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Cédric Chény, Elvis Guillam, André Nel, Vincent Perrichot. A new species of Ampulicomorpha Ashmead from Eocene French amber, with a list of fossil and extant Embolemidae (Insecta: Hymenoptera) of the world. Bulletin de la Société Géologique de France, 2020, L'ambre, 191 (1), pp.20. 10.1051/bsgf/2020020 . insu-02903496

HAL Id: insu-02903496

<https://insu.hal.science/insu-02903496>

Submitted on 21 Jul 2020

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A new species of *Ampulicomorpha* Ashmead from Eocene French amber, with a list of fossil and extant Embolemidae (Insecta: Hymenoptera) of the world

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Received: 15 May 2020 / Accepted: 22 May 2020

Abstract – Embolemidae is a cosmopolitan but species-poor group of chrysidoid wasps with a scarce fossil record, despite a long evolutionary history since at least the Early Cretaceous. Here, the new species, *Ampulicomorpha quesnoyensis* sp. nov., is illustrated and described based on a single female found in Early Eocene amber of Oise (France). The new species is compared with the three other known fossil species of the genus, and a key to all fossil species of *Ampulicomorpha* is provided. This is the third European fossil species of *Ampulicomorpha*, which suggests that the genus was once well established in Western Europe while it is more widely distributed in the Eastern Palaearctic region today. A list of all fossil and extant Embolemidae of the world, as well as a map of their geographical distribution map, are provided.

Keywords: Insecta / Hymenoptera / Chrysoidea / Paleogene / Oise amber / France

Résumé – Une nouvelle espèce d'*Ampulicomorpha* Ashmead (Hymenoptera : Chrysoidea) dans l'ambre éocène de France. Les Embolemidés sont un groupe cosmopolite mais peu diversifié de guêpes chrysoïdes au registre fossile rare, malgré une longue histoire évolutive depuis au moins le Crétacé inférieur. Une nouvelle espèce, *Ampulicomorpha quesnoyensis* sp. nov., est illustrée et décrite à partir d'une femelle trouvée dans l'ambre éocène inférieur de l'Oise (France). Elle est comparée aux trois autres espèces connues pour ce genre et une clé des espèces fossiles d'*Ampulicomorpha* est proposée. Il s'agit de la troisième espèce européenne fossile d'*Ampulicomorpha*, ce qui suggère que le genre était autrefois bien établi en Europe de l'Ouest alors qu'il est davantage présent dans l'Est de la région Paléarctique aujourd'hui. Une liste des espèces fossiles et actuelles d'Embolemidae du monde ainsi qu'une carte de leur distribution géographique sont aussi proposées.

Mots clés : insectes / hyménoptères / chrysoïdes / Paléogène / ambre de l'Oise / France

1 Introduction

Embolemidae is one of the smallest and least known families among Chrysoidea, currently with 62 extant species described in three genera (see list in Supplementary material: Appendix A): the cosmopolitan *Embolemus* Westwood, 1833 and *Ampulicomorpha* Ashmead, 1893; and *Trogloembolemus* Olmi, Mita and Guglielmino, 2014, which is known only from two troglobitic species from Japan (Mita and Olmi, 2018).

Extant embolemid wasps are parasitoids on nymphs of the planthopper families Cixiidae (for *Embolemus*) and Achilidae (for *Ampulicomorpha*), but knowledge on their biology remains very limited due to their cryptic behavior and tiny size (varying from 1 to 7 mm), making them difficult to find and observe (Olmi, 1995). Within the superfamily Chrysoidea, Embolemidae has consistently been retrieved as sister to Dryinidae (Brothers and Carpenter, 1993; Carr *et al.*, 2010; Brothers, 2011; Branstetter *et al.*, 2017), although the group has rarely been incorporated in higher-level phylogenies of Hymenoptera to place it in a broader context.

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Fig. 1. Distribution of all extant and extinct genera of Embolemidae on a present-day map (data compiled from Olmi, 1995 and all subsequent works on Embolemidae; see Appendix A in Supplementary material).

Morphologically, embolemid wasps are easily discernible from other Chrysidoidea by their 10-segmented antennae that are inserted far from the mouthparts and, in extant genera, on a frontal prominence (but prominence absent in the extinct genera *Cretembolemus* Olmi, Rasnitsyn, Brothers and Guglielmino, 2014; *Baissobius* Rasnitsyn, 1975; and *Embolemopsis* Olmi, Rasnitsyn and Guglielmino, 2010). They are also noticeable for their sexual dimorphism, as several other chrysidoid families, the males being macropterous while females are either micropterous or brachypterous in *Embolemus*, but macropterous in *Ampulicomorpha*. The distinction between males of both genera is more challenging, based only on the second cubital cell of the fore wing being closed by distinctly pigmented veins in *Ampulicomorpha*, and open or closed by weakly pigmented veins in *Embolemus*. Hence, the synonymy of both genera proposed by van Achterberg and van Kats (2000), which is still controversial as the genera seem to have different hosts and biology and the females are clearly distinct (Olmi *et al.*, 2014c; Contarini *et al.*, 2020). An ongoing molecular analysis of species of both genera will hopefully help clarify this situation (note from M. Olmi in Contarini *et al.*, 2020). Meanwhile, we keep considering *Ampulicomorpha* as a distinct, valid genus in the present work.

Fossil Embolemidae are known from rock imprints and inclusions in amber but remain infrequent, with only 11 species recognized to date (Fig. 1: eight species from five Cretaceous deposits, three species from two Eocene deposits). But we are aware of a work in progress by Perkovsky *et al.* (in prep.), in which all known fossil embolemids are reviewed and several new species are described, including new species of *Embolemus* from mid-Cretaceous Burmese (Kachin) amber as well as the oldest known embolemid, from the Early Barremian amber of the Isle of Wight (ca. 128 Ma). Interestingly, it belongs to the extinct genus *Embolemopsis*, which is otherwise known only from an Aptian-aged rock imprint from Siberia (Olmi *et al.*, 2010). So far, this is the only

genus found both as a rock imprint and an amber inclusion. Other species in rock imprints similarly belong to extinct genera, namely *Baissobius* and *Cretembolemus*, while other amber fossils belong to either *Embolemus* or *Ampulicomorpha*. Remarkably, these two extant genera are recorded as early as in the mid-Cretaceous, 100–105 Ma (including undescribed species of *Embolemus* from Kachin amber, pers. obs.). And these Burmese fossils already display a dimorphism similar to extant ones, indicating a long-term morphological stasis in these lineages.

Here we describe a new fossil species of *Ampulicomorpha* based on a single female specimen from Early Eocene Oise amber, France. This is the second species of *Ampulicomorpha* from the Eocene of Europe, and the first fossil record of the family Embolemidae in France.

2 Material and methods

The description below is based on a single individual found in amber from the Le Quesnoy outcrop, near Houdancourt in the Oise Department of the Paris Basin, France. The outcrop, dated as Ypresian in age ('Sparnacian', Early Eocene, ca. 53 Ma), has yielded a copious amount of fossiliferous amber associated with abundant plant remains and a diverse vertebrate fauna. Further details on the geology, biodiversity, and paleoenvironment can be found in Nel *et al.* (1999, 2004), Cavagnetto (2000), Brasero *et al.* (2009), or Nel and Brasero (2010).

The wasp was found preserved in an automorph, cylindrical piece of orange amber approximately 4.0 mm in diameter. The piece was partly polished to remove the opaque weathered surface using Buehler CarbiMet silicon carbide papers on a Buehler Metaserv 3000 polisher. Then, it was immersed in Canada balsam between cover slips for optimal views. Observations, measurements, and photographs were made using a Leica MZ APO stereomicroscope equipped with an ocular micrometer and a Canon 5D Mark II SLR camera.

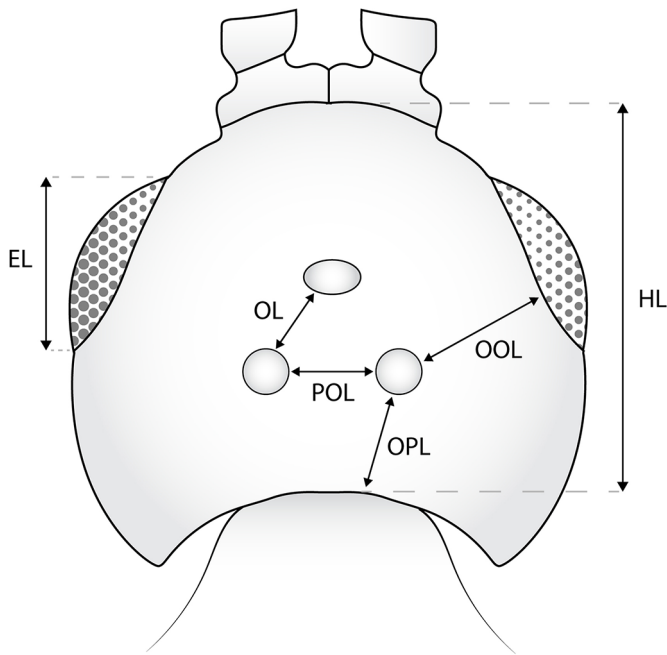


Fig. 2. Schematic line drawing of the head of an embolemid wasp, with indication of measurements used in the present study.

Helicon Focus 6.7 software was used to build composite images from a series of photographs taken at different focal planes. The resulting images and figures were processed using Adobe CC (Photoshop, Illustrator), which was also used to compose the map in [Figure 1](#).

The specimen is preserved without apparent distortion and is mostly complete, missing the tarsomeres of right mid leg, the femoro-tibial articulation of the right hind leg, the left hind leg beyond the femur, the posterodorsal portion of the mesosoma, and most of the wings except basal portions and the apical portion of the right fore and hind wings. The wings and mesosomal structures were apparently lost in an amber splintering that likely occurred during the field collecting or the washing of the amber material.

The terminology used in this study generally follows that of [Lanes *et al.* \(2020\)](#) pertaining to Bethyliidae, with additions of [Olmi \(1995\)](#) or [Olmi *et al.* \(2014c\)](#) for all the ocellar measurements, which are detailed below with other measurements and indices, and illustrated in [Figure 2](#).

- BL: body length: in dorsal view, median longitudinal line from anteriormost point of frontal projection to posteriormost point of visible gaster (\neq from gastral apex if apical gastral segments curved ventrally).
- HL: head length: in dorsal view, median longitudinal line from anteriormost point of frontal projection to posterior margin of the occiput.
- EL: eye length: maximum diameter of compound eye measured in oblique lateral view.
- OL: ocellar line: minimum distance between inner margin of lateral ocellus and median (anterior) ocellus.
- OOL: ocular-ocellar line: minimum distance from outer margin of lateral ocellus to compound eye.
- OPL: ocellar-occipital line: minimum distance from posterior edge of lateral ocellus to occipital carina.

- POL: postocellar line: minimum distance between inner margins of lateral ocelli.

This published work and the nomenclatural acts it contains have been registered in ZooBank (<http://www.zoobank.org/>, last access: 21 May 2020), with the following LSID (reference): urn:lsid:zoobank.org:pub:25DF8ED3-96F9-498A-BA08-01EE288C15F6.

3 Systematic palaeontology

Order HYMENOPTERA [Linnaeus, 1758](#)
 Suborder APOCRITA [Gerstaecker, 1867](#)
 Superfamily CHRYSIDOIDEA [Latreille, 1802](#)
 Family EMBOLEMIDAE [Förster, 1856](#)
 Genus *Ampulicomorpha* [Ashmead, 1893](#)

Type species *Ampulicomorpha confusa* [Ashmead, 1893](#): 79.
Diagnosis. See [Olmi \(1995\)](#), [Olmi *et al.* \(2014a\)](#).

Ampulicomorpha quesnoyensis sp. nov.

LSID (species): urn:lsid:zoobank.org:act:B8AC5E69-BDC9-4FDC-B22B-B270DE955B39

[Figures 3, 4](#)

Holotype. Specimen MNHN.F.A58662, female, housed in the Paleontological collection of the Muséum national d’Histoire naturelle, Paris, France.

Type locality. Le Quesnoy outcrop, Chevrières near Houdancourt, Department of Oise, France.

Type horizon. Lowermost Eocene, Ypresian, biozone MP7 of the reference mammal fauna of Dormaal (= ‘Sparnacian’, ca. 53 Ma) ([Feugueur, 1963](#); [Nel *et al.*, 1999](#); [Cavagnetto, 2000](#))

Etymology. The specific epithet is derived from the Le Quesnoy outcrop, the type locality from which the new species originates.

Diagnosis. Antenna with scape approximately $5.4\times$ as long as pedicel; mesosoma not distinctly elongate (only $1.8\times$ as long as broad); pronotum with complete median, longitudinal furrow; mesoscuto-scutellar suture medially sulcate, the sulcus bifoveate metasomal petiole elongate, approximately subequal in length to metatrochanter.

Description. Female, macropterous ([Fig. 3C](#): basal portions of all wings and apicalmost portions of the right fore and hind wings are the only preserved parts; but the fore wing reaches the second gastral segment, thus indicating macroptery). Body length 3.15 mm as visible dorsally (but gaster curved ventrally and anteriorly, total length in lateral view 4.30 mm). Head pyriform, slightly longer than high, 0.60 mm long; eye rather large, higher than long, slightly less than half as long as head (0.25 mm long). Antennae filiform, inserted on two contiguous frontal projections; scape elongate, $1.7\times$ as long as first flagellomere; first flagellomere approximately $2.5\times$ as long as broad, following flagellomeres gradually shortening except apical one which is longest, with rounded tip; length of antennomeres (in mm): 0.65, 0.12, 0.38, 0.35, 0.30, 0.28, 0.26, 0.26, 0.20, 0.24; distance between antennal sockets and clypeus 0.25 mm; ocelli conspicuous, OL = 0.08, OOL = 0.18, OPL = 0.24, POL = 0.09; occipital carina distinct in dorsal and lateral views; mandible tridentate, subrectangular, about twice as long as broad, outer surface slightly convex; maxillary palps with five visible segments, basal segment widest; labial palps not visible.

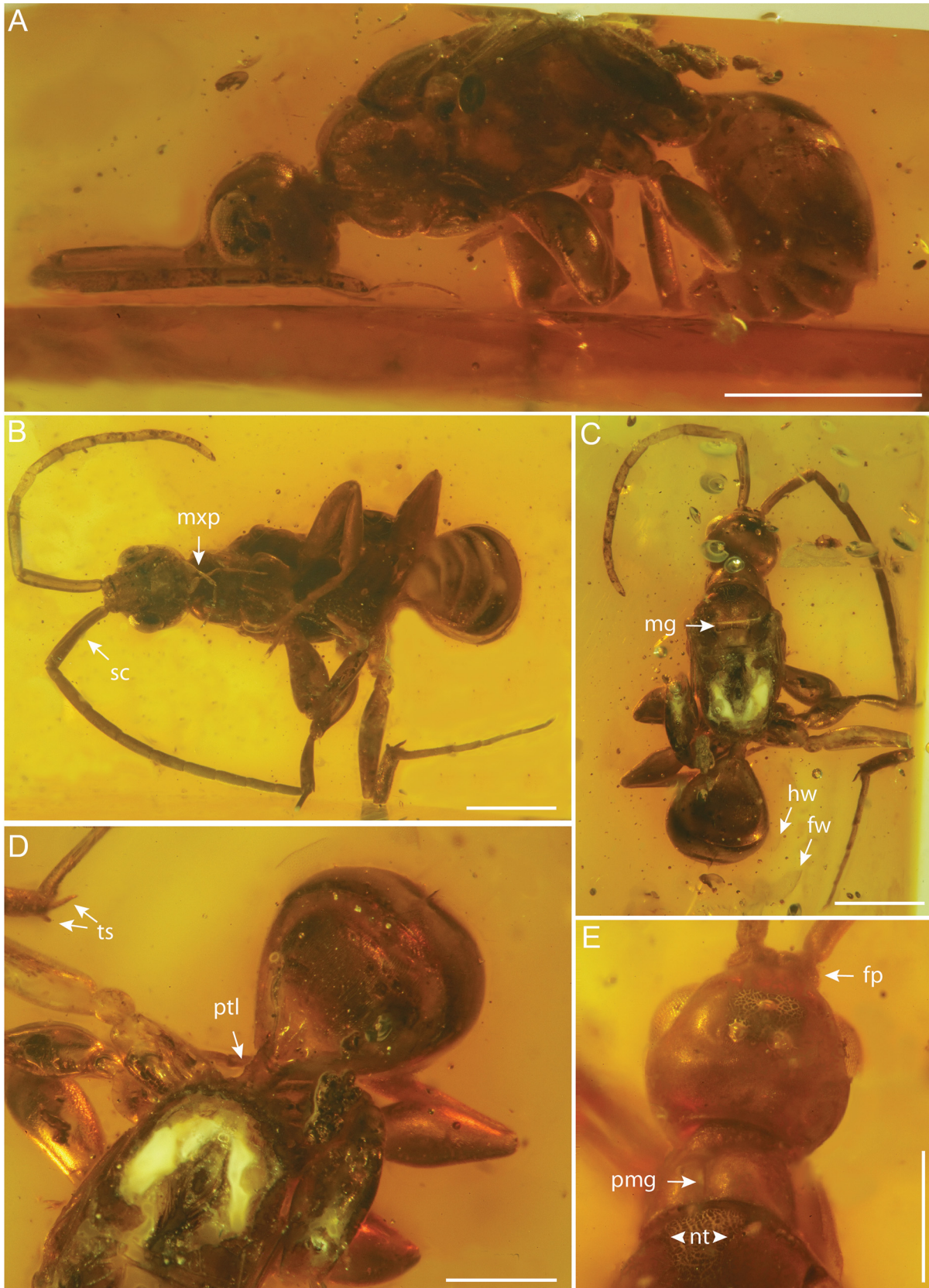


Fig. 3. *Ampulicomorpha quesnoyensis* sp. nov., holotype MNHN.F.A58662 (female), from Eocene Oise amber (France). A. Habitus in left lateral view. B. Ventral and frontal views, showing maxillary palps (mxp) and scape (sc). C. Dorsal view, showing apex of fore wing (fw) and hind wing (ha), and mesoscuto-scutellar groove (mg). D. Laterodorsal view showing metasomal petiole (ptl) and hind tibial spurs (ts). E. Dorsal view of head, pronotum and mesoscutum, showing contiguous frontal projections (fp), pronotal median groove (pmg), and notauli (ntl). Scale bars: 1 mm (A, B, C), 0.5 mm (D, E).

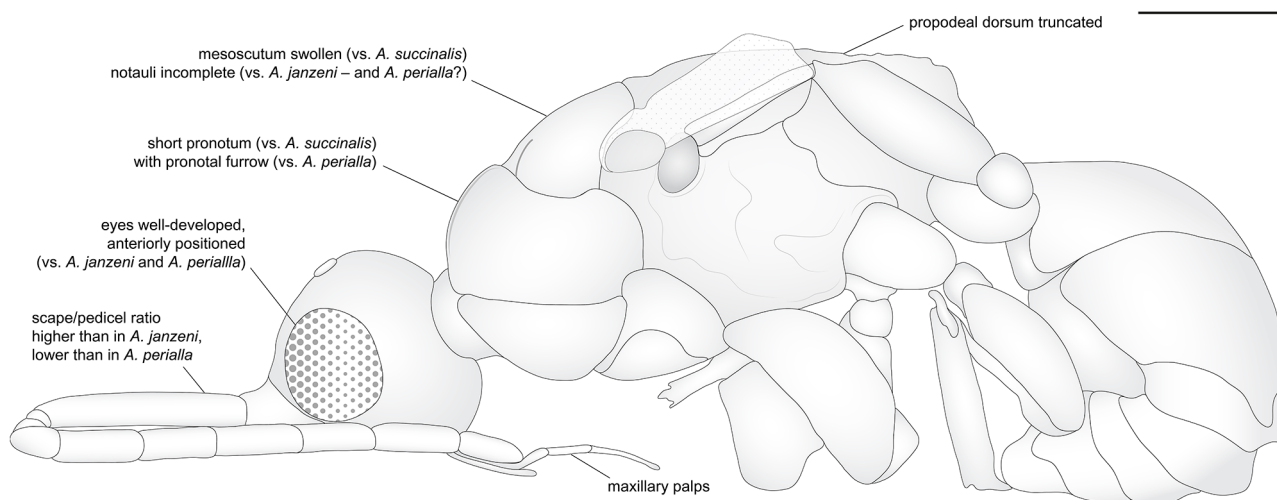


Fig. 4. *Ampulicomorpha quesnoyensis* sp. nov., holotype MNHN.F.A58662 (female), from Eocene Oise amber (France). Line drawing of the habitus in left lateral view, with indication of the differential characters compared with other fossil species of *Ampulicomorpha*. Scale bar: 0.5 mm.

Table 1. Comparison of *Ampulicomorpha quesnoyensis* sp. nov. with other fossil species of *Ampulicomorpha* (females only).

	<i>A. quesnoyensis</i> sp. nov.	<i>A. succinalis</i>	<i>A. janzeni</i>	<i>A. perialla</i>
Body length (mm)	4.3	4.1–4.8 (5.5 in lost holotype)	2.9	3.3
Eye length	0.4× head length	0.3–0.4× head length	0.3× head length	ca. 0.25× head length
Eye position	Head's anterior half	Head's anterior half	Head's midlength	Head's midlength
Scape	5.4× pedicel length	4.85–6× pedicel length	3× pedicel length	7.25× pedicel length
Pronotal furrow	Complete	Complete	Complete	Absent
Notauli	Incomplete, ca. 0.5× mesoscutal length	Incomplete, 0.25–0.3× mesoscutal length	Complete	Present, apparently complete
Fore wing	Reaching 2nd gastral segment; vein 2Cu-a not preserved	Surpassing 2nd gastral segment; vein 2Cu-a pigmented	Reaching near gastral apex; vein 2Cu-a pigmented	Surpassing 2nd gastral segment; vein 2Cu-a 'nebulous'
Petiole length	Subequal to metatrochanter	Shorter (0.6×) than metatrochanter	Subequal to metatrochanter	Shorter to or at most subequal to metatrochanter

Data taken from original descriptions, refined descriptions in Perkovsky *et al.* (in prep.), or personal examination of *A. janzeni* – holotype and additional specimens.

Mesosoma. Moderately elongate, about 1.8× as long as broad, broadest at level of mesopleura. Pronotum short; in dorsal view, approximately one eighth of mesosomal length, distinctly narrower than remaining mesosoma, with anterior pronotal margin rounded and median longitudinal pronotal furrow complete, not deep. Mesoscutum with notauli incomplete, reaching only near half of mesoscutal length, widely separated posteriorly; faint parapsidal lines not reaching anterior mesoscutal margin. Mesoscuto-scutellar suture medially sulcate, foveate. Metanotum short, transverse. Propodeum mostly missing but sculptured as evidenced by remaining carinae on few preserved lateral and posterior surfaces. Mesopleuron indistinct, apparently unsculptured. Wings almost entirely missing, venation not visible. Legs robust, all femora distinctly swollen; length of metacoxa, metatrochanter, metafemur, metatibia (in mm) = 0.50, 0.15, ca. 0.85, ca. 0.60; tibial spurs 1/2/2.

Metasoma. First gastral segment with anterior petiole approximately as long as metatrochanter (ca. 0.16 mm); first segment distinctly widening posteriorly, about as long as apical width; second gastral segment largest of metasomal segments; following segments progressively smaller, curved downward, nearly at right angle from first two segments.

4 Discussion

Female emboleimid wasps typically have the antennal scape elongate, much longer than the third antennal segment (Olmi, 1995), which clearly is the case of the newly described specimen (Figs. 3A–C). The new species, being a macropterous female with the antennae inserted on two contiguous frontal projections, is thus assignable to *Ampulicomorpha* according to Olmi (1995) or Olmi *et al.* (2014a). Additionally, the rather large eyes of the new fossil also suggest this genus

rather than *Embolemus*, which is characterized by distinctly smaller eyes in females. If the fore wing was preserved, it would likely display a second cubital cell (2Cu_{2c} *sensu* Lanes *et al.*, 2020) fully enclosed by pigmented veins.

The female of the new species differs from those of the two species of *Ampulicomorpha* described from the Cretaceous, *A. perialla* (Ortega-Blanco, Delclòs and Engel, 2011) and *A. janzeni* Olmi, Rasnitsyn, Brothers and Guglielmino, 2014, by its larger size, comparatively larger eyes, and antennal ratios (Tab. 1). The new species is more similar to the Eocene species *A. succinalis* Brues, 1933, but it differs from it, in females, by its comparatively longer metasomal petiole, longer scape (5.4× pedicel length in holotype of *A. quesnoyensis*, vs. 4.8× in specimen PIN 964/648 of *A. succinalis*, which has a similar body length), longer notauli (ca. 0.5× mesoscutal length, vs. 0.3× mesoscutal length in *A. succinalis*), and the presence of a conspicuous, foveate, mesoscuto-scutellar sulcus. Here we propose a key to fossil species of *Ampulicomorpha* based on females, to accommodate the new species. Unpublished, complementary features of *A. perialla* were kindly provided by Massimo Olmi who re-examined the type specimen for a global review of all fossil Embolemidae.

Key to fossil species of *Ampulicomorpha*:

- 1 Antenna with scape more than 7× longer than pedicel; pronotum without median longitudinal furrow . . . *A. perialla* (Ortega-Blanco, Delclòs and Engel) (Peñacerada amber)
 - Antenna with scape at most 6× longer than 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 Body length 2.9 mm; scape 3× longer than pedicel; notauli complete . . . *A. janzeni* Olmi, Rasnitsyn, Brothers and Guglielmino (Kachin amber)
 - Body length 4.3 mm; scape 5.4× longer than pedicel; notauli incomplete . . . *A. quesnoyensis* sp. nov. (Oise amber)

5 Conclusion

The newly described species of *Ampulicomorpha* adds to the scant knowledge of the evolutionary history of embolemid wasps. The current fossil record shows that the genus occurred in territories that today belong to the western Palaeartic region from, at least, the late Early Cretaceous (*A. perialla* from the Albian of Spain) until the Late Eocene (*A. succinalis* from the Priabonian of the ‘Baltic amber forest’). Today, the Palaeartic species of *Ampulicomorpha* are almost exclusively restricted to its eastern part (Olmi, 1995; Xu *et al.*, 2012; Olmi *et al.*, 2014a; Kim and Lee, 2016; Mita *et al.*, 2017), with the exception of *A. thauma* Rasnitsyn and Matveev, 1989 in the southwest of Russia (Rasnitsyn and Matveev, 1989; Olmi *et al.*, 2014a) and *A. reticulata* (van Achterberg and van Kats, 2000) in the Netherlands (originally described as *Embolemus reticulatus* but from a macropterous female, so it has been transferred in *Ampulicomorpha* by Olmi *et al.* (2014c) who rejected the synonymy of both genera). In contrast, the only genus broadly distributed today in the western Palaeartic

region is *Embolemus* (Olmi, 1994; Hansen and Olmi, 1996) (Fig. 1).

Supplementary material

Appendix A: List of fossil and extant Embolemidae of the world.

Appendix B: Supplementary references cited in Appendix A.

The Supplementary Material is available at <http://www.bsgf.fr/10.1051/bsgf/2020020/olm>.

Acknowledgements. We thank Jean-Paul Saint Martin and Simona Saint Martin, *BSGF* guest editors, for the invitation to contribute to this thematic volume on Amber. We also thank Massimo Olmi (Univ. Tuscia, Italy) for information and bibliography on embolemids; and Massimo Olmi and an anonymous reviewer for their helpful comments on the manuscript. Collection of the amber material was made possible thanks to the Lafarge-Granulat company and the Langlois-Meurinne family. This work was partly contributed by C. Chény and E. Guillam during their Master studies, and partial support was provided by Géosciences Rennes through a grant to E. Guillam. Examination of *A. janzeni* at the SMNS (Stuttgart) was made possible thanks to Karin Wolf-Schwenninger.

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Cite this article as: Chény C, Guillam E, Nel A, Perrichot V. 2020. A new species of *Ampulicomorpha* Ashmead from Eocene French amber, with a list of fossil and extant Embolemidae (Insecta: Hymenoptera) of the world, *BSGF - Earth Sciences Bulletin* 191: 20.