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The first fossil Embolemidae (Hymenoptera: Chrysidoidea) from Burmese amber (Myanmar) and Orapa Kimberlitic deposits (Botswana) and their phylogenetic significance

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The first fossil Embolemidae (Hymenoptera: Chrysidoidea) from Burmese amber (Myanmar) and Orapa Kimberlitic deposits (Botswana) and their phylogenetic significance

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Ampulicomorpha janzeni sp. nov. and *Cretembolemus orapensis* gen. et sp. nov. are described from Burmese amber (Upper Cretaceous; Lower Cenomanian) and Orapa sediments (Upper Cretaceous; Turonian), respectively. *A. janzeni* is the first embolemid species found in amber from Myanmar (c. 99 Ma). *C. orapensis* is the first fossil embolemid species found in the southern hemisphere, in Orapa Kimberlitic deposits (c. 91 Ma). A discussion on the phylogenetic significance of the above new records is presented, together with a tentative history of Embolemidae and their relations with their hosts. The new combinations *Ampulicomorpha perialla* (Ortega-Blanco *et al.*, 2011) comb. nov. (= *Embolemus periallus*) and *Ampulicomorpha reticulata* (Van Achterberg in Van Achterberg & Van Kats, 2000) comb. nov. (= *Embolemus reticulatus*) are proposed.

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Keywords: *Ampulicomorpha janzeni*; *Cretembolemus orapensis*; new genus; new species; Cixiidae; Achilidae

Introduction

Embolemidae (Hymenoptera: Chrysidoidea) is a small family of Aculeata, including four genera (*Embolemus* Westwood, 1833; *Ampulicomorpha* Ashmead, 1893; *Baissobius* Rasnitsyn, 1975; *Embolemopsis* Olmi *et al.*, 2010), distributed in all zoogeographical regions and with 55 described extant species (Guglielmino & Bückle 2013). It is one of the smallest and least known families of Chrysidoidea, but comprises a relatively derived lineage, being sister to the speciose and diverse Dryinidae (Brothers 2011). Extant species are known to parasitize nymphs of Achilidae and Cixiidae (Hemiptera: Auchenorrhyncha) (Varrone & Olmi 2012; Guglielmino & Bückle 2013) in a way similar to Dryinidae on other Auchenorrhyncha (Olmi 1996).

Fossil Embolemidae are known both from amber (Rasnitsyn & Matveev 1989; Olmi 1995, 1996; Olmi *et al.* 2011; Ortega-Blanco *et al.* 2011) and rock (Rasnitsyn 1975, 1996; Olmi *et al.* 2010). The following fossil species have been described:

Cretaceous: Baissa (Russia, Siberia, Transbaikalia; Neocomian; 130–140 Ma): *Baissobius minimus* Rasnitsyn, 1996 (Figs 1, 2); *B. parvus* Rasnitsyn, 1975 (Figs 1, 3A);

B. minutus Olmi *et al.*, 2010 (Fig. 3B); *Embolemopsis baissensis* Olmi *et al.*, 2010 (Fig. 5). Bon Tsagan (Mongolia; Aptian, Khurilt Beds; 110–115 Ma): *Baissobius carolinus* Rasnitsyn, 1996 (Figs 1, 4). Peñacerrada amber (Spain; Albian; c.110 Ma (Peñalver & Delclòs 2010)): *Ampulicomorpha perialla* (Ortega-Blanco *et al.*, 2011), comb. nov. (= *Embolemus periallus*) (Fig. 6).

Eocene: Baltic amber (Northern Europe; Priabonian; 34–37 Ma): *Ampulicomorpha succinalis* Brues, 1933 (Fig. 7); *Embolemus*[?] *breviscapus* Brues, 1933. Rovno amber (Ukraine; Priabonian; 34–37 Ma): *Ampulicomorpha succinalis* Brues, 1933 (Fig. 8) (Olmi *et al.* 2011).

In addition, the following hitherto undescribed embolemid specimens have been recorded: one compression fossil from Orapa, Botswana (Upper Cretaceous, Turonian), deposited at the Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa (Brothers & Rasnitsyn 2003); two specimens of putative embolemid-like wasps from Burmese amber deposited in the Natural History Museum, London, UK (Rasnitsyn & Ross 2000); and two specimens in Lower Miocene amber from the Dominican Republic kept at the Smithsonian Institution, Washington, DC, USA (Rasnitsyn 1996).

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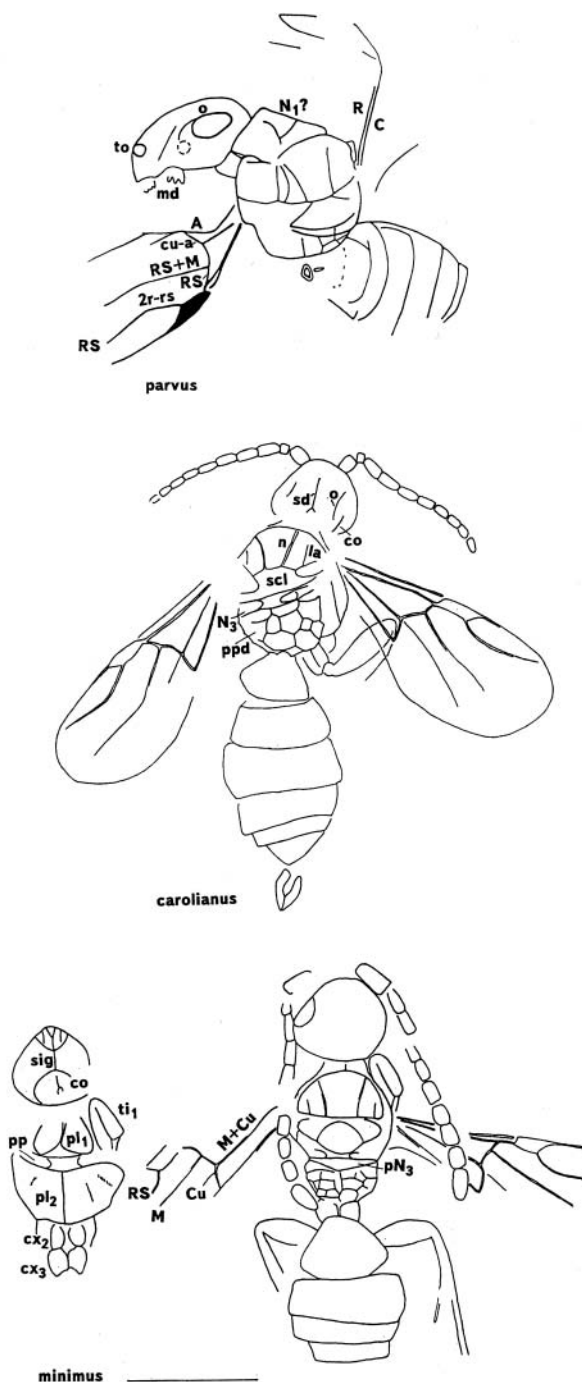


Figure 1. *Baissobius* spp., males, line drawings (from Rasnitsyn 1996). Abbreviations: 2r-rs, second radial to radial-sector crossvein; A, anal vein; C, costa; co, occipital carina; Cu, cubitus; cu-a, cubito-anal crossvein; cx, coxa; la, adlateral line; M, media; M + Cu, fused media and cubitus; md, mandible; N, notum; n, notaulus; o, eye; pl, pleuron; pN, postnotum; pp, fused prepecti; ppd, propodeum; R, radius; RS, radial sector; RS + M, fused radial sector and media; scl, scutellum; sd, dorsal cranial furrow; sig, intergenal suture; ti, tibia; to, torulus. Scale bar: 1.0 mm.

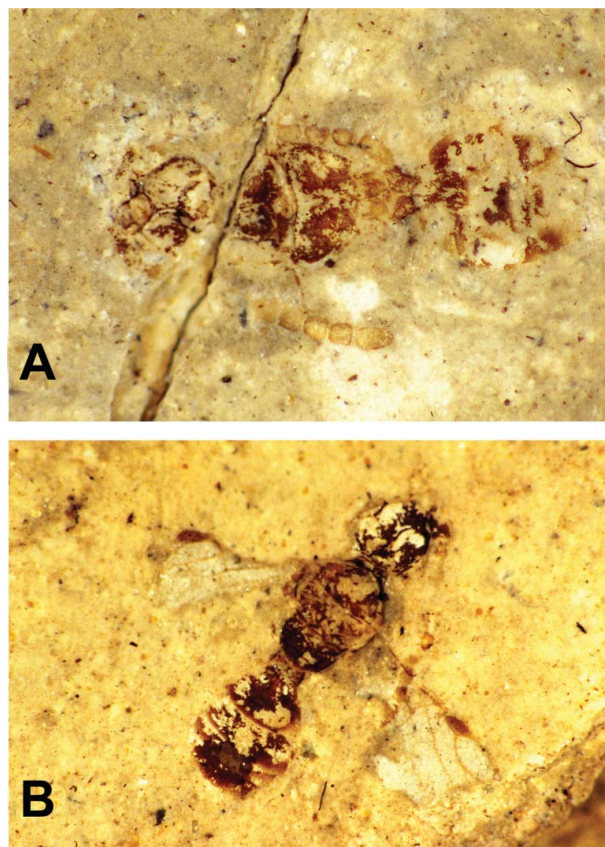


Figure 2. *Baissobius minimus* Rasnitsyn, male, holotype. **A**, part; **B**, counterpart (from Olmi *et al.* 2010). Baissa deposit. Length 3.1 mm.

One additional specimen, described in the present study, has been found in Upper Cretaceous Burmese amber (Myanmar). In addition, three of the authors (OM, APR and DJB) had the chance to study the above specimen from Orapa, Botswana; the results of that study are reported below.

Material and methods

The descriptions below follow the terminology used by Olmi (1994, 1996, 1999), Olmi *et al.* (2010) and Xu *et al.* (2012a, b, 2013). The measurements reported are relative, except for the total length (head to metasomal tip, without the antennae). Antennal and leg proportions refer to the lengths of the relevant segments or subsegments as proportions to each other, the values adjusted to eliminate fractions. POL is the distance between the inner edges of the two lateral ocelli; OL is the shortest distance between



Figure 3. *Baissobius* spp., males, holotypes. **A**, *B. parvus* Rasnitsyn, length 4.6 mm; **B**, *B. minutus* Olmi *et al.*, length 1.7 mm (from Olmi *et al.* 2010). Baissa deposit.

the edges of a lateral ocellus and the median ocellus; OOL is the distance from the outer edge of a lateral ocellus to the compound eye. 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.

Institutional abbreviations

The material studied in this paper is deposited in the following collections: **BPIP**: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; **MOLC**: Department of Plant Protection, University of Tuscia, Viterbo, Italy (Massimo Olmi’s collection); **PIN**: A. A. Borissiak Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; **SIZK**: I. I. Schmalhausen Institute of Zoology, the National Academy of Sciences of Ukraine, Kiev, Ukraine; **SMNS**: Staatliches Museum für Naturkunde Stuttgart, Abt. Paläontologie-Sektion Bernstein, Stuttgart, Germany.

Systematic palaeontology

Order **Hymenoptera** Linnaeus, 1758

Family **Embolemidae** Förster, 1856

Genus *Ampulicomorpha* Ashmead, 1893

Ampulicomorpha janzeni sp. nov.

(Figs 9, 10)

Diagnosis. Female (Fig. 9) with complete median longitudinal furrow on pronotum, extending from anterior to posterior margin; petiole about as long as metatrochanter. Male (Fig. 10) with maxillary palpus 5-segmented.

Etymology. The species is named after Mr Jens-Wilhelm Janzen (Seevetal, Germany).

Material examined. Female holotype (SMNS-BU-21) and one male paratype (SMNS-BU-22) in Upper Cretaceous Burmese amber (SMNS; gift from Mr Jens-Wilhelm Janzen).

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.



Figure 4. *Baissobius carolianus* Rasnitsyn, male, holotype, PIN 3559/4532 (from Olmi *et al.* 2010). **A**, counterpart; **B**, part. Bon Tsagan sediment. Length 3.7 mm.



Figure 5. *Embolemopsis baissensis* Olmi *et al.*, male, holotype (from Olmi *et al.* 2010). Baissa deposit. Length 2.6 mm.

Description of female holotype. Female holotype (Fig. 9). Fully winged (in Fig. 9A, B the left forewing is apparently sub-brachypterous, shortened and narrow, because it is inclined anteroposteriorly in the amber and the distal third is missing; the right forewing is complete and overlying the metasoma); length 2.9 mm. Apparently totally brown, except metasoma brown-black and legs testaceous. Both antennae missing. Head pyriform, dull, apparently hairless, with sculpture indistinct, with two frontal prominent contiguous antennal processes; occipital carina not visible; ocelli present, but only anterior ocellus visible; eye very small, approximately 0.3 times as long as head (6:21); region of face from clypeus to antennal toruli not visible; region from anterior ocellus

to frontal processes flat, not distinctly visible. Palpi not visible. Pronotum dull, granulated, hairless, apparently with strong complete median longitudinal furrow. Mesosoma about 6.1 times as long as pronotum (49:8). Pronotal tubercles not visible. Scutum, notauli, scutellum and metanotum not visible. Mesopleuron and metapleuron not visible. Mesometapleural suture not visible. Propodeum reticulate rugose, about 1.6 times as long as pronotum (13:8); propodeal keels not visible. Forewing hyaline, without dark transverse bands; marginal cell not completely visible; distal part of stigmal vein longer than proximal part; 1DC and 1SDC cells completely enclosed by pigmented veins. Hind wing not visible, because hidden under forewing. Petiole much shorter than remainder of metasoma (4:53) and as long as metatrochanter. Segments of foreleg not completely visible. Segment lengths of midleg in following proportions: coxa (10): trochanter (4): femur (11): tibia (12): tarsus (20). Segment lengths of hind leg in following proportions: coxa (8): trochanter (4): femur (22): tibia (21): tarsus (25). Tibial-spur formula unknown (only one metatibial spur visible).

Description of male paratype. Male paratype (Fig. 10). Fully winged; length 1.7 mm. Apparently totally brown, except legs brown-testaceous. Antennae filiform, articulated on two prominent contiguous frontal processes; antennomere lengths in following proportions: 12:4:16:13:15:13:13:12:10:14. Head subspheroidal, dull, apparently hairless, with sculpture indistinct; occipital carina not visible; ocelli present; POL = 2.0; OL = 1.5; OOL = 4.0; eye approximately 0.5 times as long as head (6:11); region of face from clypeus to antennal toruli not

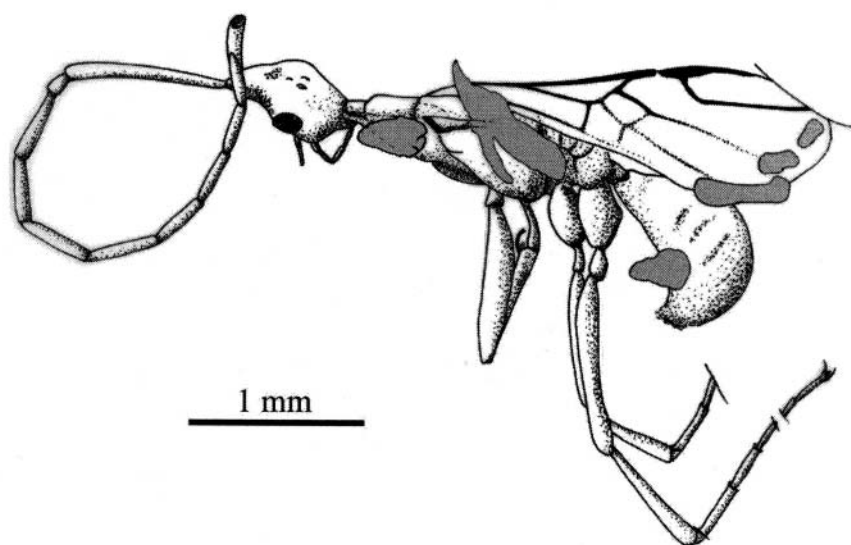


Figure 6. *Ampulicomorpha perialla* (Ortega-Blanco *et al.*), female, holotype (line drawing from Ortega-Blanco *et al.* 2011). Peñacerrada amber. Length 3.3 mm.

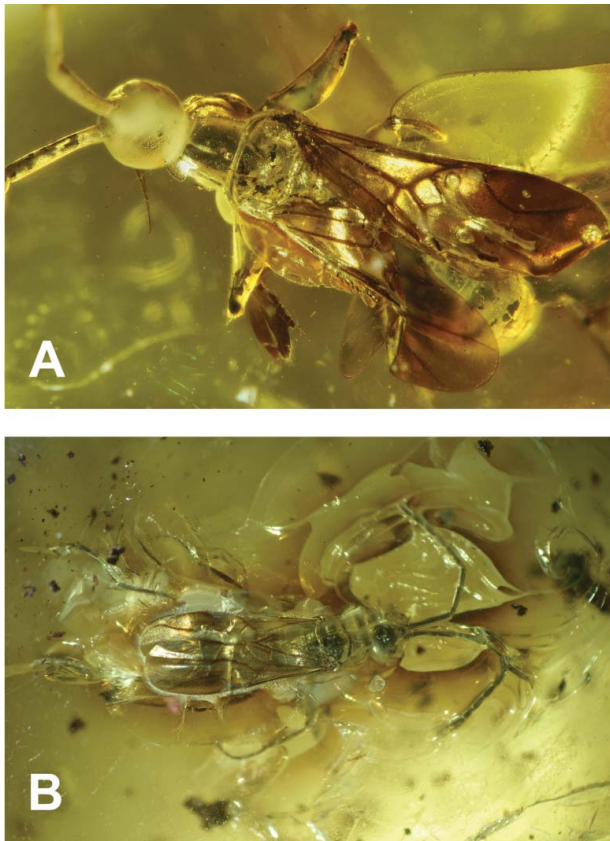


Figure 7. *Ampulicomorpha succinalis* Brues, females. **A**, MOLC/25; **B**, MOLC/26. Baltic amber. Lengths 4.4 mm.

visible; region from anterior ocellus to frontal processes flat, not distinctly visible. Maxillary palpi apparently 5-segmented; labial palpi not distinct. Mesosoma approximately 2.4 times as long as head (27:11). Pronotal tubercles not visible. Pronotum, scutum, notauli, scutellum, metanotum, propodeum not distinct. Mesopleuron and metapleuron not visible. Mesometapleural suture not visible. Forewing hyaline, without dark transverse bands; marginal cell not completely visible; distal part of stigmal vein longer than proximal part; 1DC and 1SDC cells not visible. Hind wing not visible, because hidden under forewing. Petiole much shorter than remainder of metasoma (2:26) and about as long as metatrochanter. Segment lengths of foreleg in following proportions: coxa (14): trochanter (6): femur (20): tibia (22): tarsomere 1 (14): tarsomere 2 (4): tarsomere 3 (4): tarsomere 4 (3): tarsomere 5 (6). Segment lengths of midleg in following proportions: coxa (12): trochanter (5): femur (18): tibia (16): tarsus (28). Segment lengths of hind leg in following proportions: coxa (16): trochanter (6): femur (24): tibia (30): tarsomere 1 (20): tarsomere 2 (8): tarsomere 3 (6): tarsomere 4 (4): tarsomere 5 (7). Tibial spurs 1 $\frac{1}{2}$ /2 (spurs of mesotibia not visible).

Hosts. Unknown.

Remarks. The male described above is tentatively associated with the female holotype because its morphological characters are very similar to those of the female, as in all extant and fossil species of *Ampulicomorpha*, and both specimens are from the same amber deposit.

Comparison and systematic position. There are two known fossil species of *Ampulicomorpha*: *A. perialla* (Ortega-Blanco *et al.*, 2011) comb. nov. (= *Embolemus periallus*, here assigned to *Ampulicomorpha* because it is a winged female), from Peñacerrada amber (Spain; Lower Cretaceous, Albian; c.110 Ma (Peñalver & Delclòs 2010)); and *A. succinalis* Brues, 1933, from Baltic (Northern Europe; 34–37 Ma) and Rovno (Ukraine; 34–37 Ma) ambers (Tertiary, Upper Eocene (Perkovsky *et al.* 2010; Olmi *et al.* 2011)). A third fossil assigned to an extant embolemid genus is *Embolemus breviscapus* Brues, 1933, described on the basis of two male specimens (so stated in the original description), deposited originally in the amber collection of the Albertus University in Königsberg and regarded as lost (Olmi 1996). It is better to ignore this species, because the description is insufficient and unreliable, and to regard it as a *nomen dubium*. In addition, it is not

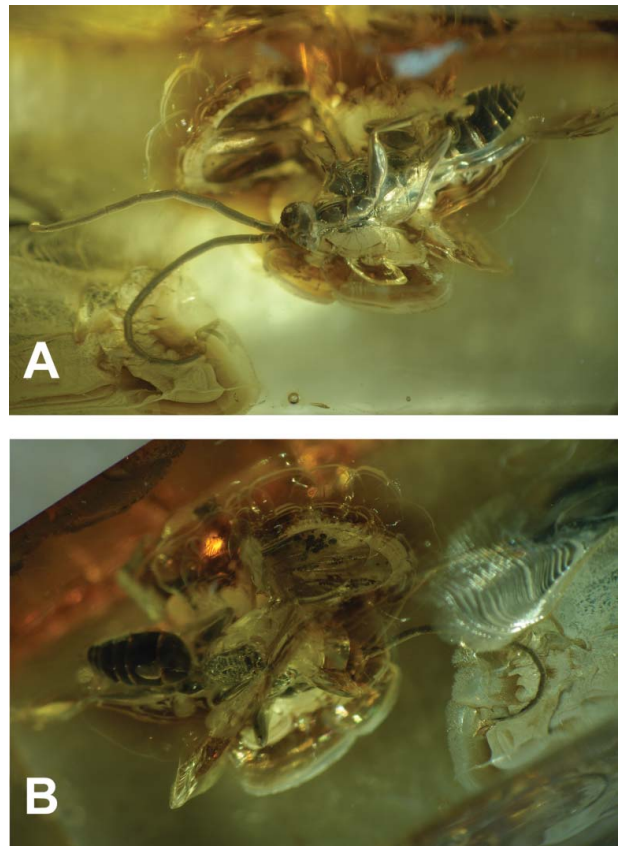


Figure 8. *Ampulicomorpha succinalis* Brues, male. **A**, ventral view; **B**, dorsal view. Rovno amber. Length 5.0 mm.

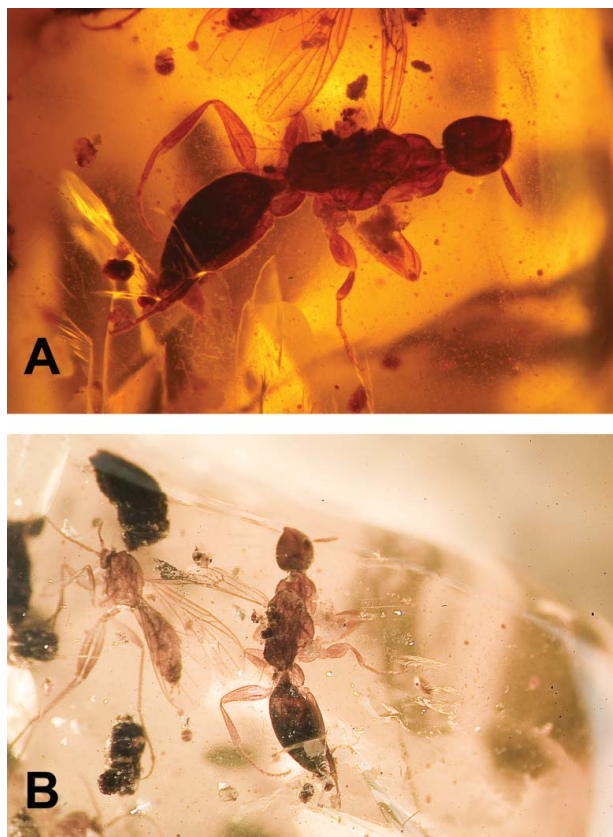


Figure 9. *Ampulicomorpha janzeni* sp. nov., female, holotype, **A, B**, dorsolateral views under: **A**, transmitted light; **B**, incident light. Burmese amber. Length 2.9 mm.

even possible to decide if it belongs to *Ampulicomorpha* or *Embolemus* Westwood, 1833, because the only drawing published by Brues is incomplete. It is likely, as even suggested by Brues (1933) himself, that it represents the male of *A. succinalis*, but this cannot be established without the type material.

Ampulicomorpha perialla is known only on the basis of a female specimen. The main difference from *A. janzeni* concerns the pronotum: without a median longitudinal furrow in *A. perialla*, but with a complete furrow in *A. janzeni*.

Both sexes of *A. succinalis* are known. The female (given as ‘♂?’ by Brues) holotype, deposited originally in the amber collection of the Albertus University in Königsberg, has to be regarded as lost (Olmi 1996). However, we know a further three female specimens from Baltic amber, one deposited in PIN and two in MOLC, that agree with the original description (Rasnitsyn & Matveev 1989; Olmi 1995). The only known male is a specimen from Rovno amber deposited in SIZK (Olmi *et al.* 2011). The main difference between the females of *A. janzeni* and *A. succinalis* concerns the petiole: about as long as the metatrochanter in *A. janzeni*, but much shorter in *A. succinalis*. The main difference between the males

concerns the maxillary palpi: 5-segmented in *A. janzeni* and 6-segmented in *A. succinalis*.

Remarks. The family Dryinidae is the sister group of Embolemidae (Brothers 2011 and references therein). Three species of Dryinidae from Burmese amber have been described: *Anteon olmii* Engel, 2003, *Hybristodryinus resinicolus* Engel, 2005 and *Ponomarenkoa ellenbergeri* Olmi, Xu & He in Xu *et al.*, 2013.

***Cretembolemus* gen. nov.**

Type species. *Cretembolemus orapensis* sp. nov.

Diagnosis. Female (Figs 11, 12): fully winged; head rounded; eye large, oval; palpal formula unknown; scape apparently not articulated on a prominent frontal process; toruli apparently at about mid-height of face; pronotum fairly long, anteriorly convex, posterior margin almost straight, sculpture not discernible; propodeum with posterolateral angles abrupt, disc apparently with three longitudinal ridges; prepectus apparently fused medially; forewing with stigmal vein forming acute angle with pterostigma, ((Rs+M) + 2-M) vein apparently very long,

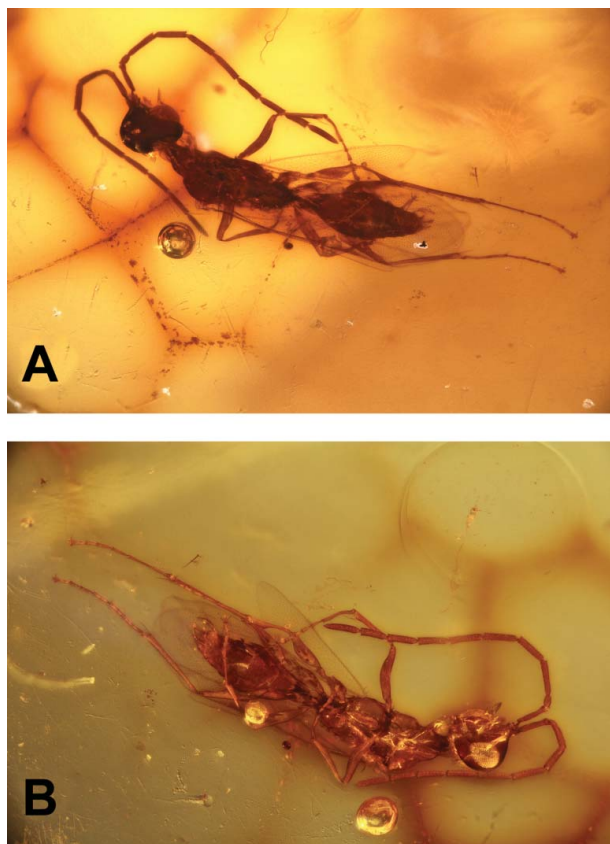


Figure 10. *Ampulicomorpha janzeni* sp. nov., male, paratype. **A**, dorsal view; **B**, ventral view. Burmese amber. Length 1.7 mm.

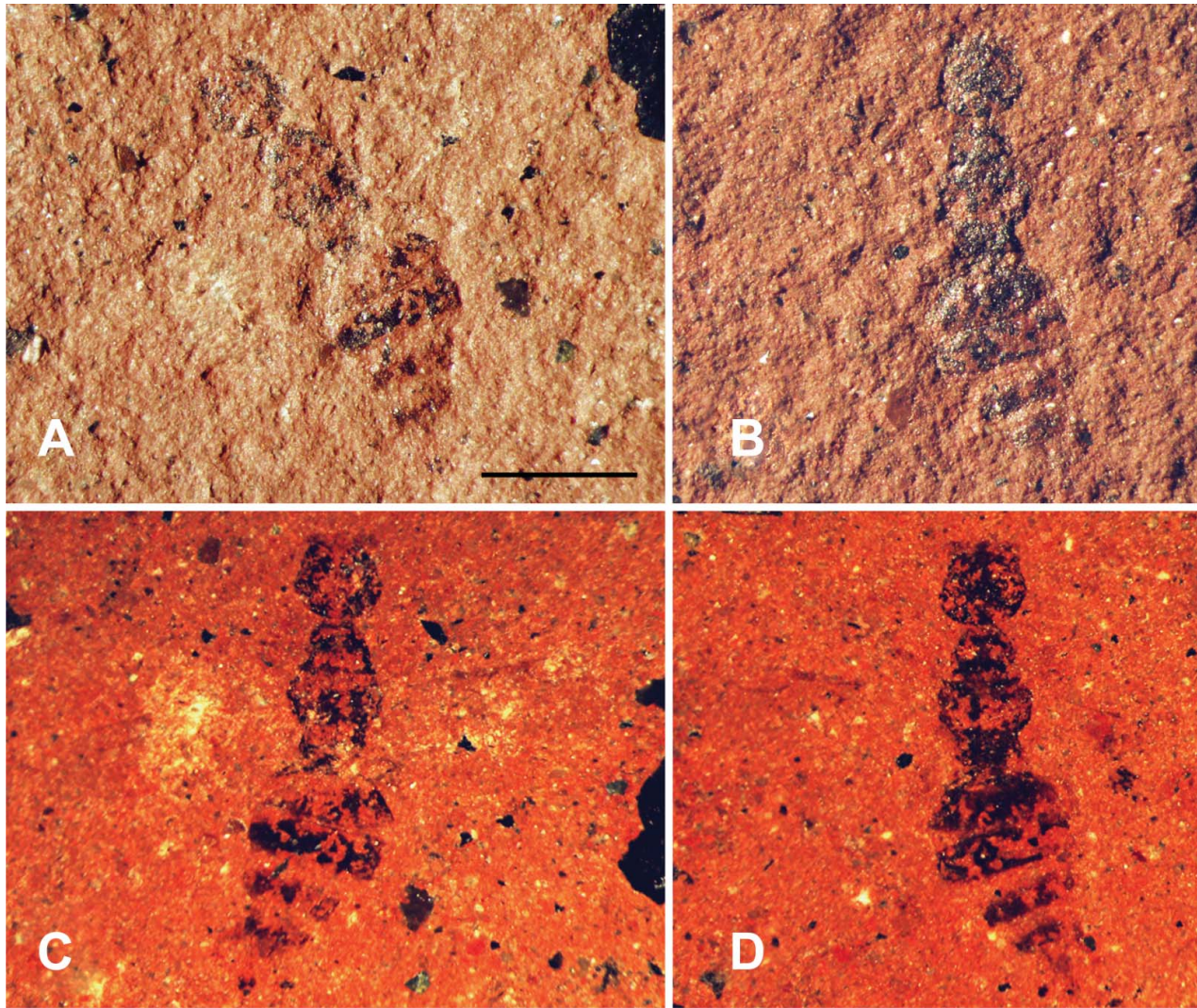


Figure 11. *Cretembolemus orapensis* gen. et sp. nov., female, holotype. **A, B**, counterpart (BP/2/27900); **A**, under oblique incident light, **B**, under cross-polarized light. **C, D**, part (BP/2/27895); **C**, under oblique incident light, **D**, under cross-polarized light. Kimberlitic deposit at Orapa (Botswana). Length 2.9 mm. Scale bar: 1.0 mm.

trace of distal region of vein Cu apparently present, sub-basal cell (SBC) broad, 1DC and 1SDC cells not visible; tibial spurs not visible. Male unknown.

Etymology. The genus name is a combination of *Cret-* (=Cretaceous) and *Embolemus* (the type genus of the family).

Remarks. In the only known specimen of *C. orapensis* sp. nov. the sting is apparently visible as a dark line and there seem to be six distinct metasomal terga. It is thus considered to be a female, confirmed by the fairly long pronotum.

Comparison and systematic position. *Cretembolemus* gen. nov. differs from the two extant genera of Embolemidae, *Embolemus* and *Ampulicomorpha*, because the

antennae are apparently not articulated on two prominent contiguous frontal processes (although the toruli seem to be close together) and the eyes are relatively much larger (eyes much reduced in *Embolemus* and *Ampulicomorpha*, see Fig. 9); in addition, females of *Embolemus* are micropterous or brachypterous. The differences from the other two fossil genera of Embolemidae, *Embolemopsis* Olmi *et al.*, 2010 and *Baissobius* Rasnitsyn, 1975 (both known only from males) follow. In *Embolemopsis* the stigmal vein forms a right angle with the pterostigma and issues from near the pterostigmal base (Fig. 5), whereas in *Cretembolemus* and in all other extant and fossil Embolemidae the stigmal vein forms an acute angle with the pterostigma (Figs 1, 6, 7, 12), and in *Cretembolemus* issues from near its apex. In *Baissobius* and *Embolemopsis* the propodeum is rounded posterodorsally (Figs 1, 3B,

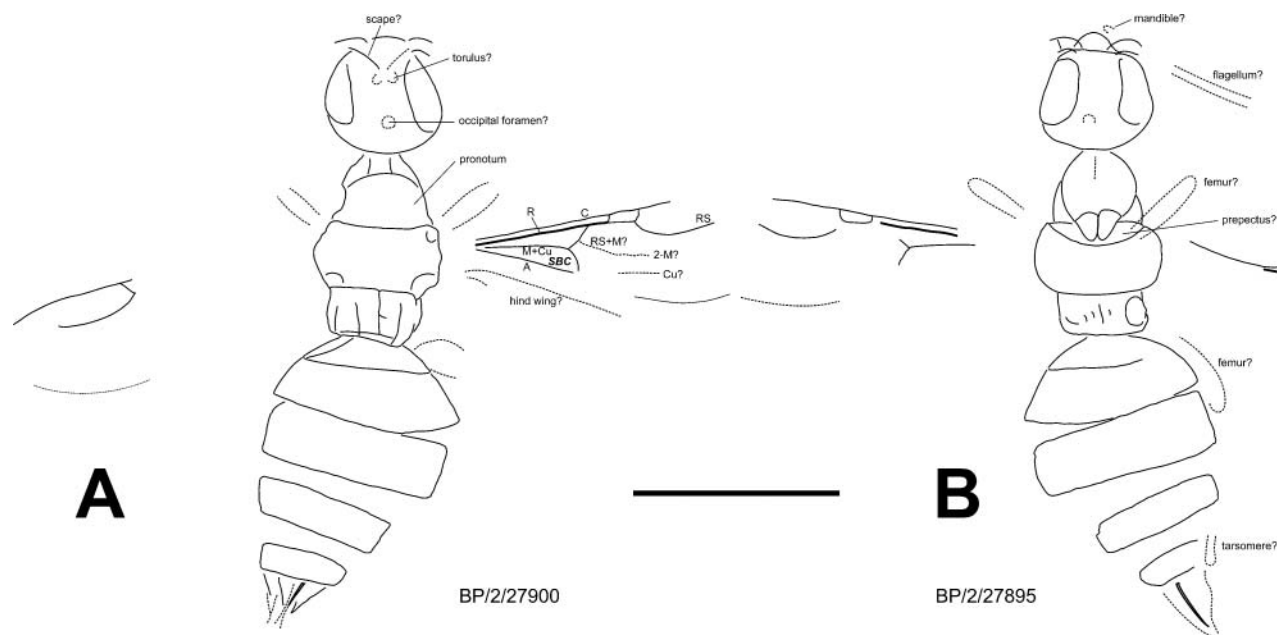


Figure 12. *Cretembolemus orapensis* gen. et sp. nov., holotype, line drawings (features only vaguely indicated shown with dotted lines); **A**, counterpart; **B**, part. Kimberlitic deposit at Orapa (Botswana). Abbreviations: 2-M, second abscissa of media; A, anal vein; C, costa; Cu, cubitus; M+Cu, fused media and cubitus; R, radius; RS, radial sector; RS+M, fused radial sector and media; SBC, subbasal cell. Scale bar: 1.0 mm.

5), whereas in *Cretembolemus* it is abrupt or even bluntly protuberant posterolaterally (Fig. 12), but this may be due to sexual dimorphism since posterolateral protrusions/angles on the propodeum are always absent in males of Embolemidae, whereas they can be present in females of some extant species (for example, in *Ampulicomorpha collinsi* Olmi, 1996, *Ampulicomorpha magna* Olmi, 1996, *Embolemus ruddii* Westwood, 1833, and *Embolemus zealandicus* Olmi, 1996) (Olmi 1996, fig. 28A). As in all extant and fossil Embolemidae, RS of *Cretembolemus* is lost between RS+M and the basal section of the stigmal vein (2r-rs); the only known trace of this section of RS is at the elbow of the stigmal vein in *Embolemopsis* (Fig. 5).

***Cretembolemus orapensis* sp. nov.**
(Figs 11, 12)

Diagnosis. See the above diagnosis of *Cretembolemus* gen. nov.

Etymology. The species is named after its type locality, Orapa (Botswana).

Material examined. Poorly preserved compression fossil: female holotype BP/2/27895 (part) and BP/2/27900 (counterpart) in Upper Cretaceous Kimberlitic deposit (BPIP).

Horizon and locality. Upper Cretaceous, Turonian (c. 91 Ma), Orapa, Botswana.

Description. Female holotype (Figs 11, 12): fully winged; length 2.9 mm as preserved. Antennae almost completely missing; scape apparently fairly long and straight (but may have been misidentified, shown only on counterpart and without distinct relief), pedicel and/or base of flagellum evident, section of right flagellum possibly indicated on counterpart. Scape apparently not articulated on a prominent frontal process, but toruli apparently close together and somewhat distant from clypeus (pale patches interpreted as toruli not distinctly margined and thus possibly misidentified as such). Head about as high as broad, with sculpture not visible. Clypeus apically convex and strongly protruding. Eye large, scarcely protruding, height about 0.6 times total height of head. Ocelli and palpi not visible. Mesosoma about 1.6 times as long as head height, about 0.6 times as long as metasoma. Pronotum transverse, about half as long as wide, about 0.9 times length of head, with anterior margin strongly and evenly convex; sculpture not evident. Meso- + metanotum about 1.2 times as long as pronotum. Notauli not visible. Propodeum about 0.7 times as long as meso- + metanotum, apparently with three longitudinal ridges on laterally margined disc and posterolateral dorsal angle bluntly abrupt. Propleura extending anterior to pronotum, forming a short neck anteriorly (possibly the result of displacement during fossilization); ventrally with median margins evident only anteriorly. Prepectus apparently indicated as a short transverse sclerite fused medially. Forewing only partly preserved; stigmal vein forming an acute angle with pterostigma and arising near its apex,

evenly curved; vein R thick and well sclerotized; ((Rs+M) + 2-M) vein apparently tubular, very long and sclerotized; trace of distal region of vein Cu apparently present; costal cell distinct, wider than vein R; subbasal cell (SBC) apparently broader than basal cell; 1DC and 1 SDC cells not visible. Hind wing with anterior margin possibly indicated but otherwise indistinguishable. Legs: forecoxa more or less conical; forefemora, hind femora and hind tarsomere possibly indicated; tibial spurs not visible. Metasoma with six segments distinguishable; first segment shorter than second, with petiole very short; terminal segment(s) acute apically, with sting weakly preserved. Male unknown.

Hosts. Unknown.

Comparison and systematic position. See *Cretembolemus* gen. nov., above.

Discussion

In Embolemidae there are two distinct groups. The first one includes the extant species of *Embolemus* and *Ampulicomorpha*, where both sexes have the antennae articulated on two prominent contiguous frontal processes far above the clypeus (apomorphic). This feature is also present in all fossil species attributed to *Ampulicomorpha*: in the Tertiary, *A. succinalis* from Baltic (34–37 Ma) and Rovno (34–37 Ma) amber; in the Cretaceous, *A. janzeni* from Burmese amber (99 Ma), and *A. perialla* from Peñacerrada amber (110 Ma) (Table 1).

The second group comprises the following compression fossils: *Baissobius* (three species from Baissa (Transbaikalia), (*B. minimus*, *B. minutus* and *B. parvus*) and Bon Tsagan (Mongolia) (*B. carolianus*)) and *Embolemopsis* (one species, *E. baissensis*, from Baissa (Transbaikalia)) (Table 1). All these species have no frontal antenniferous

processes; in addition, their antennal bases are widely spaced and do not approach closely to the head midline (both plesiomorphic characters). A further characteristic connecting all these species is their antiquity – Neocomian (*B. minimus*, *B. minutus* and *B. parvus*; *E. baissensis*; 130–140 Ma) or Aptian (*B. carolianus*; 110–115 Ma) – i.e. older than the oldest fossil species with frontal processes (*A. perialla* from the Albian, 110 Ma, and *A. janzeni* from the Cenomanian, 99 Ma). *Cretembolemus* (one species, *C. orapensis*, from Botswana) is anomalous in apparently having no antenniferous processes but with the antennal bases possibly approximated (unfortunately, the condition of the fossil does not provide certainty for either character); in addition, it is younger (Turonian, 91 Ma) than *A. perialla* and *A. janzeni*.

A first conclusion from the above discussion is that the plesiomorphic lack of frontal processes is not only generally older than their apomorphic presence, but that the apomorphic state presumably appeared in the Cretaceous and the plesiomorphic state was lost relatively soon thereafter.

The genera *Baissobius* and *Embolemopsis* are considered by Ortega-Blanco *et al.* (2011) to be ‘putative’ Embolemidae, because of the absence of the prominent contiguous frontal processes and because the main characters used for attributing them to Embolemidae (antenna 10-segmented, forewing with long tubular development of Rs+M and the distal abscissa of M ((RS+M) + 2-M) and desclerotization of Cu beyond its separation from M) are also separately present in other Aculeata, though always in combination with other features not present in Embolemidae (Ortega-Blanco *et al.* 2011). However, desclerotization of Cu is not complete in *Embolemopsis*, *Embolemus* and *Ampulicomorpha*, where cell 1m_{cu} is enclosed by tubular veins (unlike *Baissobius* and *Cretembolemus*, where 1m_{cu} is lost as well as most of the free Cu). In spite of the above doubts, the venation of *Baissobius* and *Embolemopsis* (and *Cretembolemus*) is more reminiscent of Embolemidae than any other Aculeata

Table 1. Fossil Embolemidae.

Taxon	Deposit	Age	Ma
Compression fossils			
<i>Cretembolemus orapensis</i> gen. et sp. nov.	Orapa (Botswana)	Cretaceous (Turonian)	91
<i>Baissobius carolianus</i> Rasnitsyn, 1996	Bon Tsagan (Mongolia)	Cretaceous (Aptian)	110–115
<i>B. minimus</i> Rasnitsyn, 1996	Baissa (Siberia)	Cretaceous (Neocomian)	130–140
<i>B. minutus</i> Olmi <i>et al.</i> , 2010	Baissa (Siberia)	Cretaceous (Neocomian)	130–140
<i>B. parvus</i> Rasnitsyn, 1975	Baissa (Siberia)	Cretaceous (Neocomian)	130–140
<i>Embolemopsis baissensis</i> Olmi <i>et al.</i> , 2010	Baissa (Siberia)	Cretaceous (Neocomian)	130–140
Fossils in amber			
<i>Ampulicomorpha janzeni</i> sp. nov.	Myanmar	Cretaceous (Cenomanian)	99
<i>A. perialla</i> (Ortega-Blanco <i>et al.</i> , 2011)	Peñacerrada (Spain)	Cretaceous (Albian)	110
<i>A. succinalis</i> Brues, 1933	Baltic, Rovno (Ukraine)	Eocene (Priabonian)	34–37
<i>Embolemus</i> [?] <i>brevicapus</i> Brues, 1933	Baltic	Eocene (Priabonian)	34–37
Embolemidae? (Rasnitsyn, 1996)	Dominican Republic	Miocene (Burdigalian)	16
Embolemidae? (Rasnitsyn & Ross, 2000)	Myanmar	Cretaceous (Cenomanian)	99

(Ortega-Blanco *et al.* 2011), so we consider it very probable that they belong to this family.

If the three fossil genera without frontal processes do belong to Embolemidae, the following questions arise: why are they extinct, and why were they replaced by genera and species with antennae articulated on two contiguous frontal processes?

New information on the biology of extant Embolemidae (no biological data are available for fossil species) may assist in answering these questions. However, it is first necessary to discuss the actual systematic position of the two extant genera of Embolemidae, *Embolemus* and *Ampulicomorpha*. Van Achterberg & Van Kats (2000) considered *Ampulicomorpha* and *Embolemus* as synonyms. It is sometimes very difficult to attribute a male specimen to *Ampulicomorpha* or *Embolemus*, because the length and pigmentation of the veins enclosing the 1SDC cell (and mostly the posterior spurious vein near the 1A vein) may be variable (1SDC being either closed or open 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*). In spite of the considerations of Van Achterberg & Van Kats (2000), however, we prefer to continue to consider both genera as valid, not only because in the majority of cases there are no difficulties in distinguishing them, but also because the genera seem to be biologically separated. *Embolemus* species are parasitoids of nymphs of Cixiidae (Hemiptera Auchenorrhyncha) (Fig. 13A) feeding on roots and living in the soil (Varrone & Olmi 2012). In contrast, *Ampulicomorpha* species are parasitoids of nymphs of Achilidae (Hemiptera Auchenorrhyncha) (Fig. 13B) feeding on fungus and living in rotten logs, as seen in the USA by Bridwell (1958) and Wharton (1989) (for *Ampulicomorpha confusa* Ashmead, 1893, on the host *Epiptera floridiae* (Walker, 1851)) and in Argentina by Olmi (*Ampulicomorpha schajovskoyi* De Santis & Vidal Sarmiento, 1977 reared from the achilid *Olmiana argentina* Guglielmino *et al.*, 2010 (Guglielmino & Bückle 2013; Fig. 13B)). Note that Fig. 13A, B are the only available photographs of cysts (= thylacia) of Embolemidae on their hosts, proving not only the relationships with the hosts (the embolemids were reared to the adult stage), but also confirming the close connection with Dryinidae which form similar cysts on the bodies of their hosts (Hemiptera Auchenorrhyncha) (Olmi 1994, 1999). Although Fig. 13A, B appear to show ectophagous larvae feeding on the bodies of their hosts and not included inside moulted skins forming a 'cyst', the exuvia are actually present, but are colourless and transparent, and not easily visible (Olmi, pers. obs.). A similar situation occurs also in some dryinids, mainly in the genus *Neodryinus* Perkins, 1905 (e.g. *Neodryinus typhlocybae* (Ashmead, 1893) on *Metcalfa pruinosa* (Say, 1830) (Flatidae) and *Neodryinus floridensis* Olmi, 1992,

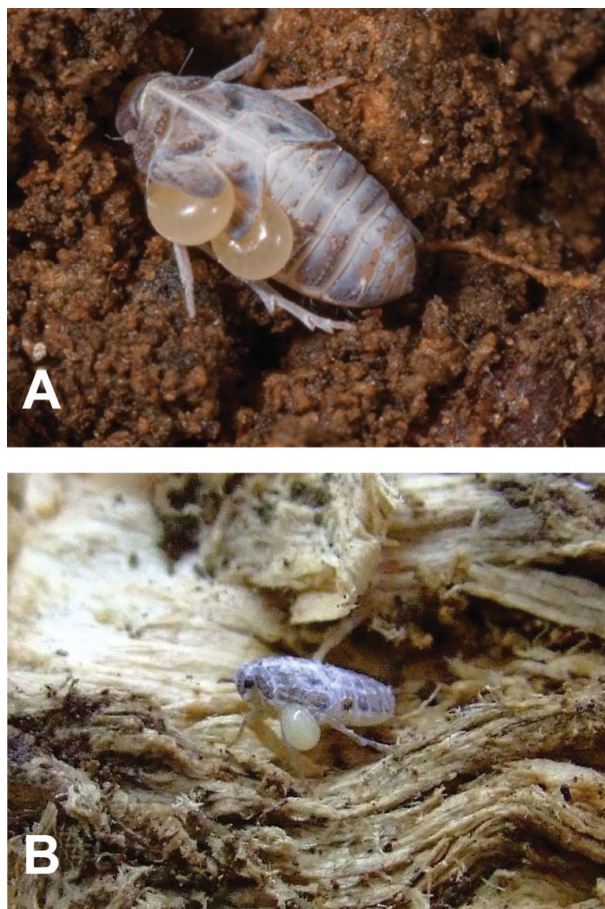


Figure 13. Homopteran nymphs with larval cysts of Embolemidae. **A**, nymph of Cixiidae with two cysts of *Embolemus ruddii* Westwood, under stone, Pont Canavese (Torino Province, Italy), 3 April 2009 (from Varrone & Olmi 2012) (length of nymph 5.0 mm); **B**, nymph of *Olmiana argentina* Guglielmino *et al.*, 2010 (Achilidae) with a cyst of *Ampulicomorpha schajovskoyi* De Santis & Vidal Sarmiento, in a rotten log, Pucará (Neuquén, Argentina), 21 November 2007 (from Guglielmino & Bückle 2013) (length of nymph 5.6 mm).

on *Ormenaria rufifascia* (Walker, 1851) (Flatidae)) (Olmi, pers. obs.).

Rasnitsyn & Matveev (1989) described *Ampulicomorpha thauma*, a new extant species from Rostov Province, Russia. No Achilidae had been reported in that area (according to A. Emeljanov), so Rasnitsyn & Matveev believed that the hosts of this species were Cixiidae feeding on roots, in addition because the type material was collected in a soil trap. However, according to Fauna Europaea (Hoch, 2013), in central and northern Russia there are two species of Achilidae (*Cixidia confinis* (Zetterstedt, 1828) and *C. lapponica* (Zetterstedt, 1828)), and the family also occurs in areas of Central Russia not far from Rostov Province. Achilidae species are considered rare, because of their particular biology, developing

in rotten logs and feeding on fungi (Guglielmino, pers. obs.). It is thus highly likely that Achilidae are not reported in Rostov Province merely because of a lack of research (as also suggested by several anomalous gaps in their distribution as reflected in *Fauna Europaea*, such as their presence in the Czech Republic and central and northern Russia, but their absence in Poland, Ukraine and Belarus). The same situation applies to *Ampulicomorpha reticulata* (= *Embolemus reticulatus* Van Achterberg in Van Achterberg & Van Kats, 2000, comb. nov.), known only from The Netherlands. In this country as well, no Achilidae species are reported, but *C. confinis* has been collected in neighbouring Germany, so its presence in The Netherlands is probable. In addition, captures of *Ampulicomorpha* species in soil traps are not rare, because both sexes fly outside the rotten logs to copulate and find new hosts; they are also frequently collected in Malaise traps (Olmi, pers. obs.).

The above biological separation explains why the evolution of extant embolemid females was so different, and supports the maintenance of separate genera for those parasitizing hosts in these different situations: micropterous or brachypterous females of *Embolemus* can easily enter the soil to parasitize nymphs of Cixiidae feeding on roots (the presence of complete wings would be an obstacle), probably following the ants feeding on the honey-dew produced by the Cixiidae nymphs; in contrast, macropterous females of *Ampulicomorpha* can easily enter the more spacious fissures of rotten logs, where they parasitize nymphs of Achilidae feeding on fungus; such colonies of Achilidae are usually not attended by ants. Conversely, males of *Embolemus* and *Ampulicomorpha* are very similar. Always macropterous, they fly to find the opposite sex (females of *Embolemus* emerge from the soil for copulation and to find new colonies of hosts; females of *Ampulicomorpha* fly outside the 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 species has been found to parasitize Achilidae, whereas adults of Cixiidae can be parasitized by species of *Dryinus* Latreille, 1804 (Olmi, pers. obs.). No dryinids are known to parasitize nymphs of Cixiidae feeding on roots in the soil; apparently this is a specialization of *Embolemus* species.

Achilidae and Cixiidae are often present in Baltic and Dominican ambers (Szwedo 2002), but both families are much older. According to Szwedo (2007), the first true Cixiidae are recorded from the Lower Cretaceous (in the Weald Clay Formation (England), Hauterivian through Barremian, 125–136 Ma (Fennah 1987; Rasnitsyn *et al.* 1998); in Lebanese amber, Hauterivian through Barremian, 120–136 Ma (Fennah 1961); and in the Crato Formation of Brazil, Aptian, 120 Ma

(Martins-Neto 1989)), so probably the origins of the group could be pushed back to the Jurassic/Cretaceous boundary (the data of Shcherbakov & 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 Early Cretaceous (Neocomian, 130 Ma, Jordanian amber (Kaddumi 2005); Aptian, 120 Ma, Crato Formation of Brazil (Hamilton 1990)). However, according to Shcherbakov (2002, p. 33) “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. This would explain why no fossils of nymphs are known, either in amber or in sediments or rocks as compression fossils.

The above history of Embolemidae, Achilidae and Cixiidae suggests that *Baissobius*, *Embolemopsis* and *Cretembolemus* species (without frontal processes) were the first embolemids to appear. Their hosts are unknown, but probably they were also nymphs of Fulgoromorpha. Achilidae are in fact rare in the Lower Cretaceous and apparently absent from pre-Aptian (Neocomian) sedimentary rocks, where *Baissobius* and *Embolemopsis* species are the most abundant (four fossils in Baissa). This indicates that *Baissobius* and *Embolemopsis* hosts (and maybe also *Cretembolemus*) were probably some planthoppers other than Achilidae. Further evidence that *Baissobius* and *Embolemopsis* species were hunting for hosts with cryptic habits is the fact that all five known fossils are males, while normally hymenopterous buried in sedimentary rocks are predominantly females (Rasnitsyn, pers. obs.). Given that terrestrial insects 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 N. America, and the Bembridge Marls in England; Rasnitsyn, pers. obs.). This implies that the Early Cretaceous Embolemidae were much more abundant than Cenozoic ones.

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 their length and mobility,

mainly in females. It seems reasonable to infer that very long mobile antennae, with increased surface area and probably more sensilla and also a greater reach, would facilitate the localization of concealed hosts, enabling specialization on these; this is additionally suggested by the fact that long stout antennae are only found in the extant Embolemidae which use such hosts, and not in the Dryinidae which utilize related but unconcealed Auchenorrhyncha as far as is known. The embolemids without such antennae (*Baissoobius*, *Embolemopsis* 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. *Cretembolemus* seems to be somewhat intermediate, apparently without antennal processes but with the toruli probably approximated and at a greater distance from the clypeus than in *Baissoobius* and *Embolemopsis*, and the antennae probably still relatively short.

Prior to the discovery of *Cretembolemus*, two morphologically clearly distinguishable groups were evident in the family Embolemidae, which might have warranted formal recognition of them, those with relatively short antennae and no frontal antenniferous processes (*Baissoobius* and *Embolemopsis*) and those with enlarged antennae and prominent processes (*Embolemus* and *Ampulicomorpha*). The apparently intermediate nature of *Cretembolemus* has produced uncertainty, however, and we prefer to defer any such proposals until additional and better-preserved specimens are available.

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