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A new *Myrmecarchaea* (Araneae: Archaeidae) species from Oise amber (earliest Eocene, France)

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Abstract – Extant Archaeidae, also known as pelican or assassin spiders, have an Austral distribution (South Africa, Madagascar and Australia), but were present in Eurasia during the Mesozoic and Cenozoic, as attested by fossils from Cretaceous Burmese amber (Ross A. 2019. *Burmese (Myanmar) amber checklist and bibliography 2018. Palaeoentomology 2(1): 22–84*) and Eocene European ambers (Wunderlich J. 2004. *Fossil spiders in amber and copal: conclusions, revisions, new taxa and family diagnoses of fossil and extant taxa. Hirschberg-Leutershausen: Ed. Joerg Wunderlich, 1893 p.*). They have been known to occur in Oise amber (Ypresian, early Eocene, MP7), from northern France. However, they are not abundant in Oise amber, and have been the subject of few studies until now. Here, we describe the only well-preserved, almost complete, archaeid fossil specimen. This adult male is described as *Myrmecarchaea antecessor* sp. nov, based on the presence of unique morphological features. The elongate petiolus and extremely long legs are characteristic of the genus *Myrmecarchaea* from the Middle Eocene Baltic amber. However, unique traits such as the thick, stout petiolus and the extremely elongated, posteriorly tapering cephalothorax distinguish it from the other species of *Myrmecarchaea*. This specimen is of high interest, as besides being a new species, it is also the first documented adult male in the genus, allowing us to observe sexual characters for the first time. Furthermore, it is the first occurrence of this genus outside Baltic amber, showing affinities between Oise and Baltic ambers, which are, otherwise, very different in their faunistic compositions, and further extends the known past range of the archaeid spiders.

Keywords: Archaeidae / Ypresian / Oise amber / Araneae / taxonomy / palaeontology

Résumé – Nouvelle espèce dans le genre *Myrmecarchaea* (Araneae: Archaeidae) de l'ambre de l'Oise (Yprésien, Eocène basal, France). Actuellement, les Archaeidae, connues sous les noms communs d'araignées-pélicans ou araignées-assassins, ont une distribution australe (Afrique du Sud, Madagascar, Australie), mais peuplaient l'Eurasie durant le Mésozoïque et le Cénozoïque, comme l'attestent les fossiles de l'ambre du Crétacé de Birmanie (Ross A. 2019. *Burmese (Myanmar) amber checklist and bibliography 2018. Palaeoentomology 2(1): 22–84*) et de l'Eocène d'Europe (Wunderlich J. 2004. *Fossil spiders in amber and copal: conclusions, revisions, new taxa and family diagnoses of fossil and extant taxa. Hirschberg-Leutershausen: Ed. Joerg Wunderlich, 1893 p.*). Leur présence est connue de longue date dans l'ambre de l'Oise (Yprésien, MP7, Eocène basal), dans le nord de la France. Néanmoins, elles n'y sont pas abondantes, et n'ont été que peu étudiées par le passé. Nous décrivons dans cette publication le seul spécimen bien préservé et presque complet. Ce mâle adulte est décrit ici comme *Myrmecarchaea antecessor* sp. nov., sur la base de caractères morphologiques uniques. Le pédicelle allongé et les pattes extrêmement longues sont caractéristiques du genre *Myrmecarchaea* de l'ambre de la Baltique, de l'Eocène moyen. Cependant, des caractères uniques comme l'épaisseur et la robustesse du pédicelle et le céphalothorax très allongé, s'affinant progressivement dans sa partie postérieure, le distinguent des autres espèces du genre *Myrmecarchaea*. Ce spécimen est particulièrement intéressant car, en plus d'appartenir à une espèce nouvelle, il est aussi le premier mâle adulte connu du genre, ce qui nous permet d'observer pour la première

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fois la structure des pièces génitales. De plus, il s'agit de la première occurrence de ce genre hors de l'ambre de la Baltique, démontrant des affinités entre ces ambres qui sont, par ailleurs, très différents dans la composition de leurs paléofaunes, et étend la répartition fossile connue de la famille.

Mots clés : Archaecidae / Yprésien / ambre de l'Oise / Araneae / taxonomie

1 Introduction

Oise amber (Ypresian, reference level MP7, 55–53 Ma) is one of the oldest known Cenozoic fossil resins (Penney, 2010), and, with more than 20,000 identified inclusions (Brasero *et al.*, 2009), is the best-known deposit from the sparsely recorded earliest Eocene. While insects have been extensively studied and described (see Brasero *et al.*, 2009, for a comprehensive list), arachnids (spiders, scorpions, mites and their relatives) are not as well-known. Penney (2006, 2007a, 2007b) described four species in the spider families Oonopidae, Selenopidae, Anapidae and Pholcidae, and also recorded the presence of the spider families Archaecidae, Hersiliidae, Segestriidae, Uloboridae and questionable Ageleidae and Tetragnathidae. A more recent study (Carbuccia *et al.*, *in press*) yielded 23 families, including the ones identified by Penney (2006, 2007a, 2007b), and a new species in the family Segestriidae. Spiders are thus quite diverse in Oise amber, although, with 296 registered specimens, they are not especially abundant, representing less than 2% of the inclusions (*ibid.*).

Except for the four aforementioned species, Oise amber spiders have mostly been identified at family level, and seldom at the species or genus level. The assemblage of Oise amber spiders, in its composition, is markedly different (Carbuccia *et al.*, *in press*) from the geographically close, albeit more recent, Central European Palaeogene ambers (Baltic, Bitterfeld and Rovno ambers). Differences between these assemblages are not surprising, as the global climate underwent some quick and drastic climatic shifts during the terminal Paleocene and early Eocene (Röhl *et al.*, 2007; Zachos *et al.*, 2008). Oise amber is indeed situated in geological time at a thermal optimum, between the PETM (Paleocene-Eocene Thermal Maximum) and the EECO (Early Eocene Climatic Optimum), two short, but extreme (Röhl *et al.*, 2007; Zachos *et al.*, 2008) global warming events that allowed the existence of paratropical environments, with taxa that would later become restricted to intertropical zones (Saupe *et al.*, 2019) occurring high latitudes. Meanwhile, the younger Baltic amber forests seem to have been a much cooler, mesothermal environment (Wolfe *et al.*, 2015; Sadowski *et al.*, 2017).

However, because of the geographic proximity of Oise and Baltic ambers, one would expect the taxa in the families shared by both of these sites to be somewhat closely related. This seems to be the case with the adult male Archaecidae from Oise amber that we describe here. The genus to which this species belongs, *Myrmecarchaea*, has thus far only been described from Baltic amber (Wunderlich, 2004), so this new species thereby extends the geographical range into western Europe, and extends its time range to basal Ypresian.

2 Material and methods

2.1 Material

The amber fragment containing the spider described herein has been excavated at the Le Quesnoy site (Oise), which is now permanently flooded and inaccessible. Oise amber occurs in clayey sands containing lignite and continental vertebrate remains, a formation known as “argiles à lignites du Soissonnais” (Nel *et al.*, 1999). These strata correspond to a hypoxic freshwater palaeoenvironment. Transport is minimal, as attested by some fossil wood fragments still associated with amber (Nel *et al.*, 1999). The vertebrate groups found in Le Quesnoy are the same as in the Dormaal reference locality (Nel *et al.*, 1999), thus allowing unequivocal dating as lowermost Eocene (MP7).

3 Methods

The amber fragment went through a preliminary observation to evaluate the quality of the sample and to locate the position of the inclusion. Then, the fragment was faceted with a Crystal Master Pro 12 polisher; and scratches and marks on the facets were polished with diatomite. Preparation of the inclusion was kept to a minimum in order to preserve, as much as possible, the general shape and structure of the amber sample, and to minimize the loss of taphonomic information.

Observations were made with a Nikon SMZ25 stereomicroscope, with optic fibre auxiliary light. The fragment was immersed in tap water (as Oise amber seems slightly soluble in ethanol) during observation. High definition photographs were taken using a Nikon D800 camera attached to the microscope, activated from a distance with Helicon Remote[®], and then stacked with Adobe[®] Photoshop CS6 and adjusted for contrast and sharpness. Drawings were made by hand using a drawing tube attached to a Wild M3C stereomicroscope. Because a different microscope was used for drawings and photographs, for the same illustrated body part, the angles may differ slightly.

4 Results

4.1 Family Archaecidae Koch and Berendt (1854)

Genus *Myrmecarchaea* Wunderlich (2004) (type species: *Myrmecarchaea petiolus* Wunderlich, 2004)

Wunderlich (2004) described the genus *Myrmecarchaea* based on the remarkably elongated petiolus, longer than the width of the carapace. He described two species, *M. petiolus* and *Myrmecarchaea pediculus*, both from Baltic amber, which was, until now, the only known occurrence of the genus. Nothing is known about their behaviour, but their peculiar morphology was interpreted as possible ant or wasp mimicry (Wunderlich, 2004).

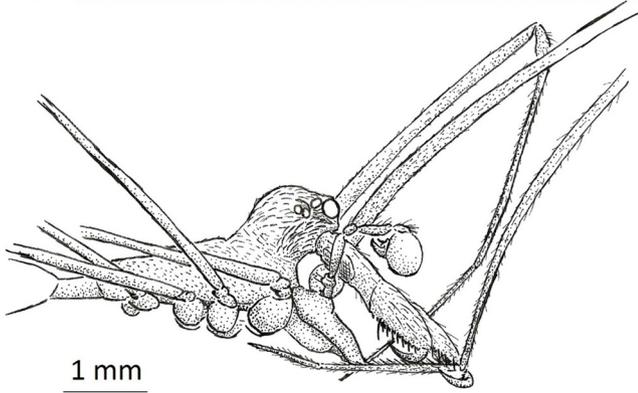
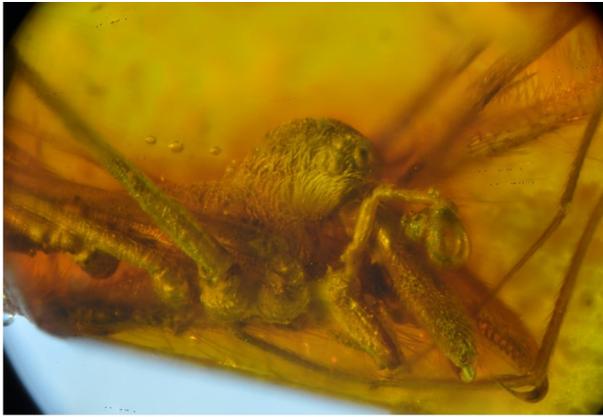


Fig. 1. *Myrmecarchaea antecessor* sp. nov., holotype MNHN.F. A71310, lateral view. (photograph and drawing: B. Carbuccia).

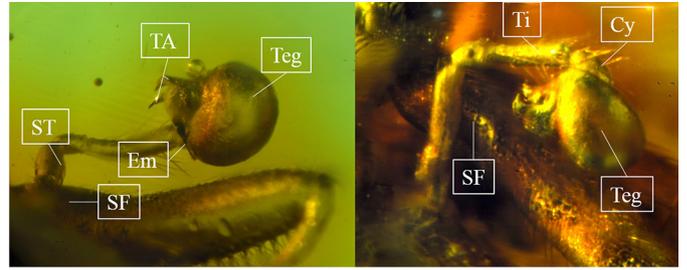


Fig. 3. *Myrmecarchaea antecessor* sp. nov., holotype MNHN.F. A71310, details of genitalia. Teg: tegulum; TA: tegular apophyses; Em: embolus; ST: stridulatory teeth; SF: stridulatory file; Ti: tibia; Cy: cymbium (photograph: B. Carbuccia).

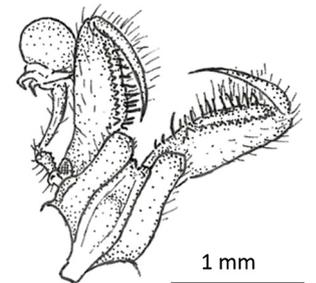


Fig. 4. *Myrmecarchaea antecessor* sp. nov., holotype MNHN.F. A71310, mouthparts (photograph and drawing: B. Carbuccia).



Fig. 2. *Myrmecarchaea antecessor* sp. nov., holotype MNHN.F. A71310, ventral view. C3: coxa 3; C4: coxa 4 (photograph: B. Carbuccia).

***Myrmecarchaea antecessor* sp. nov.**

Etymology: “antecessor”: Deverbal noun of the Latin verb “antecedo”, which means “to precede, to predate”. “Antecessor” literally means “the one which predates”, as *M. antecessor* sp. nov. is older than all the previously known *Myrmecarchaea* species.

Material: holotype MNHN.F.A71310 (PA 12262, adult male) in Oise amber, deposited in the Palaeontological collections of the Muséum National d’Histoire Naturelle (MNHN), Paris, France.

Type locality and horizon: Le Quesnoy (Oise), in the Sparnacian (lower Ypresian) “argiles à lignites du Soissonnais”.

Preservation and syninclusions: in a very clear, but broken, cylindrical amber fragment (diameter 6 mm) no syninclusions, except a very large, hairy spider leg on the left side of the specimen, partly hiding its ventral side. Very well-preserved but incomplete: posterior part of the abdomen, and parts of legs are missing.

Diagnosis: (male; female unknown) head region raised and strongly individualized, with a very short “neck”, that forms a marked angle with the thoracic part (Fig. 1). Coxae IV are separated from the coxae III by a noticeable diastema (space between coxae III and IV $2.8 \times$ the length of the space between coxae II and III), and a clear thoracic constriction between coxae III and IV (Fig. 2). Male palp (Figs. 3 and 4) with long, thin setae on the tibia and cymbium. Tegulum large, bean-shaped, embolus thick and relatively long, almost straight, with two strongly recurved, relatively large embolic apophyses. Thoracic region is very long and narrow, and markedly elongated posteriorly, the part behind coxae II represents $3/5$ of the total cephalothorax length, while it is only $1/3$ in *M. pediculus* (Fig. 5). Petiolus relatively short (less than half the length of the cephalothorax) and thick, compared to the Baltic species (Figs. 5 and 6), $2.8 \times$ longer than wide.

Description: body (chelicerae excluded) 5.0 mm long. Carapace 3.0 mm long, opisthosoma 2.0 mm long (note that the posterior part of the abdomen is broken off).

Chelicerae (Fig. 4): fairly long (1.0 mm) and robust, distal half slightly recurved, with 14 peg teeth on the promargin, the longest at the proximal end of the cheliceral furrow, and 12 true

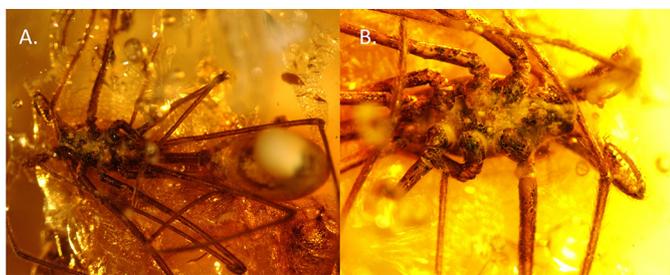


Fig. 5. *Myrmecarchaea pediculus* Wunderlich (2004), possible adult female, holotype, Geologisch Paläontologisches Institute und Museum (GPIH) specimen No. S3907/4338. A: general habitus, ventral view; B: Prosoma, ventral view (photographs: H. Wood).



Fig. 6. *Myrmecarchaea petiolus* Wunderlich (2004), juvenile male, holotype, GPIH specimen No. S3999/4337. A: general habitus, dorsal view; B: detail of the carapace (photos: H. Wood).

teeth on the retromargin. The fangs are long and slightly curved, about half as long as the basal segment.

Stridulatory apparatus (Fig. 3): same as in *Archaea paradoxa* Koch and Berendt (1854) (Fig. 7).

Mouthparts (Fig. 4), very long, labium long and narrow, fusiform, with an apical incision.

Cephalothorax (Figs. 1 and 2), very long, $2.5 \times$ longer than wide, $1.7 \times$ longer than wide in *M. pediculus* (Fig. 5). Cephalic region large, raised, protruding forward and separated from the thoracic region by a very distinct constriction forming a short and thick “neck”, unlike *M. petiolus* (Fig. 6) in which the cephalic part is not sharply raised. The “head” is globally rounded, slightly flattened at the top, without spines, and covered with short setae on the top and longer, plumose setae on the sides. Thoracic region long and narrow, markedly tapering posteriorly; coxae IV conspicuously separated from the other three (Fig. 2).

Eyes (Fig. 1): the eyes are relatively close to each other, with the anterior median eyes $2.5 \times$ larger than the other eyes and anteriorly oriented. Lateral eyes contiguous and on a small hump.

Opisthosoma (Fig. 2): petiolus (characteristic of the genus *Myrmecarchaea*) distinctly elongated, but much shorter than in the Baltic amber specimens: petiolus length is less than half of the carapace in *M. antecessor*, while in the Baltic species *M. pediculus* (Fig. 5), it is almost as long as the carapace, and $\frac{3}{4}$ of the carapace length in *M. petiolus* (Fig. 6). Rear part of the opisthosoma broken off; remaining parts suggest that it was relatively small and elongated.

Legs very long and slender; femora I and II as long as the whole body. Femur I slightly curved, with a very slight hump. Leg III shorter, femur half as long as femur I. Length of legs IV unknown, as they are incomplete.

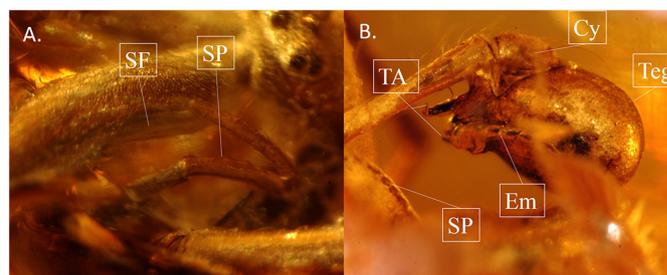


Fig. 7. *Archaea paradoxa* Koch and Berendt (1854). A: female stridulatory apparatus, Staatliches Museum für Naturkunde, Stuttgart specimen No. BB-A4000; B: male copulatory palp, Senckenberg Museum, Frankfurt Section, specimen No. SMF Be 5080. SF: stridulatory file; SP: stridulatory picks; Teg: tegulum; TA: tegular apophyses; Em: embolus; Cy: cymbium (photographs: H. Wood).

Remarks: Although the petiolus is shorter than in other *Myrmecarchaea* spp., it is still markedly more elongated (but hard to see due to its proximity to the edge of the fragment) compared to all other known archaeid species, fossil and extant. The carapace in *Myrmecarchaea* is posteriorly more elongated compared to other fossil and extant archaeids, and *M. antecessor* n. sp., compared to other *Myrmecarchaea*, has the greatest elongation. *M. antecessor* sheds light on many unknown morphological traits in this genus. As hypothesized by Wunderlich (2004), the cheliceral stridulating file is situated in the basal half of the chelicerae, very close to the base, as in *Archaea* (Fig. 7); the stridulatory apparatus is overall very similar to *Archaea paradoxa* (Fig. 7). The general structure of the male palp is also very similar to *Archaea* (Fig. 7), with the same general shape of the palpal bulb, the same orientation and shape, including a spiral of the embolus, and also with tegular apophyses in similar positions.

5 Discussion

5.1 Taxonomic placement

The genus *Myrmecarchaea* Wunderlich (2004) is diagnosed over a remarkable elongation of the petiolus, longer than the width of the carapace, and is interpreted as possible ant/wasp mimicry (Wunderlich, 2004). Very long legs and probable *Archaea*-like stridulatory organs are also mentioned as characters for the genus. *M. antecessor* sp. nov. possesses such a petiolus, although it is stouter and shorter than in the Baltic amber *Myrmecarchaea* species.

On the other hand, *M. antecessor* sp. nov. sports several unique features among *Myrmecarchaea* species, for instance the extremely elongated, tapering posterior part of the cephalothorax, with a very conspicuous diastema between the coxae III and IV. Many Archaeidae fossil genera (*Archaea*, *Baltarchaea*, *Burmesarchaea*, *Myrmecarchaea*) possess an extended, tapering posterior carapace that is truncated in extant Archaeidae, but *M. antecessor* sp. nov. is the most extreme case. A posteriorly truncated carapace is a synapomorphy of the monophyletic extant Archaeidae, and the tapering carapace observed in fossil archaeids may be a plesiomorphic trait or may be unique to Archaeidae fossils (Wood *et al.*, 2012).

M. antecessor sp. nov. also shares all the other typical *Myrmecarchaea* traits (Wunderlich, 2004), notably the extremely long legs: while incomplete, femora I are much longer than the whole body.

Besides *M. antecessor*, the genus *Myrmecarchaea* is comprised of two other species (Dunlop *et al.*, 2018): *M. petiolus* (Fig. 6), which is known from only a juvenile male specimen, and *M. pediculus* (Fig. 5), which is known from only one, possibly adult female specimen (Wunderlich, 2004). Thus, our knowledge of the genus, and of the morphological disparity among its species, is highly fragmentary. Therefore, we choose a conservative approach, including the new species in the pre-existing genus rather than creating a new monospecific taxon, as despite its peculiarities, it fits the *Myrmecarchaea* diagnosis.

However, as the morphology of adult males from the other species is unknown, some of the singularities of *M. antecessor* could actually be due to sexual dimorphism. This being said, another unidentified *Myrmecarchaea* sp., described as an immature male by Wunderlich (2004), as well as the juvenile male *M. petiolus* (Fig. 6), have a much longer petiolus. More specimens would thus be necessary for a better comprehension of this highly peculiar genus, and an improved validity of the taxonomic statements.

5.2 Archaeidae in Oise amber

The family Archaeidae is not abundant in the faunal assemblage, with only three specimens (and one moulted exoskeleton) currently registered in the MNHN collections, of which the holotype of *M. antecessor* is the most well-preserved. The two other specimens are very incomplete, with only the anterior portion of the prosoma preserved, and are likely females or juveniles due to their unmodified pedipalps. Both specimens are markedly different from the holotype of *M. antecessor*. They both seem to have smaller AME; eyes are all about the same size, and AME are widely separated. Peg teeth and true teeth also seem different, in number and repartition, from the holotype of *M. antecessor*. These differences seem to indicate Archaeidae are represented by at least two distinct taxa in Oise amber. An almost complete specimen from a private collection, that we unfortunately only saw a low-resolution picture of (de Ploëg, pers. comm.) clearly lacks the petiolus which characterizes the genus *Myrmecarchaea*. While we cannot really say much about this fossil, as we did not manage to physically observe it, it confirms the presence of several morphologically and taxonomically distinct Archaeidae in Oise amber.

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