Nevertheless, to clarify the situation, a molecular analysis of species of both genera is in preparation from one of the authors (M.O.).

Fossil Embolemidae are known from both the Cenozoic and the Cretaceous, from amber (Brues, 1933; Olmi, 1996; Olmi et al., 2010, 2014c; Ortega-Blanco et al., 2011; Perrichot and Engel, 2011;

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Rasnitsyn and Matveev, 1989; Rasnitsyn and Ross, 2000; Zhang et al., 2018; Guillam et al., 2019; Chény et al., 2020) and from rock (Brothers and Rasnitsyn, 2003; Olmi et al., 2010, 2014c; Rasnitsyn, 1975, 1996; Zhang et al., 2010) (Table 1). Only one embolemid wasp from Burmese (Kachin) amber has been described: *Ampulicomorpha janzeni* Olmi, Rasnitsyn, Brothers and Guglielmino, 2014c, based on one female and one male specimen. However, other unidentified specimens of this family were recorded as compression fossils from the Laiyang Formation (late phase of the Jehol Biota; 120–122.5 Ma) of Shandong Province in China (Zhang et al., 2010) and from Burmese amber in the collections at The Natural History Museum, London, UK (Rasnitsyn and Ross, 2000) (specimens registered with numbers NHMUK In.20151 (2) and NHMUK In.20194: In.20151 (2) is a male of *Embolemus* sp.; it is possible to see only the head, antennae and prothorax, so it is impossible to identify the species; the length of head and prothorax is 0.75 mm; In.20194 is a male of *Embolemus* sp.; the specimen is hardly visible; so it is impossible to identify it), the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (Zhang et al., 2018; Guillam et al., 2019) and in the amber collections of the American Museum of Natural History, New York, USA (Engel, pers. comm.).

Hosts of extant Embolemidae are nymphs of Achilidae and Cixiidae (Hemiptera: Auchenorrhyncha) (Olmi et al., 2014c). No fossil nymphs of these two families of planthoppers, parasitized by embolemids and showing the characteristic thylacium (Olmi et al., 2014c), are known.

In 2017–2019, the authors examined other fossil material of Embolemidae, comprising some new species from Kachin

(Myanmar) and Wealden (UK) amber. They are described in this paper. This discovery provided the opportunity to review all known fossil species of Embolemidae.

2. Material and methods

The deposits where embolemid fossils have been found are listed below.

All pieces of Burmese amber examined herein were collected from the Noiye Bum site (26° 29' N, 96° 35' E) in the Hukawng Valley of Kachin State, Myanmar. The age of Kachin amber was previously considered to be Late Albian to Cenomanian based on palynology and ammonite stratigraphy (Cruickshank and Ko, 2003). It is now radiometrically dated as 98.79 ± 0.62 Ma based on U–Pb zircon dating of the volcanoclastic matrix and shown to be earliest Cenomanian in age (Shi et al., 2012; Smith and Ross, 2018; Zhang et al., 2018; Yu et al., 2019). Kachin amber is a Burmese amber different from the recently discovered Campanian Tilin amber (Zheng et al., 2018).

The piece of Wealden amber examined herein was collected on the Isle of Wight (UK). Wealden amber (“chiltonchinese”) is in the Wessex Formation exposed by marine erosion on the southwest coast of the Isle of Wight (IoW) in southern England. The amber bed actually is a plant-debris horizon (Lignite 6) exposed by the sea on the Channel coast of the IoW near a small valley called Chilton Chine (Sweetman, 2011: text-fig. 4.17). The amber occurs occasionally in the mass of plant debris considered to have been deposited from sheet flooding on a river floodplain following seasonal wildfire and rainstorms on wooded higher ground

Table 1

Identified fossil Embolemidae. Unidentified Embolemidae are also known from Dominican amber (Burdigalian, Miocene; 16 Ma; unknown sex) (Rasnitsyn 1996) and from the Laiyang Formation (late phase of the Jehol Biota; 120–122.5 Ma) of Shandong Province in China (Zhang et al., 2010).

Taxon	Known sex	Deposit	Age	Ma
Compression fossils				
<i>Baissobius carolinianus</i> Rasnitsyn, 1996	m#	Bon Tsaagan (Mongolia)	Aptian (Lower Cretaceous)	113–125
<i>B. minimus</i> Rasnitsyn, 1996	m#	Baissa (Siberia)	Aptian (Lower Cretaceous)	113–125
<i>B. minutus</i> Olmi, Rasnitsyn & Guglielmino, 2010	m#	Baissa (Siberia)	Aptian (Lower Cretaceous)	113–125
<i>B. parvus</i> Rasnitsyn, 1975	m#	Baissa (Siberia)	Aptian (Lower Cretaceous)	113–125
<i>Cretembolemus orapensis</i> Olmi, Rasnitsyn, Brothers & Guglielmino, 2014b	f#	Orapa (Botswana)	Turonian (Upper Cretaceous)	91
<i>Embolemopsis baissensis</i> Olmi, Rasnitsyn & Guglielmino, 2010	m#	Baissa (Siberia)	Aptian (Lower Cretaceous)	113–125
Fossils in amber				
<i>Ampulicomorpha janzeni</i> Olmi, Rasnitsyn, Brothers & Guglielmino, 2014b	f#, m#	Kachin (Myanmar)	lowermost Cenomanian (Upper Cretaceous)	About 99
<i>A. perialla</i> (Ortega-Blanco, Delclòs & Engel, 2011)	f#	Peñacerrada (Spain)	Albian (Lower Cretaceous)	105
<i>A. quesnoyensis</i> Chény, Guillam, Nel & Perrichot, 2020	f#	Oise (France)	Ypresian (lowermost Eocene)	About 53
<i>A. succinalis</i> Brues, 1933	f#, m#	Baltic and Rovno	Priabonian (Eocene)	35–38
<i>Embolemopsis maryannae</i> Olmi, Jarzembowski, Capradossi & Perkovsky, sp. nov.	m#	Wealden (Isle of Wight, UK)	lower Barremian	About 128
<i>Embolemus antiquus</i> Perkovsky, Olmi, Müller, Guglielmino & Rasnitsyn, sp. nov.	m#	Kachin (Myanmar)	lowermost Cenomanian (Upper Cretaceous)	About 99
<i>E. [?] breviscapus</i> Brues, 1933	m#	Baltic	Priabonian (Eocene)	35–38
<i>E. burmensis</i> Perkovsky, Olmi, Müller, Guglielmino & Rasnitsyn, sp. nov.	m#	Kachin (Myanmar)	lowermost Cenomanian (Upper Cretaceous)	About 99
<i>E. cretaceus</i> Perkovsky, Olmi, Müller, Guglielmino & Rasnitsyn, sp. nov.	m#	Kachin (Myanmar)	lowermost Cenomanian (Upper Cretaceous)	About 99
<i>E. excitus</i> Perrichot & Engel, 2011	f#	Baltic	Priabonian (Eocene)	35–38
<i>E. ohmkuhnlei</i> Perkovsky, Olmi, Müller, Guglielmino & Rasnitsyn, sp. nov.	m#	Kachin (Myanmar)	lowermost Cenomanian (Upper Cretaceous)	About 99
<i>E. zherikhini</i> Perkovsky, Olmi, Müller, Guglielmino & Rasnitsyn, sp. nov.	m#	Kachin (Myanmar)	lowermost Cenomanian (Upper Cretaceous)	About 99
<i>Ponomarenkoa burmensis</i> Perkovsky, Olmi, Müller, Guglielmino & Rasnitsyn, sp. nov.	m#	Kachin (Myanmar)	lowermost Cenomanian (Upper Cretaceous)	About 99
<i>P. ellenbergeri</i> Olmi, Xu & He, in Xu, Olmi & He, 2013	m#	Kachin (Myanmar)	lowermost Cenomanian (Upper Cretaceous)	About 99
<i>P. polonica</i> (N. Ponomarenko, 1988)	m#	Baltic	Priabonian (Eocene)	35–38

(Sweetman, 2011: text-fig. 4.9). Arthropod inclusions are uncommon, but at least four orders of insects and spiders have been found (Jarzembowski et al., 2008). The amber is of early Barremian age (about 128 Ma) and generally considered to be of extinct coniferous origin (Bray and Anderson, 2008). The Wealden amber of the Isle of Wight is nationally important because it is the first *in situ* amber deposit in the UK to yield insect inclusions (Austen and Batten, 2018).

The pieces from Baltic amber examined herein were collected in unknown localities on the coast of the Baltic sea, mainly on the Sambia Peninsula (Russia) (Eocene, Priabonian, 35–38 Ma). More importantly, the piece including an achilid parasitized by dryinids was collected in Yantarnyi, Kaliningrad region.

The pieces from Rovno amber examined herein were collected in the Rovno region (Ukraine), the embolemid female in the basin of the Styr River (Eocene, Priabonian, 35–38 Ma) (Martynova et al., 2019), the embolemid male and achilid from Klesov.

The piece of Álava amber examined herein was collected in Peñacerrada near Álava, Basque Country, Spain (Lower Cretaceous, Albian, about 105 Ma) (Olmi et al., 2014c).

The piece of Oise amber including the holotype of *Ampulicomorpha quesnoyensis* Chény, Guillaum, Nel and Perrichot, 2020 (not examined here), was collected in Le Quesnoy outcrop, Chevières near Houdancourt, Department of Oise, France (lowermost Eocene, Ypresian, biozone MP7 of the reference mammal fauna of Dormaal (= 'Sparnacian', ca. 53 Ma) (Chény et al., 2020).

The compression fossil from Orapa, Botswana, examined here was collected in a Kimberlitic deposit (Upper Cretaceous, Turonian, 91 Ma) (Olmi et al., 2014c).

The compression fossils from Baissa (Siberia) examined herein were collected on the left bank of the Vitim River, Western Transbaikalia, 3 km down-stream from the former lodge at Baissa, 45 air km upstream from Romanovka Village, found in marls of the Zaza Formation (Lower Cretaceous, Aptian, 113–125 Ma) (Olmi et al., 2010).

The compression fossil from Bon Tsaagan examined herein was collected in Central Mongolia, 5–8 km N of Bon Tsaagan Nuur Lake, outcrop 87, bed 8, in Bayanhongor Aimag, in the Bon-Tsaagan Member of the Dzun-Bain Formation (Lower Cretaceous, Aptian, 113–125 Ma) (Olmi et al., 2010). The composition of the insect fossil fauna suggests a distinctly younger age of the Bon-Tsaagan deposits compared to those of Baissa (Dmitriev, 2017).

The terminology used throughout the text is that of Olmi (1996) revised by Azevedo et al. (2018) and Lanes et al. (2020). The following abbreviations are used: POL, distance between the inner edges of the two lateral ocelli; OL, shortest distance between the edge of a lateral ocellus and the median ocellus; OOL, distance from the outer edge of a lateral ocellus to the compound eye. The names of cells and veins of the fore wing are here used in the sense of Azevedo et al. (2018). In Olmi (1996) and Olmi et al. (2010, 2014c) different names were used. The correspondence between old and new names is as follows (the first name is the old name): basal cell (BC) = radial cell (R); subbasal cell (SBC) = first cubital cell (1Cu); marginal cell = second radial 1 cell (2R1); first discal cell (1DC) = first medial cell (1M); first subdiscal cell (1SDC) = second cubital cell (2Cu); stigmal vein = second radial cross and radial sector (2r-rs&Rs); metacarp = poststigmal abscissa of radial 1 (PostabR1). In the text, cells and veins are named by their respective abbreviations, including costal cell (C) and Radial Sector + Median vein (Rs + M). The term “metapectal-propodeal complex” is here used in the sense of Kawada et al. (2015). It corresponds to the term “propodeum” *sensu* Olmi (1996). The terms “disc of metapectal-propodeal complex” and “propodeal declivity” *sensu* Kawada et al. (2015) and Olmi et al. (2019), used here, correspond to the terms “dorsal surface of propodeum” and

“posterior surface of propodeum”, *sensu* Olmi (1996). The term “ADOs” (= Antennal Dorsal Organs) is here used in the sense of Riolo et al. (2016). It corresponds to the term “rhinaria” *sensu* Olmi (1999). According to Riolo et al. (2016), ADOs are sensory structures.

All types of Embolemidae fossil species were examined personally by the authors, excluding those of *Ampulicomorpha quesnoyensis* Chény, Guillaum, Nel & Perrichot, 2020, and *Embolemus breviscapus* Brues, 1933.

Because of the nature of the fossils and distortions sometimes caused by artefacts, the word ‘apparently’ is used when describing characters for which there is slight uncertainty about the true condition or where a false impression is obtained at first sight.

One of the authors (EAJ) checked the English language of this paper.

The material studied in the present paper is deposited in the following collections: **AMNH**: American Museum of Natural History, New York (USA); **DAFS**: Department of Agriculture and Forest Science (DAFNE), University of Tuscia, Viterbo (Italy); **ESI**: Evolutionary Studies Institute (former Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg (South Africa); **MCNA**: Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz (Spain); **PAS MZ**: Polish Academy of Sciences, Museum of the Earth, Warsaw (Poland); **NHMUK**: Natural History Museum, London (United Kingdom); **PIN**: A. A. Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (Russia); **SIZK**: I. I. Schmalhausen Institute of Zoology, National Academy of Sciences of the Ukraine, Kiev (Ukraine); **SMF**: Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (Germany); **SMNS**: Staatliches Museum für Naturkunde Stuttgart, Abt. Paläontologie-Sektion Bernstein, Stuttgart (Germany).

3. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Suborder Apocrita Gerstaecker, 1867

Superfamily Chrysidoidea Latreille, 1802

Family Embolemidae Förster, 1856

Embolemoidae (sic) Förster, 1856: 94

Type genus: *Embolemus* Westwood, 1833, according to Art. 63 of ICZN (1999) (the type of each taxon of a family-group is that nominal genus upon which the family-group name is based).

Diagnosis. Female: micropterous (habitus in figs 5, 6 in Olmi, 1996), or brachypterous (habitus in fig. 31 in Olmi, 1996), or macropterous (habitus in figs 1, 2 in Olmi, 1996); third segment of maxillary palpus much larger than other segments; antenna composed of 10 antennomeres; antennae of most extant species and fossil species articulated on two prominent contiguous frontal processes far above the clypeus (see figs 1, 2 in Olmi, 1996); antennae rarely not articulated on prominent frontal processes (only in *Cretembolemus* Olmi, Rasnitsyn, Brothers and Guglielmino, 2014c) (see figs 11, 12 in Olmi et al., 2014c); antennae without ADOs; in macropterous species, fore wing with long tubular development of Rs + M and distal abscissa of M ((RS + M)&M) and desclerotization of Cu beyond its separation from M (desclerotization complete or partial); tibial spurs 1/2/2. **Male:** macropterous (Figs 1–6; habitus also in figs 3, 4, 7, 8 in Olmi, 1996); third segment of maxillary palpus much larger than other segments; antenna composed of 10 antennomeres; antennae of extant species and fossil species in Upper Cretaceous and Cenozoic amber articulated on two prominent contiguous frontal processes far above the clypeus (see figs 3, 4, 7, 8 in Olmi, 1996); antennae of Lower Cretaceous compression fossils not articulated on contiguous frontal prominences (see figs 1, 3, 6, 7 in Olmi et al., 2010); fore wing with long tubular development of Rs + M and the distal abscissa of M ((RS + M)&M) and desclerotization of

Cu beyond its separation from M (desclerotization complete or partial); tibial spurs 1/2/2.

Distribution. Worldwide.

Hosts. Nymphs of Cixiidae feeding on roots and living in the soil (Varrone and Olmi, 2012) and Achilidae feeding on fungus and living in rotten logs (Bridwell, 1958; Wharton, 1989; Guglielmino and Bückle, 2013; Olmi et al., 2014c).

World genera. Seven genera are known.

World species. Eighty-five species are known, including 64 extant (Olmi, 1996; Azevedo and Amarante, 2006; Olmi et al., 2014a; Olmi et al., 2020a) and 21 fossil species (Olmi et al., 2010, 2014b, c; Perrichot and Engel, 2011; Chény et al., 2020; present paper) (Table 1).

Key to the genera of extant and fossil Embolemidae.

Females.

1. Antennae not articulated on two frontal prominences (Figs 11, 12 in Olmi et al., 2014c)..... *Cretembolemus* Olmi, Rasnitsyn, Brothers and Guglielmino (fossil)
- Antennae articulated on two contiguous frontal prominences situated far from the clypeus (see figs 1, 2, 5, 6 in Olmi, 1996).... 2
2. Macropterous (see figs 1, 2 in Olmi, 1996)..... *Ampulicomorpha* Ashmead (extant and fossil)
- Micropterous (see figs 5, 6 in Olmi, 1996) or brachypterous (see fig. 31 in Olmi, 1996)..... 3
3. Head with anterior region tapering (see figs 6, 7 in Olmi et al., 2014b); eye greatly reduced (see figs 6, 7 in Olmi et al., 2014b); mesoscutellum narrow, alutaceous, trapezoidal, with shorter posterior base (see fig. 6 in Olmi et al., 2014b); metanotum reduced to narrow longitudinal carina forming a bridge

upon the anterior region of the metapectal-propodeal complex (see fig. 6 in Olmi et al., 2014b).....

..... *Trogloembolemus* Olmi, Mita and Guglielmino (extant)

- Head with anterior region not tapering (see fig. 8 in Olmi et al., 2014b); eye of normal size (see fig. 6 in Olmi, 1996); mesoscutellum subcircular (see fig. 5 in Olmi, 1996); metanotum short and transverse (see fig. 5 in Olmi, 1996).....

..... *Embolemus* Westwood (extant and fossil)

Remarks. Females of *Baissobius* Rasnitsyn, *Embolemopsis* Olmi, Rasnitsyn and Guglielmino and *Ponomarenkoa* Olmi are unknown.

Males.

1. Bases of antennae widely spaced and not articulated on contiguous frontal prominences (Fig. 1; see also figs 1, 3, 4, 6, 7 in Olmi et al., 2010) (fossil)..... 2
- Antennae articulated on two contiguous frontal prominences (Fig. 3; see also figs 3, 4, 7, 8 in Olmi, 1996) (extant and fossil).... 4
2. Fore wing with 1M and 2Cu cells not enclosed by pigmented veins (see figs 6, 7 in Olmi et al., 2010).....
- *Baissobius* Rasnitsyn (fossil)
- Fore wing with 1M and 2Cu cells enclosed by pigmented veins (Figs 1A, 5A; see also fig. 1 in Olmi et al., 2010)..... 3
3. Lateral ocelli touching occipital carina (Fig. 1A; see also fig. 1 in Olmi et al., 2010).....
- *Embolemopsis* Olmi, Rasnitsyn and Guglielmino (fossil)
- Lateral ocelli distant from occipital carina (Fig. 5A).....
- *Ponomarenkoa* Olmi (fossil)
4. Fore wing with both 2Cu and 1M cells enclosed by well pigmented veins (see figs 3, 4 in Olmi, 1996).....
- *Ampulicomorpha* Ashmead (extant and fossil)
- Fore wing with 2Cu open or enclosed by less pigmented vein (Figs 2A, B; see also figs 7, 8 in Olmi, 1996); 1M cell closed by well or little pigmented veins (Figs 2A, B; see also figs 7, 8 in Olmi, 1996)..... *Embolemus* Westwood (extant and fossil)

Remarks. Males of *Cretembolemus* and *Trogloembolemus* are unknown.

Genus *Ampulicomorpha* Ashmead.

(Habitus in figs 1–4 in Olmi, 1996)

Ampulicomorpha Ashmead 1893: 79.

Type species: *Ampulicomorpha confusa* Ashmead, 1893, by original designation.

Diagnosis. Female: macropterous (see figs 1, 2 in Olmi, 1996). Antenna with scape much longer than first flagellomere (see figs 1, 2 in Olmi, 1996). Head subspheroidal, with dorsal side swollen (see figs 1, 2 in Olmi, 1996), occasionally pyriform and flat. Palpal formula variable: 6/3, 6/2, 5/2, 4/2, rarely 2/1. Posterior surface of pronotum with strong median complete or incomplete longitudinal furrow (see fig. 1 in Olmi, 1996). Fore wing with 2Cu cell completely enclosed by pigmented veins (see fig. 2 in Olmi, 1996) (veins less pigmented than those enclosing C, R, 1Cu cells; occasionally 2Cu cell partly open and not completely enclosed by pigmented veins).

Male: macropterous (see figs 3, 4 in Olmi, 1996). Head always subspheroidal (see figs 3, 4 in Olmi, 1996), never pyriform, with dorsal side swollen (see fig. 4 in Olmi, 1996). Antenna with scape usually shorter than first flagellomere (see figs 3, 4 in Olmi, 1996), occasionally longer. Palpal formula variable: 6/3, 6/2, 5/2. Posterior surface of pronotum with strong median complete or incomplete longitudinal furrow. Fore wing with 2Cu cell completely enclosed by pigmented veins (see figs 3, 4 in Olmi, 1996) (veins less pigmented than those enclosing C, R, 1Cu cells; occasionally 2Cu cell partly open and not completely enclosed by pigmented veins).

Hosts. Nymphs of Achilidae (Hemiptera: Auchenorrhyncha).

Distribution. Worldwide.

World species. Genus comprises 24 extant species (unpublished data) and 4 fossil species recorded from Kachin (Myanmar) amber

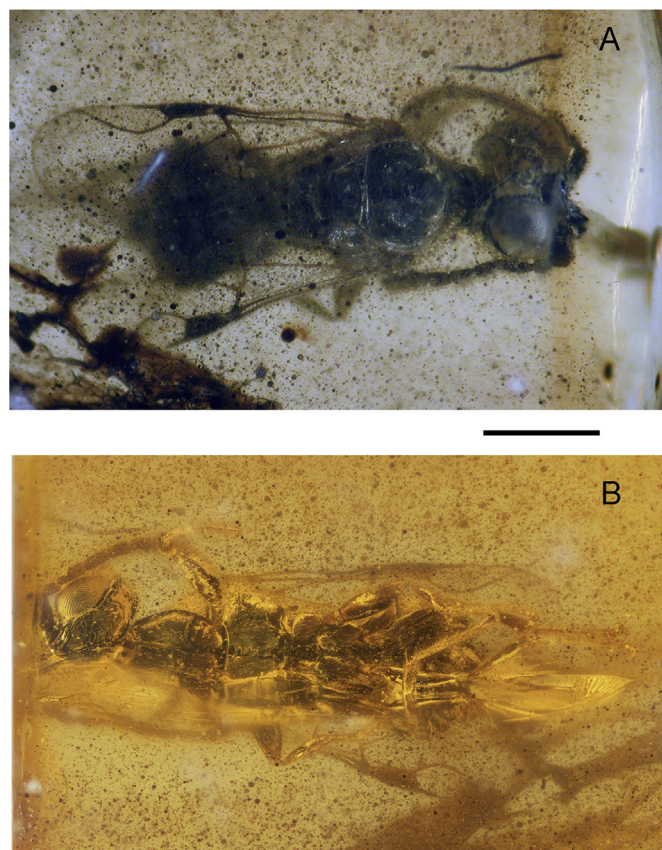


Fig. 1. *Embolemopsis maryannae* sp. nov.: male holotype (NHMUK 28344) in dorsal (A) and ventral (B) view. Scale bar: A: 0.5 mm; B: 0.4 mm.

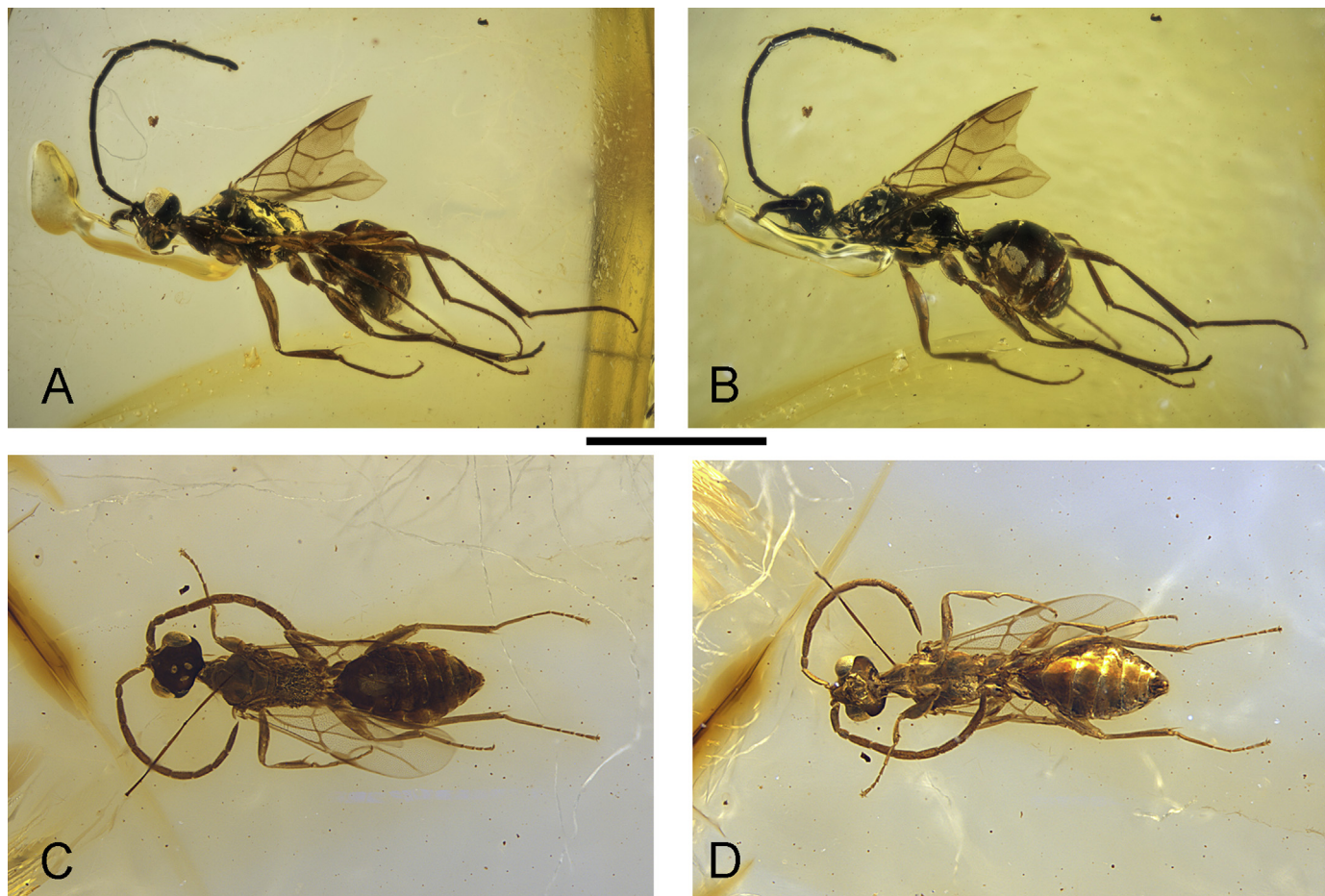


Fig. 2. *Embolemus antiquus* sp. nov.: male holotype (DAF2901) in lateroventral (A) and laterodorsal (B) view. *Embolemus burmensis* sp. nov.: male holotype (DAF2902) in dorsal (C) and ventral (D) view. Scale bar: A, B: 1.6 mm; C, D: 1.3 mm.

(*A. janzeni* Olmi, Rasnitsyn, Brothers and Guglielmino, 2014c), Álava amber (*A. perialla* (Ortega-Blanco, Delclòs and Engel, 2011), Oise amber (*A. quesnoyensis* Chény, Guillaum, Nel & Perrichot, 2020) and Baltic and Rovno amber (*A. succinalis* Brues, 1933) (Table 1).

Remarks. In *Ampulicomorpha*, males strongly differ from females, thus the association of opposite sexes based on morphological characters is impossible. Only DNA analysis or rearings can solve the problem of association of the opposite sexes of single species.

Key to the fossil species of *Ampulicomorpha*.

Females.

1. Antenna with scape more than seven times as long as pedicel; pronotum without median longitudinal furrow.....
..... *A. perialla* (Ortega-Blanco, Delclòs and Engel) (Álava amber)
- Antenna with scape at most six times as long as pedicel; pronotum with complete median longitudinal furrow..... 2
2. Metasomal petiole much shorter than metatrochanter.....
..... *A. succinalis* Brues (Baltic and Rovno amber)
- Metasomal petiole about as long as metatrochanter..... 3
3. Notauli complete..... *A. janzeni* Olmi, Rasnitsyn, Brothers and Guglielmino (Kachin amber)
- Notauli incomplete, reaching about 0.5 length of mesoscutum. . .
A. quesnoyensis Chény, Guillaum, Nel & Perrichot (Oise amber)

Males.

1. Fore wing apparently completely darkened. . . *A. succinalis* Brues (Baltic and Rovno amber)

– Fore wing hyaline, not darkened. . . *A. janzeni* Olmi, Rasnitsyn, Brothers and Guglielmino (Kachin amber)

Remarks. The male of *A. perialla* is unknown.

Ampulicomorpha janzeni Olmi, Rasnitsyn, Brothers and Guglielmino.

(Habitus in figs 9, 10 in Olmi et al., 2014c)

Ampulicomorpha janzeni Olmi, Rasnitsyn, Brothers and Guglielmino, 2014c: 625.

Diagnosis. Female (see fig. 9 in Olmi et al., 2014c) with scape less than six times as long as pedicel; pronotum with complete median longitudinal furrow, extending from anterior to posterior margin; metasomal petiole about as long as metatrochanter. Male (see fig. 10 in Olmi et al., 2014c) with maxillary palpus 5-segmented; fore wing hyaline, not darkened.

Material examined. Holotype f#, SMNS-BU-21 (SMNS) and 1m# paratype, SMNS-BU-22 (SMNS). Other material: 1f#, same locality as holotype, DAF3000 (DAFS). In Upper Cretaceous Kachin (Burmese) amber.

Horizon and locality. Lower Cenomanian (98.79 ± 0.62 Ma; Grimaldi et al., 2002 based on insect inclusions; Shi et al., 2012 based on zircon analyses), SW of Tanai City, Hukawng Valley, Tanai Township, Kachin State, northern Myanmar.

Description of female holotype. Macropterous (see fig. 9 in Olmi et al., 2014c; left fore wing apparently sub-brachypterous, shortened and narrow, because it is inclined antero-posteriorly in the amber and

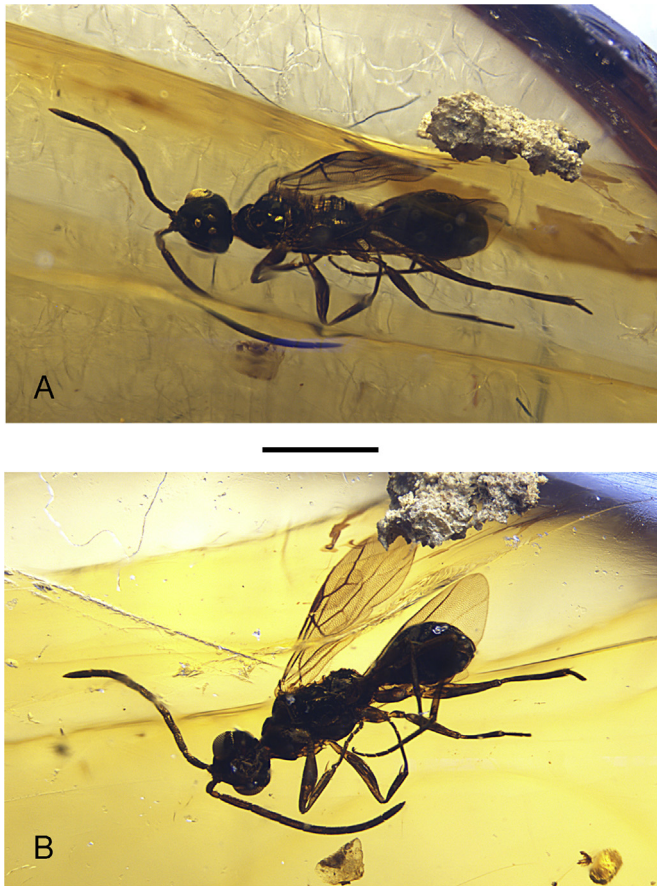


Fig. 3. *Embolemus cretacicus* sp. nov.: male holotype (DAF2907) in dorsal (A) and lateroventral (B) view. Scale bar: A: 0.9 mm; B: 1.0 mm.

the distal third is missing; right fore wing complete); length 2.9 mm. Description in Olmi et al. (2014c).

Other material: f#, DAF3000, similar to holotype, but antenna testaceous, with antennomeres in following proportions: 27:9:11:11:12:11:11:10:17. Pronotum dull, granulated, hairless, with deep complete median longitudinal furrow. Notauli complete, posteriorly separated; minimum distance between notauli much shorter than antennomere 2 (5:9). Fore wing hyaline, without dark transverse bands; stigmal vein 2r-rs&Rs with distal part much longer than proximal part (21:10).

Description of male paratype. Macropterous (see fig. 10 in Olmi et al., 2014c); length 1.7 mm. Description in Olmi et al. (2014c).

Hosts. Unknown.

Remarks. The male quoted above is tentatively associated with the female holotype because its morphological characters are very similar to those of the female and both specimens are from the same amber deposit.

Ampulicomorpha perialla (Ortega-Blanco, Delclòs and Engel)

(Habitus in figs 1, 2 in Ortega-Blanco et al., 2011)

Embolemus periallus Ortega-Blanco, Delclòs and Engel, 2011: 37.

Ampulicomorpha perialla (Ortega-Blanco, Delclòs and Engel): Olmi et al., 2014c: 5.

Diagnosis. Female (see figs 1, 2 in Ortega-Blanco et al., 2011) with scape more than seven times as long as pedicel; pronotum without median longitudinal furrow. Male unknown.

Material examined. Holotype f#, MCNA 12709. In Lower Cretaceous Álava amber.

Horizon and locality. Albian (about 105 Ma), Peñacerrada (Peñacerrada I = Moraza, Burgos), Álava, Spain.

Description of female holotype (see figs 1, 2 in Ortega-Blanco et al., 2011). Macropterous; length 3.3 mm. Apparently black. Head punctate, flat dorsoventrally, two times longer than broad. Antenna filiform, articulated on two prominent contiguous frontal processes; scape 10 times longer than apical width and 7.25 times as long as pedicel; pedicel slightly longer than wide, as wide as scape; flagellomeres elongate, about five times longer than wide, progressively shortening. Palpus not completely visible (only two labial and five maxillary palpomeres visible). Mesosoma about three times as long as broad. Pronotum elongate, without longitudinal medial furrow. Mesoscutum about as long as pronotal collar. Notauli apparently faintly present. Mesoscutellum not visible. Fore wing darkened, with 1M and 2Cu cells enclosed by pigmented veins; marginal cell 2R1 not completely visible; stigmal vein 2r-rs&Rs with distal part longer than proximal part. Legs elongate, with femora longer than one-half of mesosoma. Metasoma as long as two-thirds of mesosoma. Tibial spurs 1/2/2. **Male:** unknown.

Hosts. Unknown.

Ampulicomorpha quesnoyensis Chény, Guillaum, Nel and Perrichot. (Habitus in figs 3, 4 in Chény et al., 2020)

Ampulicomorpha quesnoyensis Chény, Guillaum, Nel and Perrichot, 2020: 20.

Diagnosis. Female (see figs 3, 4 in Chény et al., 2020) with scape about 5.4 as long as pedicel; pronotum with complete median longitudinal furrow; metasomal petiole about as long as metatrochanter; notauli incomplete, reaching about $0.5 \times$ length of mesoscutum.

Remarks. The female holotype (MNHN.FA58662), deposited in the Natural History Museum of Paris (France), was not examined. Description in Chény et al., 2020. From Oise Department, France (lowermost Eocene, Ypresian, ca. 53 Ma).

Ampulicomorpha succinalis Brues.

(Habitus in fig. 7 in Olmi et al., 2014c)

Ampulicomorpha (sic) *succinalis* Brues, 1933: 114.

Ampulicomorpha succinalis Brues: Rasnitsyn and Matveev, 1989: 657.

Diagnosis. Female (see fig. 7 in Olmi et al., 2014c) with scape less than six times as long as pedicel; pronotum with complete median longitudinal furrow, extending from anterior to posterior margin; metasomal petiole much shorter than metatrochanter. Male (see fig. 8 in Olmi et al., 2014c) with fore wing darkened.

Material examined. Holotype f# probably lost (originally in the amber collection of the Albertus University in Königsberg). Other material: 4f#f# from Baltic amber in DAFS (DAF2998, DAF2999), PIN (PIN 964/648) and SMNS (BB-2418); 1f# from Rovno amber in SIZK (SIZK W-302); 1m# from Rovno amber in SIZK (SIZK K-1973 from Klesov locality). In Upper Eocene Baltic and Rovno amber.

Horizon and locality. Priabonian (35–38 Ma), Northern and Eastern Europe.

Description of female from Baltic amber (PIN 964/648). Macropterous; length 4.4 mm (holotype 5.5 mm (Brues, 1933)). Colour not distinctly visible; apparently colour of body black. Antennae geniculate, filiform; antennomeres in following proportions: 34:7:17:16:15:14:14:14:12:12; antennae articulated on strong frontal processes; area from antennal toruli to clypeus not visible. Head apparently dull and alutaceous, without visible sculpture, with dorsal side swollen; occipital carina completely visible in dorsal side of head, not visible in lateral and ventral sides; ocelli distinct; POL = 3; OL = 3; OOL = 9; OPL = 9; TL = 13; eye large, approximately 0.4 as long as head (13:33). Maxillary and labial palpus not visible. Pronotum apparently dull, alutaceous, unsculptured, anteriorly crossed by strong transversal impression,

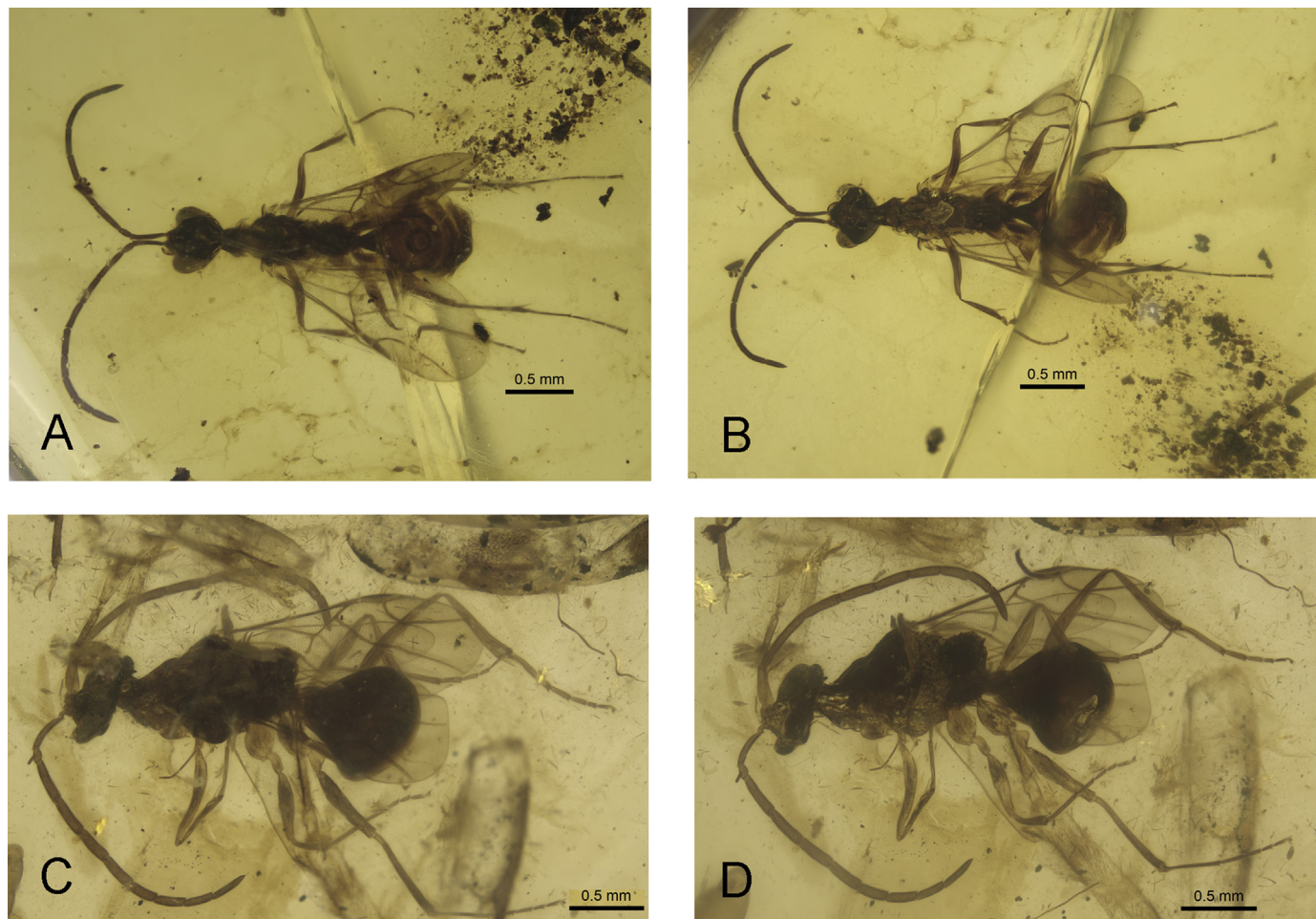


Fig. 4. *Embolemus ohmkuhnlei* sp. nov.: male holotype (PIN 5620/87) in dorsal (A) and ventral (B) view. *Embolemus zherikhini* sp. nov.: male holotype (PIN 5620/88) in dorsolateral (C) and lateroventral (D) view.

shorter than mesoscutum (19:21); disc of pronotum very long, with strong median longitudinal furrow; pronotal tubercle apparently reaching tegula. Mesoscutum dull, alutaceous, apparently unsculptured. Notauli incomplete, reaching approximately 0.3 length of mesoscutum. Mesoscutellum not distinctly visible, much shorter than mesoscutum (8:21), longer than metanotum (8:2). Metanotum not distinctly visible, apparently rugose, very short. Metapectal-propodeal complex not visible, because hidden under wings, much shorter than metasoma (27:63). Fore wing fully developed, hyaline, without dark transverse bands; marginal cell 2R1 open; distal part of stigmal vein 2r-rs&Rs longer than proximal part (21:18); 2Cu and 1M cells completely enclosed by pigmented veins. Hind wing not distinctly visible. Ventral side of body not visible. Tibial spurs not visible. **Other material:** 2 f## from Baltic amber in DAFS (DAF2998, DAF2999) (see fig. 7 in Olmi et al., 2014c): macropterous, length 4.1 mm; apparently totally black, except antennae brown. Antenna geniculate, filiform; antennomeres in following proportions: 30:5:16:13:11:11:10:10:9:11; antennae shorter than body, articulated on two strong frontal processes; antennal toruli very far from upper margin of clypeus. Head pyriform, dull, granulate, apparently unsculptured; occipital carina not completely visible; ocelli distinct; POL = 3; OL = 3; OOL = 9; OPL = 8; TL = 10; greatest breadth of posterior ocelli shorter than OL (2:3); eye very small, approximately 0.33 as long as head (13:29); region of frons from clypeus to antennal toruli with two longitudinal and median sutures only partly visible; region

from anterior ocellus to frontal processes flat, not distinctly visible. Palps only partly visible. Third palpomere of maxillary palpus broadened. Pronotum dull, granulated, apparently unsculptured, with strong complete median longitudinal furrow; posterior surface of pronotum shorter than mesoscutum (10:18); pronotal tubercles reaching tegulae. Mesoscutum dull, granulate, apparently unsculptured. Notauli very short, approximately $0.25 \times$ length of mesoscutum. Parapsidal furrows distinct. Mesoscutellum dull, granulate, apparently unsculptured, much shorter than mesoscutum (8:18). Metanotum not visible, because hidden under wings. Mesopleura and metapleura not visible. Meso-metapleural suture not visible. Metapectal-propodeal complex almost completely invisible because hidden under wings; disc of metapectal-propodeal complex partly visible through wings, reticulate rugose, with two median longitudinal subparallel keels apparently not forming basal areola at anterior margin of metapectal-propodeal complex; propodeal declivity not visible. Fore wing weakly darkened, with marginal cell 2R1 open; distal part of stigmal vein 2r-rs&Rs longer than proximal part (20:15); 1M and 2Cu cells completely enclosed by pigmented veins. Hind wings not visible, because hidden under fore wings. Metasomal petiole much shorter than metasoma (5:60) and shorter than hind trochanter (5:8). Tibial spurs 1/2/2. **F# from Rovno amber in SIZK, SIZK W-302** (see fig. 3 in Martynova et al., 2019): as the above female; macropterous; length 4.8 mm. Body apparently black, metasoma blackish. Antenna composed of 10 antennomeres, filiform, geniculate. Antennomeres in following

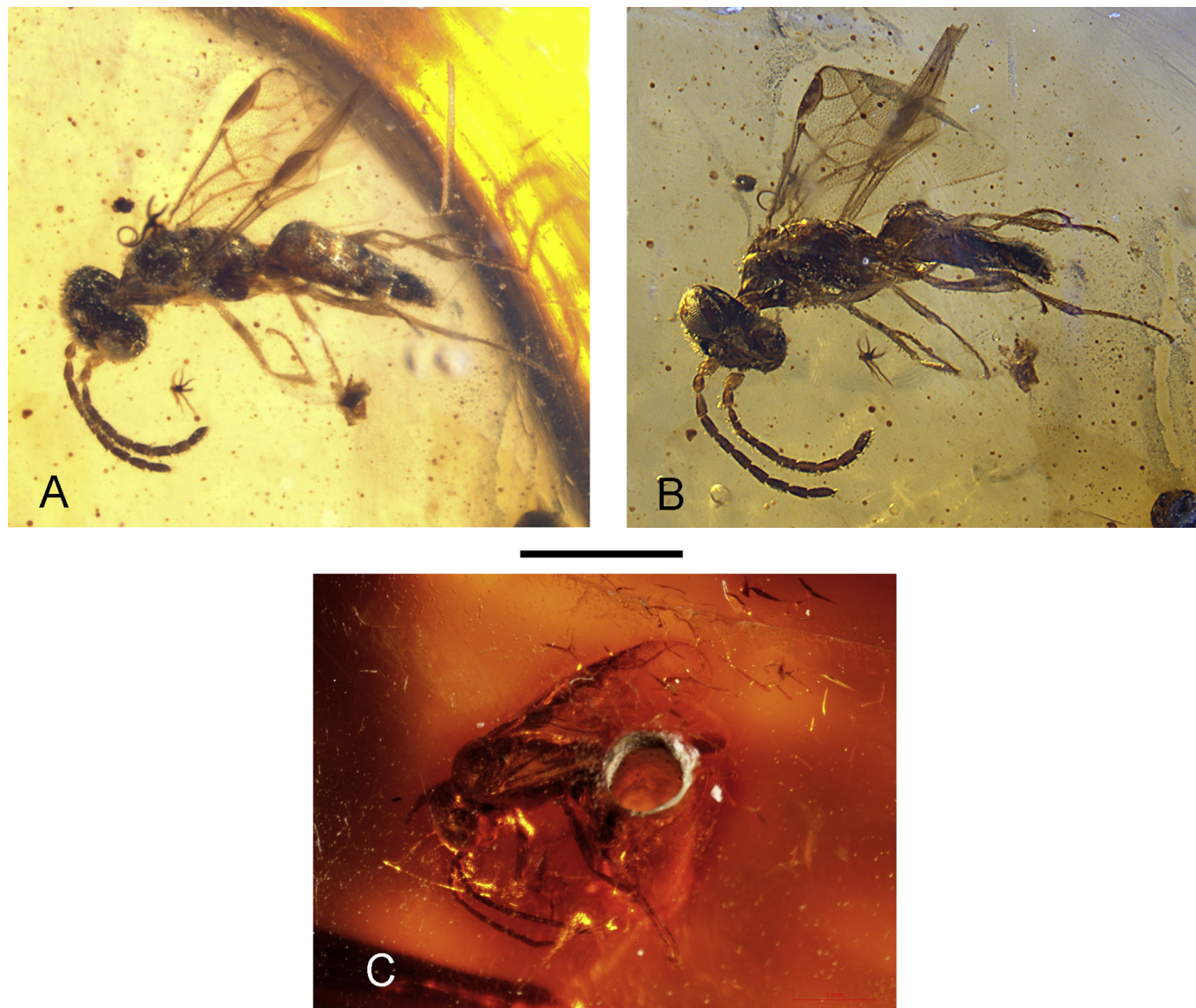


Fig. 5. *Ponomarenkoa burmensis* sp. nov.: male holotype (DAF2800) in dorsolateral (A) and lateroventral (B) view. C: *Ponomarenkoa polonica* (N. Ponomarenko): male holotype (PAS MZ 8736) in dorsolateral view. Scale bar: A, B: 0.6 mm; C: 1.7 mm.

proportions: 38:7:21:20:18:18:17:16:15:18. Head dull, micro-punctate. Palps only partly visible; maxillary palpus composed of 6 palpomeres; third maxillary palpomere broader than other palpomeres. Occipital carina complete. Pronotum about as long as mesoscutum, crossed by transverse shallow groove anteriorly and with deep median longitudinal groove. Pronotal tubercle reaching tegula.

Description of male from Rovno amber (SIZK K-1973 from Klesov locality) (see figs 1–3 in Olmi et al., 2011). Macropterous; length 5.0 mm. Colour apparently black, except palpus brown and metasoma brown-testaceous. Antenna filiform, not geniculate; antennomeres in following proportions: 12:4:35:28:26:24:22:22:19:20; antennae articulated on strong frontal processes; distance from antennal toruli to clypeus very large. Head apparently dull and granulate, with dorsal side swollen; frontal line apparently absent; occipital carina complete; ocelli distinct; POL, OL, OOL, OPL not measurable (ocelli observable only in lateral view); TL = 10; eye large, in dorsal view approximately 0.5 as long as head (14:29);

region of frons from clypeus to antennal toruli only partly visible; mandibles partly visible, but teeth not visible. Palpal formula 6/3 (but labial palpus not distinctly visible). Pronotum only observable in lateral view, with lateral regions dull, granulate; pronotal tubercle reaching tegula. Mesoscutum, notauli, mesoscutellum and metanotum not visible. Metapectal-propodeal complex completely reticulate rugose, with areolae very large, and dorsal surface sculptured by two irregular median longitudinal keels (area between these keels reticulate rugose). Metapectal-propodeal complex much shorter than metasoma (36:83), much longer than petiole (36:5). Fore wing fully developed, apparently completely darkened; marginal cell 2R1 open; distal part of stigmal vein 2r-rs&Rs longer than proximal part (25:20); 2Cu and 1M cells completely enclosed by pigmented veins. Hind wing partly visible. Foreleg ratio: 20 (coxa): 8 (trochanter): 39 (femur): 32 (tibia): 20 (tarsomere 1): 5 (tarsomere 2): 5 (tarsomere 3): 6 (tarsomere 4): 5 (tarsomere 5). Mid leg ratio: 20 (coxa): 5 (trochanter): 33 (femur): 35 (tibia): 21 (tarsomere 1): 7 (tarsomere 2): 6 (tarsomere 3): 5 (tarsomere 4): 7 (tarsomere 5).

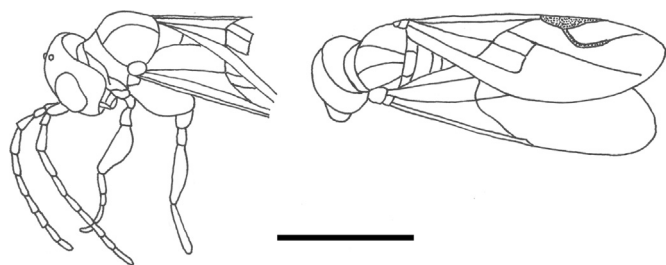


Fig. 6. *Ponomarenkoa polonica* (N. Ponomarenko): male holotype (PAS MZ 8736) in dorsolateral view (redrawn and corrected from N. Ponomarenko, 1988). Scale bar: 1.9 mm.

Hind leg ratio: 22 (coxa): 8 (trochanter): 49 (femur): 50 (tibia): 25 (tarsomere 1): 9 (tarsomere 2): 9 (tarsomere 3): 6 (tarsomere 4): 6 (tarsomere 5). Tibial spurs 1/2/2.

Hosts. Unknown.

Genus *Baissobius* Rasnitsyn.

(Habitus in figs 2–7 in Olmi et al., 2010)

Baissobius Rasnitsyn, 1975: 128.

Type species: *Baissobius parvus* Rasnitsyn, 1975, by monotypy and original designation.

Diagnosis. Male: macropterous (see figs 2–7 in Olmi et al., 2010); dorsal side of head swollen; bases of antennae widely spaced and not articulated on contiguous frontal prominences (see figs 6, 7 in Olmi et al., 2010); fore wing with 1M and 2Cu cells not enclosed by pigmented veins; stigmal vein 2r-rs&Rs forming acute angle with pterostigma. **Female:** unknown.

Hosts. Unknown.

Distribution. Mongolia, Transbaikalia.

World species. Genus comprises four fossil species, among which one species is recorded from Lower Cretaceous marl in Bon Tsaagan (Mongolia) (*B. carolianus* Rasnitsyn, 1996) and three species are known from Lower Cretaceous Baissa (Siberia) marl (*B. minimus* Rasnitsyn, 1996; *B. minutus* Olmi, Rasnitsyn and Guglielmino, 2010; *B. parvus* Rasnitsyn, 1975).

Key to the fossil species of *Baissobius* (females unknown)

Males.

1. Pterostigma less than three times as long as broad (see figs 2, 4 in Olmi et al., 2010)..... 2
- Pterostigma more than three times as long as broad (see figs 5–7 in Olmi et al., 2010)..... 3
2. Fore wing with Rs + M vein very long, reaching to over half distance between R cell and distal margin (see fig. 2 in Olmi et al., 2010). . . *B. minimus* Rasnitsyn
- Fore wing with Rs + M vein shorter, not reaching half distance between R cell and distal margin (see fig. 4 in Olmi et al., 2010) *B. minutus* Olmi, Rasnitsyn and Guglielmino
3. Fore wing with stigmal vein 2r-rs&Rs showing an angle between proximal and distal parts (see fig. 5 in Olmi et al., 2010) *B. parvus* Rasnitsyn
- Fore wing with stigmal vein 2r-rs&Rs regularly curved (see figs 6, 7 in Olmi et al., 2010)..... *B. carolianus* Rasnitsyn

Baissobius carolianus Rasnitsyn.

(Habitus in figs 6, 7 in Olmi et al., 2010)

Baissobius carolianus Rasnitsyn, 1996: 186.

Diagnosis. Male (see figs 6, 7 in Olmi et al., 2010): macropterous; fore wing with stigmal vein 2r-rs&Rs regularly curved; pterostigma more than three times as long as broad.

Material examined. Holotype m#, PIN 3559/4523, Bon Tsaagan marl (Mongolia).

Horizon and locality. Aptian (113–125 Ma), Central Mongolia (5–8 km N Bon Tsaagan, Nuur Lake, outcrop 87, bed 8, in Bayanhongor Aimag), Bon-Tsaagan Member of Dzun-Bain Formation.

Description of male holotype (see figs 6, 7 in Olmi et al., 2010). Macropterous; length 3.7 mm. Antenna filiform, slightly geniculate, slender; antennomeres in following proportions: 9:3:7:8:8:7:6:6:5:5:6; length/breadth ratio of antennomere 8: 6:3; 9: 5.5:3; 10: 6:3. Head anteriorly narrowed; eye possibly half as long as head. Pronotum not visible. Notauli complete; minimum distance between notauli longer than antennal segment 2 (7:3). Fore wing with stigmal vein 2r-rs&Rs regularly curved. Length/breadth ratio of pterostigma: 21:5 (4.2). Ratios between body regions: head (27): mesoscutum (15): mesoscutellum (10): metanotum (5): metapectal-propodeal complex (20): metasoma (95): fore wing (100). Legs almost completely invisible (only the left foreleg is partly visible). Maxillary palpus and tibial spurs not visible. **Female:** unknown.

Hosts. Unknown.

Baissobius minimus Rasnitsyn.

(Habitus in figs 3, 4 in Olmi et al., 2010)

Baissobius minimus Rasnitsyn, 1996: 186.

Diagnosis. Male (see figs 3, 4 in Olmi et al., 2010): macropterous; fore wing with Rs + M vein very long; pterostigma less than three times as long as broad.

Material examined. Holotype m#, PIN 4210/1195. Baissa (Siberia).

Horizon and locality. Aptian (113–125 Ma), Siberia (left bank of Vitim River, Western Transbaikalia, 3 km down-stream from the former lodge at Baissa, 45 air km upstream from Romanovka Village), marls of Zaza Formation.

Description of male holotype (see figs 3, 4 in Olmi et al., 2010). Macropterous; length 3.1 mm. Antenna very thick; antennomeres 7–10 in following proportions: 7:6.5:6:11 (rest of antenna not visible); length/breadth ratio of antennomeres 7–10: 7: 7:6; 8: 6.5:6; 9: 6:5; 10: 11:6. Notauli not visible. Fore wing only partly visible. Fore wing with Rs + M vein very long, extending over half-way distance between R cell and distal margin of fore wing. Length/breadth ratio of pterostigma: 12:5 (2.4). Ratios between body regions: head (28): eyes (11): pronotum (2.5): mesoscutum (16): mesoscutellum + metanotum (18): metapectal-propodeal complex (14): metasoma (51). **Female:** unknown.

Hosts. Unknown.

Baissobius minutus Olmi, Rasnitsyn and Guglielmino.

(Habitus in fig. 2 in Olmi et al., 2010)

Baissobius minutus Olmi, Rasnitsyn and Guglielmino, 2010: 23.

Diagnosis. Male (see fig. 2 in Olmi et al., 2010): macropterous; fore wing with Rs + M vein very short; pterostigma less than three times as long as broad.

Material examined. Holotype m#, PIN 4210/1203. Baissa (Siberia).

Horizon and locality. Aptian (113–125 Ma), Siberia (left bank of Vitim River, Western Transbaikalia, 3 km down-stream from the former lodge at Baissa, 45 air km upstream from Romanovka Village), marls of Zaza Formation.

Description of male holotype (see fig. 2 in Olmi et al., 2010). Macropterous; length 1.7 mm. Antennae and head missing. Pronotum not distinctly visible. Notauli present, not distinctly visible, apparently incomplete. Fore wing with 1M and 2Cu cells not enclosed by pigmented veins, with Rs + M vein very short, not reaching half distance between R cell and distal margin of fore wing. Length/breadth ratio of pterostigma: 24:12 (2.0). Ratios between body regions: mesoscutum (14): mesoscutellum (8): metanotum (2): metapectal-propodeal complex (18): metasoma (57): fore wing (70). Legs almost completely invisible (only one hind leg

is partly visible). Maxillary palpus and tibial spurs not visible. **Female:** unknown.

Hosts. Unknown.

Baissobius parvus Rasnitsyn.

(Habitus in fig. 5 in Olmi et al., 2010)

Baissobius parvus Rasnitsyn, 1975: 128.

Diagnosis. Male (see fig. 5 in Olmi et al., 2010): macropterous; fore wing with stigmal vein 2r-rs&Rs showing an angle between proximal and distal parts; pterostigma more than three times as long as broad.

Material examined. Holotype m#, PIN 1989/2597 Baissa (Siberia).

Horizon and locality. Aptian (113–125 Ma), Siberia (left bank of Vitim River, Western Transbaikalia, 3 km down-stream from the former lodge at Baissa, 45 air km upstream from Romanovka Village), marls of Zaza Formation.

Description of male holotype (see fig. 5 in Olmi et al., 2010). Macropterous; length 3.7 mm. Antenna filiform, slightly geniculate, slender; antennomeres in following proportions: 9:3:7:8:8:7:6:6:5:5:6; length/breadth ratio of antennal segment 8th: 6:3; 9th: 5.5:3; 10th: 6:3. Head anteriorly narrowed; eyes possibly half as long as head. Pronotum not visible. Notauli complete; minimum distance between notauli longer than antennal segment 2 (7:3). Fore wing with stigmal vein 2r-rs&Rs showing an angle between proximal and distal parts. Length/breadth ratio of pterostigma: 21:5 (4.2). Ratios between body regions: head (27): mesoscutum (15): mesoscutellum (10): metanotum (5): metapleural-propodeal complex (20): metasoma (95): fore wing (100). Legs almost completely invisible (only the left fore leg is partly visible). Maxillary palpus and tibial spurs not visible.

Female: unknown.

Hosts. Unknown.

Genus *Cretembolemus* Olmi, Rasnitsyn, Brothers and Guglielmino. (Habitus in figs 11–12 in Olmi et al., 2014c)

Cretembolemus Olmi, Rasnitsyn, Brothers and Guglielmino, 2014c: 628.

Type species: *Cretembolemus orapensis* Olmi, Rasnitsyn, Brothers and Guglielmino, 2014c, by monotypy and original designation.

Diagnosis. Female (see figs 11–12 in Olmi et al., 2014c): macropterous. [Head rounded; eye large, oval; palpal formula unknown; scape apparently not articulated on prominent frontal process; toruli apparently at about mid-height of face; pronotum fairly long, anteriorly convex, posterior margin almost straight, with sculpture not discernible; metapleural-propodeal complex with posterolateral angles abrupt, disc apparently with three longitudinal ridges; prepectus apparently fused medially; fore wing with stigmal vein 2r-rs&Rs forming acute angle with pterostigma, ((Rs + M)&M) vein apparently very long, trace of distal region of vein Cu apparently present, first cubital cell (1Cu) broad, 1M and 2Cu cells not visible; tibial spurs not visible.] (Olmi et al., 2014c, pp. 6–7). **Male:** unknown.

Hosts. Unknown.

Distribution. Botswana.

World species. Genus comprises one fossil species from Upper Cretaceous Kimberlitic deposit (Orapa, Botswana) (*C. orapensis* Olmi, Rasnitsyn, Brothers and Guglielmino, 2014c).

Cretembolemus orapensis Olmi, Rasnitsyn, Brothers and Guglielmino.

(Habitus in figs 11–12 in Olmi et al., 2014c)

Cretembolemus orapensis Olmi, Rasnitsyn, Brothers and Guglielmino, 2014c: 630.

Diagnosis. See the above diagnosis of the genus *Cretembolemus*.

Material examined. Holotype f#, ESI (= BPIP)/2/27895 (part) and ESI (= BPIP)/2/27900 (counterpart). In Upper Cretaceous Kimberlitic deposit (Orapa, Botswana).

Horizon and locality. Turonian (about 91 Ma), Orapa, Botswana.

Description of female holotype (see figs 11–12 in Olmi et al., 2014c). Macropterous; length 2.9 mm as preserved. Description in Olmi et al. (2014c). **Male:** unknown.

Hosts. Unknown.

Genus *Embolemopsis* Olmi, Rasnitsyn and Guglielmino.

(Habitus in Fig. 1; see also fig. 1 in Olmi et al., 2010)

Embolemopsis Olmi, Rasnitsyn and Guglielmino, 2010: 22.

Type species: *Embolemopsis baissensis* Olmi, Rasnitsyn and Guglielmino, 2010, by monotypy and original designation.

Diagnosis. Male (Fig. 1; see also fig. 1 in Olmi et al., 2010): macropterous. Dorsal side of head swollen; bases of antennae widely spaced and not articulated on contiguous frontal prominences; antennal toruli touching posterior margin of clypeus; palpal formula 6/3; pronotum not distinctly visible, so that it is not possible to see if it has a median longitudinal furrow; fore wing with three basal cells (C, R, 1Cu) enclosed by pigmented veins, with 1M and 2Cu cells enclosed by pigmented veins; PostabR1 shorter than pterostigma; tibial spurs 1/2/2. **Female:** unknown.

Hosts. Unknown.

Distribution. Siberia (Baissa marl; compression fossil) and Isle of Wight (UK; Wealden amber).

World species. Genus comprises one fossil species from Early Cretaceous Baissa marl (*Ep. baissensis* (Olmi, Rasnitsyn and Guglielmino, 2010)) and one species from Wealden amber (*Ep. maryannae* sp. nov., Olmi, Jarzembowski, Capradossi and Perkovsky).

Key to the fossil species of Embolemopsis (females unknown)

Males.

1. Fore wing with stigmal vein 2r-rs&Rs forming right angle with pterostigma (see fig. 1 in Olmi et al., 2010)..... *Ep. baissensis* Olmi, Rasnitsyn and Guglielmino (from Baissa marl)
- Fore wing with stigmal vein 2r-rs&Rs forming acute angle with pterostigma (Fig. 1)..... *Ep. maryannae* sp. nov., Olmi, Jarzembowski, Capradossi and Perkovsky (from Wealden amber)

Embolemopsis baissensis Olmi, Rasnitsyn and Guglielmino.

(Habitus in fig. 1 in Olmi et al., 2010)

Embolemopsis baissensis Olmi, Rasnitsyn and Guglielmino, 2010: 23.

Diagnosis. Male of *Embolemopsis* (see fig. 1 in Olmi et al., 2010) with bases of antennae widely spaced and not articulated on contiguous frontal prominences; fore wing with stigmal vein 2r-rs&Rs forming right angle with pterostigma; 1M and 2Cu cells enclosed by pigmented veins.

Material examined. Holotype m#, PIN 4210/7095. Baissa (Siberia).

Horizon and locality. Aptian (113–125 Ma), Siberia (left bank of Vitim River, Western Transbaikalia, 3 km down-stream from the former lodge at Baissa, 45 air km upstream from Romanovka Village), marls of Zaza formation.

Description of male holotype (see fig. 1 in Olmi et al., 2010). Macropterous; length 2.6 mm. Dorsal side of head swollen; bases of antennae widely spaced and not articulated on contiguous frontal prominences; palpal formula unknown; pronotum short, not distinctly visible; median longitudinal furrow of pronotum not visible; fore wing with 1M and 2Cu cells enclosed by pigmented veins; stigmal vein 2r-rs&Rs regularly curved, forming right angle with pterostigma, composed of distinct proximal and distal parts; petiole very short; tibial spurs unknown. **Female:** unknown.

Hosts. Unknown.

Embolemopsis maryannae sp. nov., Olmi, Jarzembowski, Capradossi and Perkovsky.

LSID urn:lsid:zoobank.org:act:6E1DCC89-62C9-4573-973A-6CD181536313 (Fig. 1)

Diagnosis. Male with fore wing with cells 1M and 2Cu (Fig. 1A) present; vein Rs + M longer than pterostigma (19:10); vein M long, reaching about half of distance between R cell and distal margin of fore wing; stigmal vein 2r-rs&Rs forming acute angle with pterostigma (Fig. 1A).

Etymology. The species is named in memory of Mrs Mary Ann Mantell (née Woodhouse), 1795–1869, early amateur palaeontologist from Wealden.

Material examined. Holotype m#, NHMUK II 3111 (NHMUK). In Lower Cretaceous Wealden amber, UK.

Horizon and locality. Early Barremian (about 128 Ma, Jarzembowski, 1999; Baranov et al., 2019), plant debris bed above Chilton Chine sandstone, Wessex Formation, SW coast of Isle of Wight, UK.

Description of male holotype (Fig. 1). Macropterous; length 1.8 mm. Black, except antenna, metasoma and legs brown. Antenna setose, composed of 10 antennomeres. Ratio of antennomeres: 7:3:5:4:4:5:5:4:4:6. Head shiny, apparently punctate, unsculptured among punctures. Distance between toruli about same as between toruli and eyes. Occiput concave. Occipital carina complete, laterally not reaching eyes. Lateral ocelli touching occipital carina. Frontal line not visible. POL = 3; OL = 3; OOL = 4; TL = 3; greatest breadth of lateral ocellus: 3. Length of head: 0.3 mm. Length of mesosoma: 0.9 mm. Ratios of mesosoma: 6 (pronotum): 16 (mesoscutum): 8 (mesoscutellum): 2 (metanotum): 9 (metapectal-propodeal complex). Pronotum very short, wedging in the occiput, little visible in dorsal view. Mesoscutum shiny, apparently weakly granulate. Notauli incomplete, reaching about 0.5 × length of mesoscutum. Mesoscutellum shiny, apparently weakly granulate. Metanotum dull, with sculpture not visible. Metapectal-propodeal complex reticulate rugose, with disc longer than propodeal declivity (6:3) in dorsal view. Disc of metapectal-propodeal complex with sides protruding posterolaterally. Mesosternum not visible. Length of fore wing: 1.4 mm. Fore wing hyaline, without dark transverse bands and three basal cells (C, R, 1Cu) enclosed by pigmented veins. Pterostigma distinct, longer than broad (10:4). Stigmal vein (2r-rs&Rs) regularly curved, forming acute angle with pterostigma (Fig. 1A). 2R1 cell open. Metacarp (PostabR1) shorter than pterostigma (5:10). Cells 1M and 2Cu enclosed by pigmented veins less pigmented than veins enclosing C, R and 1Cu cells). Vein Rs + M longer than pterostigma (19:10). Vein M long, reaching about half of distance between R cell and distal margin of fore wing. Length of metasoma: 0.6 mm. Ratio of fore leg: coxa (5): trochanter (6): femur (15): tibia (7): tarsus (15). Ratio of mid leg: coxa (7): trochanter (3): femur (16): tibia (10): tarsus (18). Ratio of hind leg: coxa (10): trochanter (4): femur (16): tibia (16): tarsus (21). Tibial spurs 1/2/2. **Female:** unknown.

Hosts. Unknown.

Remarks. *Ep. maryannae* sp. nov. is the oldest known embolemid wasp. In addition, it is the first hymenopteran described from Wealden amber.

Genus *Embolemus* Westwood.

(Habitus in figs 2–4; see also figs 5–8, 31 in Olmi, 1996)

Embolemus Westwood, 1833: 444.

Type species: *Embolemus ruddii* Westwood, 1833, by monotypy.

Diagnosis. Female (see figs 5, 6, 31 in Olmi, 1996): usually micropterous (see figs 5, 6 in Olmi, 1996), occasionally brachypterous (see fig. 31 in Olmi, 1996). Head with dorsal side almost flat. Maxillary palpus 3- or 5-segmented; labial palpus 2-segmented; third segment of maxillary palpus broadened. Ocelli absent or very reduced. Eyes normal, not reduced. Antenna geniculate; scape much longer than first flagellomere. Pronotum without or with track of median longitudinal furrow. Tibial spurs 1/2/2 (usually both mesotibial spurs easily visible, but in female of *Em. africanus* Risbec, 1957 one of two mesotibial spurs very short and visible only

on microscopic slide). **Male** (Figs 2–4; see also figs 7, 8 in Olmi, 1996): fully winged. Head with dorsal side swollen. Maxillary palpus 4- or 6-segmented; labial palpus 2- or 3-segmented; third segment of maxillary palpus broadened. Face from clypeus to antennal toruli with two subantennal sulci (*sensu* Richards 1977). Ocelli distinct. Antenna not geniculate; scape shorter or slightly longer than first flagellomere. Fore wing usually with C, R and 1Cu cells enclosed by strongly pigmented veins, but 1M cell enclosed by more or less pigmented veins; 2Cu cell usually open or enclosed by slightly pigmented veins; 2R1 cell usually open, rarely closed; media vein (M) always visible and pigmented. Tibial spurs 1/2/2.

Hosts. Nymphs of Cixiidae (Hemiptera: Auchenorrhyncha).

Distribution. Worldwide.

World species. Genus comprises 38 extant published species (unpublished data) and seven fossil published species, among which two species are recorded from Baltic amber (*Em. breviscapus* Brues, 1933; *Em. excitus* Perrichot and Engel, 2011) and five are described here from Kachin (Myanmar) amber. Note that *Embolemus periallus* (Ortega-Blanco, Delclos and Engel, 2011) from Peñacerrada amber (Spain), described from one macropterous female, was transferred to the genus *Ampulicomorpha* by Olmi et al. (2014c).

Remarks. In *Embolemus*, males strongly differ from females, thus the association of opposite sexes based on morphological characters is impossible. Only DNA analysis or rearings can solve the problem of association of the opposite sexes of one species.

Key to the fossil species of *Embolemus*.

Females.

Only the brachypterous female of *Em. excitus* Perrichot and Engel (from Baltic amber) (see figs 1, 2 in Perrichot & Engel, 2011) is known.

Males.

1. Fore wing hyaline, not darkened (Figs 2C, D).....
..... *Em. burmensis* sp. nov. (from Kachin amber)
– Fore wing slightly darkened (Figs 2A, B, 3)..... 2
2. Head with posterior margin very convex (Fig. 4A).....
..... *Em. ohmkuehnlei* sp. nov. (from Kachin amber)
– Head with posterior margin almost rectilinear, not convex (Figs 3A, 4C, D)..... 3
3. Fore wing with 1M and 2Cu cells poorly visible, because surrounded by slightly pigmented veins (Figs 4C, D).....
..... *Em. zherikhini* sp. nov. (from Kachin amber)
– Fore wing with 1M and 2Cu cells distinctly visible (Fig. 3A)..... 4
4. Head with POL much shorter than OOL (2:7) (Fig. 3A); notauli complete, posteriorly separated.....
..... *Em. cretacicus* sp. nov. (from Kachin amber)
– Head with POL slightly shorter than OOL (3:4); notauli incomplete, reaching about 0.5 × length of mesoscutum. . . *Em. antiquus* sp. nov. (from Kachin amber)

Remarks. *Em. breviscapus* Brues, 1933, whose holotype is lost, has not been included in the key, because its original description is unreliable, and no additional specimens are known.

***Embolemus antiquus* sp. nov.**, Perkovsky, Olmi, Müller, Guglielmino and Rasnitsyn.

LSID urn:lsid:zoobank.org:act:04965F37-B7F4-4771-8CD7-CD38A2B4B24C (Figs 2A, B)

Diagnosis. Male of *Embolemus* (Figs 2A, B) with POL slightly shorter than OOL (3:4), notauli incomplete, reaching about 0.5 × length of mesoscutum, fore wing slightly darkened.

Etymology. The name of this species derives from the Latin adjective *antiquus*, meaning “old”, because it’s a very old fossil species.

Material examined. Holotype m#, DAF2901 (DAFS) and 1m# paratype, DAF3001 (DAFS). In Upper Cretaceous Kachin (Myanmar) amber.

Horizon and locality. Lower Cenomanian (98.79 ± 0.62 Ma; Grimaldi et al., 2002 based on insect inclusions; Shi et al., 2012 based on zircon analyses), SW of Tanai City, Hukawng Valley, Tanai Township, Kachin State, Northern Myanmar.

Description of male holotype (Figs 2A, B). Macropterous; length 2.6 mm. Apparently totally black, except antenna and metasoma brown; legs brown-testaceous. Antenna filiform, articulated on two prominent contiguous frontal processes; antennomeres in following proportions: 10:4:15:13:13:10:10:6:8. Head subspheroidal, shiny, apparently unsculptured, with sculpture indistinct; occipital carina not visible; lateral ocelli located behind imaginary straight line joining posterior edges of eyes; POL = 3; OL = 2; OOL = 4; TL = 2; greatest breadth of lateral ocellus as long as POL; eye approximately 0.5 times as long as head (9:17); region of face from clypeus to antennal toruli with two longitudinal and median subparallel sutures; region from anterior ocellus to frontal processes flat, not distinctly visible. Palpal formula apparently 6/3. Mesosoma less than three times as long as head (46:17). Pronotal tubercle reaching tegula. Pronotum, mesoscutum, mesoscutellum and metanotum with sculpture not distinct. Mesoscutum longer than pronotum (13:7). Notauli incomplete, reaching about $0.5 \times$ length of scutum. Mesoscutellum shorter than mesoscutum (6:13), longer than metanotum (6:2). Mesopleuron and metapleuron unsculptured. Metapectal-propodeal complex apparently reticulate rugose, longer than mesoscutum (19:13). Fore wing completely slightly darkened, with distal third missing; 2R1 cell apparently open; Rs vein longer than 2r-rs, not completely visible, because broken; 1M and 2Cu cells only partly bordered by strongly pigmented veins (Fig. 2). Hind wing not visible, because hidden under fore wing. Metasomal petiole much shorter than remaining part of metasoma (1:37) and much shorter than metatrochanter (1:5). Proleg ratio: coxa (9): trochanter (7): femur (25): tibia (20): tarsomere 1 (12): tarsomere 2 (5): tarsomere 3 (4): tarsomere 4 (3): tarsomere 5 (4). Mesoleg ratio: coxa (13): trochanter (5): femur (21): tibia (25): tarsomere 1 (14): tarsomere 2 (7): tarsomere 3 (4): tarsomere 4 (3): tarsomere 5 (4). Metaleg ratio: coxa (15): trochanter (5): femur (27): tibia (34): tarsomere 1 (15): remaining metatarsomeres not distinct. Tibial spurs 1/2/2. Male paratype: same characters as holotype; length 1.8 mm. **Female.** Unknown.

Hosts. Unknown.

***Embolemus breviscapus* Brues.**

(Habitus in Plate 11, fig. 65, in Brues, 1933)

Embolemus breviscapus Brues, 1933: 113.

This species was described on the basis of two male specimens from Baltic amber, deposited in the amber collection of the Albertus University in Königsberg. They are regarded as lost (Olmi, 1996). Because its description is insufficient and unreliable, it is best to regard this species as a *nomen dubium*. It is therefore not treated further here.

***Embolemus burmensis* sp. nov.**, Perkovsky, Olmi, Müller, Guglielmino and Rasnitsyn.

LSID urn:lsid:zoobank.org:act:18552E08-7993-4474-9263-DC58582486E1 (Figs 2C, D)

Diagnosis. Male of *Embolemus* (Figs 2C, D) with POL much shorter than OOL (2.5:6), notauli incomplete, reaching about $0.7 \times$ length of mesoscutum, fore wing hyaline, not darkened.

Etymology. The species is named *burmensis*, because it was found in mid-Cretaceous Burmese amber.

Material examined. Holotype m#, DAF2902 (DAFS) and 4 m#m# paratypes, DAF2903, DAF2904, DAF2905, DAF2906 (DAFS). In Upper Cretaceous Kachin (Myanmar) amber.

Horizon and locality. Lower Cenomanian (98.79 ± 0.62 Ma; Grimaldi et al., 2002 based on insect inclusions; Shi et al., 2012 based on

zircon analyses), SW of Tanai City, Hukawng Valley, Tanai Township, Kachin State, Northern Myanmar.

Description of male holotype (Figs 2C, D). Macropterous; length 2.6 mm. Apparently totally brown, except antennae and legs brown-testaceous. Antenna filiform, articulated on two prominent contiguous frontal processes; antennomeres in following proportions: 11:5:9:10:9:9:8:8:12. Head subspheroidal, shiny, apparently unsculptured, with sculpture indistinct; occipital carina not visible; lateral ocelli located behind imaginary straight line joining posterior edges of eyes; POL = 2.5; OL = 3; OOL = 6; greatest breadth of lateral ocellus as wide as OL; eye approximately 0.5 times as long as head (12:21); region of frons from clypeus to antennal toruli not distinct; region from anterior ocellus to frontal processes flat, not distinctly visible. Palpal formula apparently 6/3. Mesosoma more than twice as long as head (50:21). Pronotal tubercle reaching tegula. Pronotum shorter than mesoscutum (8:15). Mesoscutum dull, alutaceous, much longer than mesoscutellum (15:7). Notauli incomplete, reaching about $0.7 \times$ length of mesoscutum. Mesoscutellum alutaceous, longer than metanotum (7:3). Mesopleuron and metapleuron with sculpture not distinct. Meso-metapleural suture not distinct. Metapectal-propodeal complex completely reticulate rugose, longer than mesoscutum (17:15). Disc of metapectal-propodeal complex longer than propodeal declivity (12:5). Fore wing hyaline, not darkened; 2R1 cell open; Rs vein longer than 2r-rs (17:11); 1M and 2Cu cells only partly bordered by strongly pigmented veins. Hind wing not visible, because hidden under fore wing. Metasomal petiole much shorter than remaining part of metasoma (4:59) and slightly shorter than metatrochanter (4:5). Proleg ratio: coxa (9): trochanter (7): femur (21): tibia (19): tarsomere 1 (11): tarsomere 2 (4): tarsomere 3 (3): tarsomere 4 (2): tarsomere 5 (4). Protrochanter much longer than broad (7:3) (greatest breadth). Mesoleg ratio: coxa (11): trochanter (5): femur (19): tibia (18): tarsomere 1 (11): tarsomere 2 (5): tarsomere 3 (4): tarsomere 4 (3): tarsomere 5 (4). Metaleg ratio: coxa (15): trochanter (5): femur (34): tibia (25): tarsomere 1 (16): tarsomere 2 (7): tarsomere 3 (5): tarsomere 4 (4): tarsomere 5 (4). Tibial spurs 1/2/2. Paratypes: 4m#m#, same characters as holotype, 1.6–1.9 mm. **Female.** Unknown.

Hosts. Unknown.

Remarks. The male of *Ampulicomorpha janzeni*, recorded from Kachin amber, can be confused with *Embolemus burmensis*, from the same deposit, having both fore wings hyaline, not darkened. However, the two species can be distinguished easily by the OOL/POL ratio: OOL twice as long as POL in *A. janzeni*, more than three times as long as POL in *Em. burmensis*.

***Embolemus cretacticus* sp. nov.**, Perkovsky, Olmi, Müller, Guglielmino and Rasnitsyn.

LSID urn:lsid:zoobank.org:act:5A07269E-26F6-4BF6-972C-7D3D690F74F0 (Fig. 3)

Diagnosis. Male of *Embolemus* (Fig. 3) with POL much shorter than OOL (2:7), notauli complete, posteriorly separated, fore wing slightly darkened.

Etymology. The species is named *cretacticus*, because it was found in Upper Cretaceous Burmese amber.

Material examined. Holotype m#, DAF2907 (DAFS) and 3 m#m# paratypes, DAF2908 (two males in the same piece), DAF2909 (DAFS). In Upper Cretaceous Kachin (Myanmar) amber.

Horizon and locality. Lower Cenomanian (98.79 ± 0.62 Ma; Grimaldi et al., 2002 based on insect inclusions; Shi et al., 2012 based on zircon analyses), SW of Tanai City, Hukawng Valley, Tanai Township, Kachin State, Northern Myanmar.

Description of male holotype (Fig. 3). Macropterous; length 2.6 mm. Apparently totally black, except antenna and legs brown-

testaceous. Antenna filiform, articulated on two prominent contiguous frontal processes; antennomeres in following proportions: 8:5:14:14:12:11:10:10:9:12. Head subspheroidal, shiny, apparently unsetose, with sculpture indistinct; occipital carina not visible; lateral ocelli located behind imaginary straight line joining posterior edges of eyes; POL = 2; OL = 3; OOL = 7; TL = 5; greatest breadth of lateral ocellus wider than POL (4:2); eye approximately 0.5 times as long as head (12:25); region of frons from clypeus to antennal toruli not distinct; region from anterior ocellus to frontal processes flat, not distinctly visible. Palpal formula apparently 6/3. Mesosoma approximately twice as long as head (53:25). Pronotal tubercle reaching tegula. Pronotum, mesoscutum, mesoscutellum and metanotum with sculpture not distinct. Notauli not particularly distinct, apparently complete, posteriorly separated. Mesopleuron and metapleuron with sculpture not distinct. Meso-metapleural suture not distinct. Metapectal-propodeal complex apparently reticulate rugose. Fore wing completely slightly darkened; 2R1 cell open; Rs vein longer than 2r-rs (30:12); 1M and 2Cu cells only partly bordered by strongly pigmented veins (Fig. 22). Hind wing partly visible, because partly hidden under fore wing. Metasomal petiole much shorter than remaining part of metasoma (3:50) and much shorter than metatrochanter (3:6). Proleg ratio: coxa (9): trochanter (10): femur (28): tibia (22): tarsomere 1 (14): tarsomere 2 (5): tarsomere 3 (4): tarsomere 4 (4): tarsomere 5 (6). Mesoleg ratio: coxa (15): trochanter (8): femur (25): tibia (22): tarsomere 1 (10): tarsomere 2 (5): rest of mesotarsus missing. Metaleg ratio: coxa (17): trochanter (6): femur (33): tibia (34): tarsomere 1 (17): tarsomere 2 (8): tarsomere 3 (6): tarsomere 4 (5): tarsomere 5 (6). Tibial spurs 1/2/2. Paratypes: 3m#m#, same characters as holotype, 1.9–2.2 mm. **Female.** Unknown.

Hosts. Unknown.

Embolemus excitus Perrichot and Engel.

(Habitus in figs 1, 2 in Perrichot & Engel, 2011)

Embolemus excitus Perrichot and Engel, 2011: 2.

Diagnosis. Brachypterous female of *Embolemus* (see figs 1, 2 in Perrichot & Engel, 2011) with POL = OL, notauli absent, disc of metapectal-propodeal complex rugose, with two subparallel longitudinal keels from posterior to anterior margin.

Material examined. Holotype f#, SMF-Be-806. In Eocene Baltic amber.

Horizon and locality. Priabonian (35–38 Ma). Northern and Eastern Europe.

Description of female holotype (see figs 1, 2 in Perrichot & Engel, 2011). Brachypterous; length 4.2 mm (4.9 mm according to the original description). Colour apparently testaceous. Antenna geniculate, filiform, shorter than head + mesosoma + metasoma; antennomeres in following proportions: 38:5:15:17:13:13:12:12:10:15. Head slightly pyriform (length/breadth ratio: 28:25), alutaceous, apparently unsetose, with dorsal side slightly convex; anterior region of dorsal side slightly tapering; occipital carina complete; ocelli present (not evident, according to the original description); POL = 5; OL = 5; eye very small, approximately 0.18 as long as head (5:28); convergent longitudinal and median sutures usually present in *Embolemus* species in region of face from clypeus to antennal toruli not distinct. Maxillary palpus apparently 6-segmented (5-segmented, according to the original description), with third segment broadened. Labial palpus not visible (2 palpomeres, according to the original description). Pronotum dull, alutaceous, apparently unsetose, without lateral carinas; anterior collar not visible, because hidden under posterior region of head; disc long, apparently without median longitudinal groove; pronotal tubercle reaching tegula. Mesoscutum large, subrectangular, alutaceous, without traces of median furrow. Notauli apparently absent. Parapsidal lines short, present near lateral margins of scutum.

Mesoscutellum ovoidal, alutaceous. Metanotum very short and transverse. Meso-metapleural suture complete. Mesopleuron and metapleuron dull, alutaceous, not rugose. Metapectal-propodeal complex dull; disc rugose, with two subparallel longitudinal keels from posterior to anterior margins, with spiracles normally prominent, and two lateral pointed apophyses on sides of propodeal declivity, with median depression situated at border between disc and propodeal declivity. Propodeal declivity dull, strongly reticulate rugose, with three longitudinal keels. Fore wing short, much longer than tegula (6:58), reaching middle region of first metasomal tergite. Fore wing with pterostigma, stigmal vein, costal, radial and first cubital cells; veins barely pigmented; stigmal vein 2r-rs&Rs apparently reaching margin of fore wing. Hind wing absent. Metasomal petiole short. Tibial spurs 1/2/2. **Male:** unknown.

Hosts. Unknown.

Remarks. It is possible that *Em. excitus* is the opposite sex of *Em. breviscapus*.

Embolemus ohmkühnlei sp. nov., Perkovsky, Olmi, Müller, Guglielmino and Rasnitsyn.

LSID urn:lsid:zoobank.org:act:096219B3-F806-46BC-9897-AF31998F7384 (Figs 4A, B)

Diagnosis. Male of *Embolemus* (Figs 4A, B) with head ovoidal, characterized by posterior margin very convex; fore wing slightly darkened (Fig. 4A).

Etymology. The species is named after Dr. Christoph Öhm-Kühnle, from Herrenberg (Germany), who donated the holotype of the new species to PIN to his named collection #5620.

Material examined. Holotype m#, PIN5620/87 (PIN). In Upper Cretaceous Kachin (Myanmar) amber.

Horizon and locality. Lower Cenomanian (98.79 ± 0.62 Ma; Grimaldi et al., 2002 based on insect inclusions; Shi et al., 2012 based on zircon analyses), SW of Tanai City, Hukawng Valley, Tanai Township, Kachin State, Northern Myanmar.

Description of male holotype (Figs 4A, B). Macropterous; length 2.5 mm. Apparently brown, except antenna and legs brown-testaceous. Antenna filiform, articulated on two prominent contiguous frontal processes; antennomeres in following proportions: 12:4:12:10:9:9:8:7:5:7. Head ovoidal, shiny, apparently unsetose, with sculpture indistinct, apparently partly crushed; occipital carina not visible; lateral ocelli located slightly behind imaginary straight line joining posterior edges of eyes; lateral ocellus apparently with long peduncle connecting it to vertex (shape maybe caused by crushing); POL = 2; OL = 2; OOL = 5; TL = 7; greatest breadth of lateral ocellus not measurable, because of crushing; eye approximately 0.5 times as long as head (11:20); region of frons from clypeus to antennal toruli not distinct; region from anterior ocellus to frontal processes crushed, with sculpture not distinct. Palpal formula apparently 6/3. Mesosoma approximately twice as long as head (44:20). Mesosoma longer than metasoma (44:36). Pronotal tubercle not visible because prothorax partly crushed. Pronotum shorter than mesoscutum (8:13), with sculpture not distinct. Mesoscutum apparently granulate. Notauli not completely distinct, because mesoscutum crushed, apparently reaching 0.5 × length of mesoscutum. Mesoscutellum and metanotum with sculpture not distinct. Mesopleuron and metapleuron with sculpture not distinct. Meso-metapleural suture not distinct. Metapectal-propodeal complex apparently reticulate rugose. Fore wing completely slightly darkened; 2R1 cell open; Rs vein longer than 2r-rs (22:5); 1M and 2Cu cells only partly bordered by pigmented veins (Figs 4A, B) (just a hint of Anal (A) and Cubital (Cu) veins present). Hind wing not visible, because hidden under fore wing. Metasomal petiole very short, not very distinct. Proleg ratio: coxa (9): trochanter (4): femur (22): tibia (15): tarsomere 1

(10): tarsomere 2 (5): tarsomere 3 (3): tarsomere 4 (3): tarsomere 5 (3). Mesoleg ratio: coxa (10): trochanter (4): femur (18): tibia (14): tarsomere 1 (12): tarsomere 2 (5): tarsomere 3 (4): tarsomere 4 (3): tarsomere 5 (4). Metaleg ratio: coxa (10): trochanter (4): femur (24): tibia (20): tarsomere 1 (17): tarsomere 2 (6): tarsomere 3 (5): tarsomere 4 (3): tarsomere 5 (4). Tibial spurs 1/2/2. **Female.** Unknown. **Hosts.** Unknown.

Embolemus zherikhini sp. nov., Perkovsky, Olmi, Müller, Guglielmino and Rasnitsyn.

LSID urn:lsid:zoobank.org:act:023C04F9-4602-4218-844E-88870697BED6 (Figs 4C, D)

Diagnosis. Male of *Embolemus* (Figs 4C, D) with posterior margin of head almost rectilinear, not convex; fore wing slightly darkened, with 1M and 2Cu cells little visible because surrounded by poorly pigmented veins.

Etymology. The species is named after Dr. Vladimir V. Zherikhin, the famous Russian palaeontologist and evolutionary biologist.

Material examined. Holotype m#, PIN5620/88 (PIN, donated by Dr. Christoph Öhm-Kühnle). In Upper Cretaceous Kachin (Myanmar) amber.

Horizon and locality. Lower Cenomanian (98.79 ± 0.62 Ma; Grimaldi et al., 2002 based on insect inclusions; Shi et al., 2012 based on zircon analyses), SW of Tanai City, Hukawng Valley, Tanai Township, Kachin State, Northern Myanmar.

Description of male holotype (Figs 4C, D). Macropterous; length 2.5 mm. Apparently brown, except antennae and legs brown-testaceous. Antenna filiform, articulated on two prominent contiguous frontal processes; antennomeres in following proportions: 10:4:12:11:10:10:10:8:8:10. Head subspheroidal, shiny, apparently unisetose, with sculpture indistinct; occipital carina not visible; ocelli not distinct; region of frons from clypeus to antennal toruli not distinct; region from anterior ocellus to frontal processes not distinct. Palpal formula apparently 6/3. Mesosoma approximately three times as long as head (50:15). Mesosoma longer than metasoma (50:37). Pronotal tubercle not reaching tegula. Pronotum shorter than mesoscutum (12:15), with sculpture not distinct. Mesoscutum apparently granulate. Notauli not completely distinct, apparently reaching 0.5 × length of mesoscutum. Mesoscutellum and metanotum with sculpture not distinct. Mesopleuron and metapleuron with sculpture not distinct. Meso-metapleural suture not distinct. Metapetal-propodeal complex apparently reticulate rugose. Fore wing completely slightly darkened; 2R1 cell closed; Rs vein longer than 2r-rs (19:8); 1M and 2Cu cells only partly bordered by little pigmented veins. Hind wing not visible, because hidden under fore wing. Metasomal petiole very short, not very distinct. Proleg ratio: coxa (10): trochanter (5): femur (27): tibia (19): tarsomere 1 (14): tarsomere 2 (6): tarsomere 3 (5): tarsomeres 4 and 5 not distinct. Mesoleg ratio: coxa (10): trochanter (6): femur (19): tibia (19): tarsomere 1 (12): tarsomere 2 (6): tarsomere 3 (4): tarsomere 4 (3): tarsomere 5 (3). Metaleg ratio: coxa (13): trochanter (6): femur (24): tibia (30): tarsomere 1 (15): tarsomere 2 (7): tarsomere 3 (6): tarsomere 4 (4): tarsomere 5 (5). Tibial spurs 1/2/2. **Female.** Unknown.

Hosts. Unknown.

Genus *Ponomarenkoa* Olmi.
(Habitus in Figs 5, 6)

Laberites N. Ponomarenko, 1988: 107 (type species not designated, not available according to article 13.3 of ICZN, 1999).

Ponomarenkoa Olmi, 2010: 31 (new name for *Laberites* N. Ponomarenko, 1988)

Type species: *Ponomarenkoa polonica* (N. Ponomarenko, 1988) (= *Laberites polonicus* N. Ponomarenko, 1988), by original designation.

Diagnosis. Male (Figs 5, 6): macropterous. Dorsal side of head swollen; bases of antennae widely spaced and not articulated on contiguous frontal prominences; antennal toruli touching posterior margin of clypeus; palpal formula 6/3; pronotum not distinctly visible, so that it is not possible to see if it has a median longitudinal furrow; fore wing with three basal cells (C, R, 1Cu) enclosed by pigmented veins, with 1M and 2Cu cells enclosed by pigmented veins; PostabR1 shorter than pterostigma; tibial spurs 1/2/2. **Female:** unknown.

Hosts. Unknown.

Distribution. Baltic and Burmese amber.

World species. Genus comprises three species, one from Baltic and two from Burmese amber.

Remarks. Olmi (1991) described the new subfamily Laberitinae, based on *Laberites* N. Ponomarenko, 1988, and attributed it to the family Dryinidae (Hymenoptera, Chrysidoidea). At description time, this genus included two species, *L. polonicus* N. Ponomarenko, 1988 (from Baltic amber) and *L. antiquus* (N. Ponomarenko, 1981) (from Taimyr amber). N. Ponomarenko, however, did not really want to describe a new genus; for this reason, she did not designate a type species. N. Ponomarenko in fact simply used a collective name to include the two above species considered of uncertain generic position (A. Ponomarenko pers. comm.). Olmi (2010), after the separation of *L. antiquus*, attributing it to the genus *Dryinus* Latreille, 1804, abandoned a “collective” group concept for *L. polonicus* and proposed a formal genus name, *Ponomarenkoa* Olmi, 2010, and new subfamily Ponomarenkoinae for it. However, now the status of *Ponomarenkoa* has to be changed, following a re-examination of the holotype of *P. polonica*. This specimen clearly shows a tibial spur formula 1/2/2 that is typical of Embolemidae (in Dryinidae the mesotibia never has two spurs). In addition, the M vein is very long and 1M and 2Cu cells are enclosed by pigmented veins, all characters not found in Dryinidae, but common in Embolemidae. For the above reasons, the genus *Ponomarenkoa* is here attributed to Embolemidae.

Key to the fossil species of *Ponomarenkoa* (females unknown)

Males.

- 1 Head with POL much longer than OPL.....
..... *P. burmensis* sp. nov. (from Kachin amber)
- Head with POL about as long as, or shorter than OPL..... 2
- 2 Head with POL about as long as OPL.....
..... *P. ellenbergeri* Olmi, Xu and He (from Kachin amber)
- Head with POL shorter than OPL.....
..... *P. polonica* (N. Ponomarenko) (from Baltic amber)

Ponomarenkoa burmensis sp. nov., Perkovsky, Olmi, Müller, Guglielmino and Rasnitsyn.

LSID urn:lsid:zoobank.org:act:98A8F7FA-7FC7-433C-A11E-3FDE150B377C (Habitus in Fig. 5A, B)

Diagnosis. Male of *Ponomarenkoa* (Fig. 5A, B) with POL much longer than OPL; fore wing with stigmal vein 2r-rs&Rs forming acute angle with pterostigma (Fig. 5A, B).

Etymology. This species is named after Burma (= Myanmar), where the species was collected.

Material examined. Holotype m#, DAF2800 (DAFS). In Upper Cretaceous Kachin (Myanmar) amber.

Horizon and locality. Lower Cenomanian (98.79 ± 0.62 Ma; Grimaldi et al., 2002 based on insect inclusions; Shi et al., 2012 based on zircon analyses), SW of Tanai City, Hukawng Valley, Tanai Township, Kachin State, Northern Myanmar.

Description of male holotype (Fig. 5A, B). Macropterous; length 2.0 mm. Fore wing slightly shorter than mesosoma + metasoma. Length of mesosoma + metasoma: 1.6 mm. Colour brown, except scape, pedicel and legs testaceous. Antenna composed of ten antennomeres, filiform, about three times as long as head (45:14).

Antennal setae much shorter than breadth of antennomeres. Antennomeres in following proportions: 5:5:6:6:6:6:5:5:5:7. Head shiny, swollen, apparently unsculptured. Clypeus not visible. Mandible not completely visible, one of teeth very long and sharp. Eye normally protruding, apparently bare. Occipital carina complete. Temple distinct, much shorter than POL (2:6). POL = 6; OL not visible; OOL = 4; OPL = 4; TL = 2; greatest breadth of lateral ocellus less than OOL (3:4); frontal line not visible. Propleura very long, forming “neck” between head and pronotum (as in *Scolebythidae*), deeply inserted in occiput. Maxillary and labial palpus not visible. Pronotum much shorter than head (7:14) and mesoscutum (7:11); pronotal tubercle reaching tegula. Mesoscutum apparently bare and unsculptured. Notauli complete, posteriorly separated; minimum distance between notauli approximately as long as greatest breadth of lateral ocelli. Mesoscutellum apparently unsculptured, shorter than mesoscutum (8:11). Metanotum shorter than mesoscutellum (2:8), apparently unsculptured. Metapectal-propodeal complex not clearly distinct, apparently rugose. Fore wing hyaline, without dark transverse bands, with normal venation of *Ponomarenkoa* species, with three basal cells (C, R, 1Cu) clearly enclosed by pigmented veins; 1M and 2Cu cells enclosed by pigmented veins; pterostigma narrow, much longer than broad (17:4); 2R1 cell open; distal part (Rs) of 2r-rs&Rs vein much longer than proximal part (2r-rs) (14:9); distal part (Rs) of 2r-rs&Rs vein not S-shaped; stigmal vein 2r-rs&Rs forming acute angle with pterostigma. Metasomal petiole distinct, much shorter than metapectal-propodeal complex (1:10). Proleg ratio: 7 (coxa): 3 (trochanter): 15 (femur): 13 (tibia): 9 (tarsomere 1): 3 (tarsomere 2): 2 (tarsomere 3): 2 (tarsomere 4): 4 (tarsomere 5). Mesoleg ratio: 7 (coxa): 3 (trochanter): 14 (femur): 16 (tibia): 6 (tarsomere 1): 4 (tarsomere 2): 2 (tarsomere 3): 2 (tarsomere 4): 3 (tarsomere 5). Metaleg ratio: 10 (coxa): 6 (trochanter): 21 (femur): 23 (tibia): 11 (tarsomere 1): 4 (tarsomere 2): 3.5 (tarsomere 3): 2 (tarsomere 4): 3 (tarsomere 5). Tibial spurs 1/2/2. **Female.** Unknown. **Hosts.** Unknown.

Ponomarenkoa ellenbergeri Olmi, Xu and He.

(Habitus in plate 137 in Xu et al., 2013)

Ponomarenkoa ellenbergeri Olmi, Xu and He, in Xu, Olmi and He, 2013: 434.

Diagnosis. Male of *Ponomarenkoa* (see plate 137 in Xu et al., 2013) with POL about as long as OPL; fore wing with stigmal vein 2r-rs&Rs forming acute angle with pterostigma.

Material examined. Holotype m#, SMNS BU-108 (SMNS). In Upper Cretaceous Kachin (Myanmar) amber. Paratype: same locality, label as holotype, 1m#, DAF1854 (DAFS).

Horizon and locality. Lower Cenomanian (98.79 ± 0.62 Ma; Grimaldi et al., 2002 based on insect inclusions; Shi et al., 2012 based on zircon analyses), SW of Tanai City, Hukawng Valley, Tanai Township, Kachin State, Northern Myanmar.

Description of male (see plate 137 in Xu et al., 2013). Macropterous; length 2.7–2.8 mm (holotype 2.7 mm). Fore wing shorter than mesosoma + metasoma. Length of mesosoma + metasoma: 2.4 mm. Colour brown. Antenna composed of ten antennomeres, filiform, about five times as long as head (55:11). Antennal setae very short, much shorter than breadth of antennomeres. Antennomeres in following proportions: 6:5:6:6:6:6:5:5:5:7 (holotype); 5:5.5:6:5:5:6:6:6:5:5:7 (paratype). Head shiny, smooth, apparently unsculptured. Clypeus not visible. Mandible with teeth not completely visible, one of teeth very long and sharp. Eye normally protruding, apparently bare. Occipital carina complete. Temple distinct, very short. POL = 3; OL = 2; OOL = 5; OPL = 3; TL = 1; greatest breadth of lateral ocellus as wide as OL; frontal line not visible. Palpal formula 6/3. Propleura very long, forming “neck”

between head and pronotum, deeply inserted in occiput. Pronotum much shorter than head (3:18) and mesoscutum (3:14); pronotal tubercle reaching tegula. Mesoscutum apparently bare, apparently unsculptured. Notauli complete, posteriorly separated; minimum distance between notauli approximately as great as greatest breadth of lateral ocelli. Mesoscutellum apparently unsculptured, shorter than mesoscutum (8:14). Metanotum shorter than mesoscutellum (3:8), apparently unsculptured. Metapectal-propodeal complex not clearly distinct, apparently rugose. Fore wing hyaline, without dark transverse bands, with three basal cells (C, R, 1Cu) clearly enclosed by pigmented veins. 1M and 2Cu cells enclosed by pigmented veins. Pterostigma narrow, much longer than broad (15:3); 2R1 cell closed; distal part (Rs) of 2r-rs&Rs vein much longer than proximal part (2r-rs) (21:9); distal part (Rs) of 2r-rs&Rs vein not S-shaped; stigmal vein 2r-rs&Rs forming acute angle with pterostigma. Metasomal petiole distinct, much shorter than metapectal-propodeal complex (4:10). Proleg ratio: 10 (coxa): 7 (trochanter): 14 (femur): 10 (tibia): 10 (tarsomere 1): 9 (remaining tarsomeres). Mesoleg ratio: 7 (coxa): 4 (trochanter): 16 (femur): 12 (tibia): 20 (tarsus). Metaleg ratio: 12 (coxa): 5 (trochanter): 20 (femur): 20 (tibia): 23 (tarsus). Tibial spurs 1/2/2. **Female.** Unknown.

Hosts. Unknown.

Ponomarenkoa polonica (N. Ponomarenko)

(Habitus in Figs 5C, 6)

Laberites polonicus N. Ponomarenko, 1988: 107.

Ponomarenkoa polonica (N. Ponomarenko): Olmi, 2010: 31.

Diagnosis. Macropterous male of *Ponomarenkoa* (Figs 5C, 6) with POL shorter than OPL; fore wing with stigmal vein 2r-rs&Rs forming acute angle with pterostigma.

Material examined. Holotype m#, 8736 (PAS MZ) from Kaliningrad Region. In Eocene Baltic amber.

Horizon and locality. Priabonian (35–38 Ma). Northern Europe.

Description of male holotype (Figs 5C, 6). Macropterous; length 4.7 mm. Fore wing longer than body. Length of body without wings: 3.5 mm. Colour not distinctly visible, apparently black, except ventral side of antennae and part of legs apparently lighter. Antenna composed of ten antennomeres, filiform, more than twice as long as head: 108:48 (head measured in dorsal view from occipital carina behind ocelli to distal apex of mandibles). Antennal setae very short, much shorter than breadth of antennomeres. Antennomeres in following proportions: 10:6:13:13:13:12:10:10:9:12. Antennal toruli apparently touching margins of clypeus. Distance between antennal toruli apparently like that between eyes and antennal toruli. Head apparently granulate. Clypeus with anterior margin rounded, not bidentate. Mandible with teeth not visible. Eye normally protruding, apparently bare. Malar space with furrow joining lower corner of eye to base of mandible. Occipital carina complete. Temple distinct, prominent. POL = 7; OL = 4; OOL = 7; OPL = 8; TL = 10; greatest breadth of lateral ocellus as wide as OL; frontal line apparently absent. Palpus not completely distinct. Pronotum short, granulate, much shorter than head (7:48), much shorter than mesoscutum (7:30); pronotal tubercle reaching tegula. Mesoscutum apparently bare, with posterior surface apparently punctate, unsculptured among punctures, and anterior half rugose. Notauli complete, posteriorly separated; minimum distance between notauli approximately as great as greatest breadth of lateral ocellus. Mesoscutellum apparently punctate, unsculptured among punctures, shorter than mesoscutum (14:30). Metanotum shorter than mesoscutellum (5:14), apparently as sculptured as mesoscutum. Metapectal-propodeal complex not distinct through amber, because of amber thickness and because

concealed under wings. Fore wing apparently hyaline, without dark transverse bands, with usual three basal cells (C, R, 1Cu) clearly enclosed by pigmented veins. 1M and 2Cu cells enclosed by pigmented veins. Pterostigma narrow, much longer than broad (37:8); 2R1 cell open; distal part (Rs) of 2r-rs&Rs vein much longer than proximal part (2r-rs) (28:11); 2r-rs&Rs vein reaching margin of fore wing with distal part less thick than rest of vein; distal part (Rs) of 2r-rs&Rs vein slightly S-shaped; stigmal vein 2r-rs&Rs forming acute angle with pterostigma (Figs 5C, 6); M vein very long almost reaching fore wing margin. Metasoma without distinct petiole. Proleg ratio: 10 (coxa): 10 (trochanter): 33 (femur): 20 (tibia): 17 (tarsal segment 1): 5 (tarsal segment 2): 5 (tarsal segment 3): 5 (tarsal segment 4): 5 (tarsal segment 5). Mesoleg ratio: 14 (coxa): 8 (trochanter): 35 (femur): 30 (tibia): 19 (tarsal segment 1): 9 (tarsal segment 2): 8 (tarsal segment 3): 5 (tarsal segment 4): 10 (tarsal segment 5). Metaleg ratio: 19 (coxa): 16 (trochanter): 35 (femur): 33 (tibia): 13 (tarsal segment 1): 11 (tarsal segment 2): 9 (tarsal segment 3): 5 (tarsal segment 4): 11 (tarsal segment 5). Tibial spurs 1/2/2. **Female.** Unknown.

Hosts. Unknown.

4. Discussion

Embolemidae can be divided morphologically into the following three groups: the first group includes all species with the antennae of both sexes articulated on two contiguous frontal prominences situated far from the clypeus (Fig. 3; see figs 1–8 in Olmi, 1996) (this character is considered a synapomorphy (Olmi et al., 2014c) present in all extant and fossil Embolemidae belonging to the genera *Embolemus*, *Ampulicomorpha* and *Trogloembolemus* (see Table 1)); the second group includes species with the bases of the antennae widely spaced and not articulated on contiguous frontal prominences (Figs 5, 6) (this character is considered a plesiomorphy (Olmi et al., 2014c) present only in compression fossils belonging to the genus *Baissobius* and in amber and compression fossils of *Embolemopsis* and *Ponomarenkoa*); the third group includes the genus *Cretembolemus*, with one compression fossil species from Botswana (Upper Cretaceous, Turonian, 91 Ma): *C. orapensis* (see figs 11, 12 in Olmi et al., 2014c) (this genus cannot be included in the previous two groups because apparently the frons has no antenniferous processes (plesiomorphy), but the bases of the antennae are quite close (although the bad condition of the fossil does not provide certainty about these characters)).

The characters of the above three groups show not only that the plesiomorphic lack of antenniferous processes is older than their apomorphic presence, but also that the apomorphic state was present in the Cretaceous and the plesiomorphic state was lost relatively soon thereafter (Olmi et al., 2014c). We are reluctant to consider subfamilies for the above three groups for the following reasons: the third group (*Cretembolemus*) is based on a fossil in too “poor” condition to be sure about its morphological characters; the second group is based only on males (we prefer to wait for the discovery of the opposite sex before a discussion on superspecific characters; the males are distinctly characterized, but lack synapomorphies, and the resulted subfamily should be explicitly paraphyletic).

The biology of the extant species of Embolemidae has to be considered insufficiently known mainly because the number of species studied from a biological point of view is too small. For the moment, we know that *Ampulicomorpha* species parasitize nymphs of Achilidae feeding on fungi and living in rotten logs (Bridwell, 1958; Wharton, 1989; Olmi, 1996; Guglielmino and Bückle, 2013;

Olmi et al., 2014c) and the hosts of *Embolemus* species are nymphs of Cixiidae feeding on roots and living in the soil (Varrone and Olmi, 2012; Olmi et al., 2014c). The hosts of *Trogloembolemus* are unknown, although it is supposed that they are nymphs of planthoppers living in caves or in deep soil and rock interstices (Olmi et al., 2014b; Mita and Olmi, 2018). Note that all known hosts of Embolemidae are Fulgoromorpha. In the species of Dryinidae parasitizing Fulgoromorpha, antennae of females usually have special structures, named ADOs, that might mediate the antennal responses to vibratory stimuli. In Embolemidae, ADOs are absent, not only in extant, but also in fossil species, indicating a very old separation between the evolutionary lines of Dryinidae and Embolemidae, considered sister families in all phylogenetic analyses (Carpenter, 1999; Branstetter et al., 2017). ADOs are in fact absent in the oldest known fossil female of Embolemidae (*Ampulicomorpha perialla* from Peñacerrada amber; 105 Ma), but are present in the oldest known fossil females of Dryinidae parasitizing Fulgoromorpha (*Dryinus* and *Hybristodryinus* species from Kachin amber; about 99 Ma) (Perkovsky et al., 2019; Martynova et al., 2020).

The above biological separation between *Ampulicomorpha* and *Embolemus* explains why we continue to consider these two genera separate in spite of the difficulties to distinguish the males morphologically. As in Dryinidae, female morphology of Embolemidae experienced deeper changes due to course of evolution than the male one. Females of *Embolemus* are micropterous or brachypterous; they can easily enter the soil to parasitize nymphs of Cixiidae feeding on roots (the presence of complete wings would be an obstacle), probably following ants feeding on the honey-dew produced by the cixiid nymphs (Van Achtenberg and Van Kats, 2000; Holzinger, 2009; Lőrinczi, 2012). In contrast, females of *Ampulicomorpha* are macropterous; they have difficulties in entering the soil, but can easily enter the broad internal spaces of rotten logs, where they parasitize nymphs of Achilidae feeding on fungi; such colonies of Achilidae are usually not attended by ants. In contrast, males of *Embolemus* and *Ampulicomorpha* are very similar. They are always macropterous and fly to find the opposite sex. In the genus *Embolemus*, micropterous and brachypterous females emerge from the soil for copulation and walk to find new host colonies. Also in the genus *Ampulicomorpha*, macropterous females emerge from rotten logs for copulation and to find new hosts, when the wood conditions become less favourable for Achilidae, which need logs with fungus and the correct degree of rottenness.

In the sister family, Dryinidae, no extant species have been found to parasitize nymphs or adults of Achilidae (Guglielmino et al., 2013), but we know an adult of *Protepiptera kaweckii* Usinger, 1939 (Achilidae: Achilini) parasitized by an unknown species of dryinid wasps in Baltic amber (**new record**; Fig. 7; in PIN (catalogue number 964/1326); host identified by Dmitry Shcherbakov). The shape and the brown colour of the two thylacia present on this specimen indicate that they hosted dryinid larvae (thylacia formed by embolemids are different, being white and smooth (see fig. 13 in Olmi et al., 2013)). Achilids were common and diverse in Baltic amber (Brysz and Szewdo, 2018) and big extinct dryinids, such as species of *Harpactosphacion* Haupt, 1944, were adapted to the new hosts. *P. kaweckii* is the commonest Baltic achilid with tegmen length 6.3–8.0 mm and only such big dryinids as *Harpactosphacion* could capture it. With the switch to climatic seasonality after the Priabonian both Baltic amber Achilini (Emeljanov and Shcherbakov, 2009) and their parasitoids appear to become extinct. *P. kaweckii* is reported here for the first time from Klesov (Rovno amber) (**new record**; identified by Dmitry Shcherbakov); if *Harpactosphacion* should be found in Rovno amber as well, this record would support our hypothesis that *P. kaweckii* should be a possible host of *Harpactosphacion*.

In contrast to Achilidae, extant adults of Cixiidae can be parasitized by species of *Dryinus* Latreille (Olmi et al., 2014c). No dryinids are known to parasitize nymphs of Cixiidae feeding on roots in the soil; apparently this is a specialization of *Embolemus* species.

Previously, the only embolemid wasp found in Burmese (Kachin) amber was the aforementioned *Ampulicomorpha janzeni*, known from both macropterous sexes. In the present paper, we add five new species of *Embolemus* based on macropterous males (*Em. antiquus* sp. nov., *Em. burmensis* sp. nov., *Em. cretacicus* sp. nov., *Em. ohmkuhnlei* sp. nov., *Em. zherikhini* sp. nov.). The biology of fossil Embolemidae is unknown. If we imagine that the hosts and biology of the species living in Burmese amber forests were the same as the extant embolemids, we can conclude that the discovery of males of *Embolemus* shows that, probably in the same environment and at the same time, there were micropterous or brachypterous females, possibly with the same hosts. Of course females of *Embolemus* not only do not fly, but they walk on/in the soil, so that there is little chance to find them in amber pieces.

Achilidae and Cixiidae are present in Burmese amber (Szwedo, 2002; Brysz and Szwedo, 2018; Ross, 2019). However, both families are much older. The first true Cixiidae are recorded from the Lower Cretaceous (in the Weald Clay Formation (England) (Ross and Cook, 1995)), Barremian, 125.5–130 Ma (Fennah, 1987; Rasnitsyn et al., 1998; see also; Brysz and Szwedo, 2019); in Lebanese amber, Barremian, 126–130 Ma (Fennah, 1961; Maksoud and Azar, 2020); and in the Crato Formation of Brazil, latest Aptian, 114 Ma (Brysz and Szwedo, 2019)), so probably the origin of the group could be pushed back to the Jurassic/Cretaceous boundary. The data of Shcherbakov and Popov (2002) related to Cixiidae found in pre-Cretaceous (Upper Jurassic) deposits actually refer to taxa now not attributed to this family (Szwedo, 2007). Achilidae, the first mycetophagous planthoppers, apparently appeared in the Lower Cretaceous (lower Barremian, 130 Ma, Jordanian amber (Kaddumi, 2005; Maksoud and Azar, 2020); latest Aptian, 114 Ma, Crato Formation of Brazil (Hamilton, 1990; Brysz and Szwedo, 2019)).

According to Shcherbakov (2002) “until the mid-Cretaceous most fulgoroids were represented by Cixiidae and their allies and probably lived in the soil or rotten wood at the nymphal stage”. All known fossils of Achilidae and Cixiidae are adults. This suggests that already from the Jurassic/Cretaceous boundary Achilidae nymphs were probably living in rotten logs and Cixiidae nymphs on

roots in the soil (anyway in concealed sites). This would explain why no fossils of nymphs are known, either as amber inclusions or as compression fossils (Olmi et al., 2014c).

The above history of Embolemidae, Achilidae and Cixiidae suggests that *Baissobius*, *Embolemopsis*, *Ponomarenkoa* and *Cretembolemus* species (without frontal antennal processes) were the first embolemids to appear. Their hosts are unknown, but probably they were nymphs of some planthoppers other than Achilidae. Achilidae are in fact rare in the Lower Cretaceous and apparently absent from Barremian and Aptian Laurasian faunas, where *Baissobius* and *Embolemopsis* species are the most abundant. *Baissobius*, *Embolemopsis* and *Ponomarenkoa* species were probably parasitizing hosts with cryptic habits, because all known fossils are macropterous males, although normally hymenopterans present in sedimentary rocks are females (Olmi et al., 2014c). Given that terrestrial insects often come to their burial sites (water bodies) by flying (ignoring entombment in resin), this implies that females were weak fliers at best, and probably hunting within a substrate.

Another consideration is that for *Baissobius*, *Embolemopsis* and *Cretembolemus* we already have six fossils in sedimentary rocks, for *Embolemus* and *Ampulicomorpha* none, despite the Cenozoic insect record in sedimentary rocks generally being good (at least as complete as for the Cretaceous, as shown by huge collections from the Eocene of Green River and Florissant in North America, and the Bembridge Marls in England (Olmi et al., 2014c)). On the other hand, Cixiidae are very diverse in Bembridge Marls, being represented by 10 genera and 12 species (Szwedo et al., 2019).

It is interesting to discuss the distribution of Dryinidae and Embolemidae in the Cretaceous and Cenozoic, in comparison with Scolebythidae (Hymenoptera: Chrysidoidea). Biologically Scolebythidae are known as gregarious parasitoids of cerambycid and anobiid larvae in wood (Engel, 2015); so they live in concealed sites. During the Early Cretaceous, Embolemidae were much more abundant than in the Cenozoic. Seven Lower Cretaceous embolemids (Table 1) and four scolebythid species are known vs. two dryinid species (Martynova et al., 2019). In the Upper Cretaceous the situation is very different: nine embolemid species (Table 1) and four scolebythid species (Zhang et al., 2020) vs. 31 dryinid species (Olmi et al., 2020b; Tribull et al., 2020, this paper). Cenozoic embolemids are represented by 62 extant and five extinct species (Table 1), scolebythids by six extant and four extinct species (Engel, 2015); dryinids by 1880 extant (Olmi, 2020) and 38 extinct (Martynova et al., 2019; Perkovsky et al., 2020a; this paper) species.

The reason for this difference between embolemids and dryinids is that embolemids have no chelae. They could act with some difficulties in open spaces. The subterranean environment or the inside of trunks are the unique environments where they can be effective, because their hosts cannot escape (their hosts are good jumpers as nymphs). The success of the dryinids depends on the fact that they act in open spaces. The open environment grants more opportunities, with or without (*Aphelopus*) chelae. *Aphelopus* species enjoy success only because their nymphal hosts do not jump or jump with difficulty.

Surely Dryinidae and Embolemidae began their evolution in concealed sites. When some taxa (dryinids) passed to open spaces, this passage was the beginning of a big explosion concerning dryinids. Embolemids, continuing to stay in concealed environments, remained in this situation, as well as scolebythids. This explains the high diversity of dryinids and in contrast the lower diversity of embolemids and scolebythids. Of course, the above radiation also had victims: this is demonstrated by the genus *Raptodryinus* Olmi, Perkovsky, Martynova, Contarini, Bückle and Guglielmino, 2020 (Dryinidae). Provided with an extraordinary new type of chela, it is one of the new taxa arising during the transition from concealed to open spaces in an effort to adapt to open spaces. This



Fig. 7. *Proteptiptera kaweckii* Usinger (Achilidae): adult (PIN 964/1326) with two thylacia of Dryinidae. Scale bar: 2.6 mm.

modification had no success maybe because the unique unknown hosts, that *Raptodryinus* could capture with its special chela, disappeared (Olmi et al., 2020b).

From the Early Cretaceous, the first embolemids with frontal processes appeared. They were characterized by very long stout antennae articulated on two pronounced contiguous frontal processes at some distance above the clypeus, effectively increasing the length and mobility of embolemid antennae, mainly in females. Very long mobile antennae, with increased surface area and maybe more sensilla and also a greater reach, would probably facilitate the localization of concealed hosts, enabling specialization on these; this is additionally suggested by the fact that long stout antennae are always found in the extant Embolemidae which use such hosts, and usually not in the Dryinidae which attack related but unconcealed Auchenorrhyncha as far as is known (Olmi et al., 2014c). The few Dryinidae with very long antennae (females of *Harpactosphecion*; *Thaumatomyrus* Perkins, 1905; and *Pseudodryinus* Olmi, 1991) have thinner antennae, provided with sense organs not present in Embolemidae (ADOs in *Harpactosphecion* and *Pseudodryinus*; tufts of long setae in *Pseudodryinus* and *Thaumatomyrus*) probably involved in host recognition. The embolemids without such antennae (*Baissobius*, *Embolemopsis*, *Ponomarenkoa* and *Cretembolemus*) may have become less successful because of environmental changes, perhaps including increasing concealment of their hosts, but there is no real evidence to support this idea. Interestingly, extinct Cretaceous genera of Sclerogibbidae (Hymenoptera: Chrysidoidea) with frontal processes and very long antennae, suitable to explore from outside the silk galleries of the webspinners, strongly dominated at least from the Aptian to early Cenomanian (Perkovsky et al., 2020b).

Cretembolemus seems to be intermediate between embolemids without and with antennal processes, because apparently it does not show antennal processes, but the toruli are probably approximated and at a greater distance from the clypeus than in *Baissobius*, *Embolemopsis* and *Ponomarenkoa*. In addition, the antennae are probably relatively shorter. The general meaning of the above characters and the consequence on the hosts is uncertain.

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