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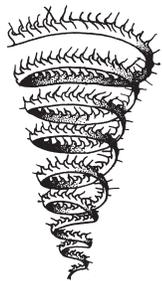
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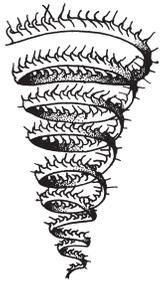
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A NEW GENUS AND SPECIES OF PEMPHREDONINE WASP IN LATE CRETACEOUS VENDEAN AMBER (HYMENOPTERA: CRABRONIDAE)

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ABSTRACT

A new genus and species of pemphredonine wasp is described and figured in Late Cretaceous (Cenomanian to Santonian) amber from Vendée, in northwestern France. *Menopsila dupeae* n. gen. and sp., is based on a partial male preserved in a small sliver of translucent amber. The genus is placed incertae sedis within the Pemphredonini, as it intermingles features, likely plesiomorphies, of various lineages within the tribe. It likely represents a stem group to one or more of the constituent subtribes, yet it is arguably most similar to the Spilomenina.

Keywords: Insecta, Apoidea, Sphéciformes, Pemphredoninae, Cretaceous, France

RÉSUMÉ

Un nouveau genre et une nouvelle espèce de guêpe pemphredonine sont décrits de l'ambre crétacé supérieur (Cénomanien à Santonien) de Vendée, nord-ouest de la France. *Menopsila dupeae* n. gen. et sp., est basé sur un mâle fragmentaire préservé dans un minuscule morceau d'ambre translucide. Le genre est placé incertae sedis au sein des Pemphredonini, car mêlant des caractères probablement plésiomorphes de plusieurs lignées de cette tribu. Il représente vraisemblablement un groupe souche de l'une ou plus des sous-tribus constitutives des Pemphredonini, mais il est sans doute plus proche des Spilomenina.

Mots-clés: Insecte, Apoïdes, Sphéciformes, Pemphredonine, Crétacé, France

INTRODUCTION

Pemphredonines comprise a widespread group of medium-sized to minute apoid wasps that typically prey on Auchenorrhyncha, Sternorrhyncha, Thysanoptera, or Collembola (Bohart & Menke, 1976). They are abundant in many terrestrial habitats and exhibit a variety of nesting tactics, utilizing tunnels in both soil and twigs for rearing progeny. They are further notable in a number of respects. For example, the only known apoid wasps to show a high degree of social behavior, *Microstigmus* and *Arpactophilus*, occur in this group (Matthews & Naumann, 1989; Matthews, 1991). The latter has undergone a remarkable radiation in the Australasian region where it

is represented by 43 named (Menke, 1989; Bohart, 1999; Pulawski, 2013) and numerous undescribed species (Matthews & Naumann, 2002; Ohl & Bennett, 2009).

Bohart and Menke (1976) divided the Pemphredoninae into the tribes Psenini and Pemphredonini. They further arranged the latter among the subtribes Ammoplanina, Pemphredonina, and Stigmia. Four genera of the Stigmia sensu Bohart and Menke (1976) have since been removed and comprise the Spilomenina (Menke, 1989; Prentice, 1998; Melo, 1999; Pulawski, 2013 – although refer to Antropov, 2011, for an alternative arrangement of tribes and subtribes). The cladistic analyses of Prentice (1998) and Melo (1999) provided strong support for this basic arrangement, but the rela-

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tionships between the pemphredonine subtribes are unknown and untested. Prentice (op. cit.) did, however, posit two possible partial reconstructions based on conflicting character data: Ammoplanina + (Pemphredonina + Stigmina + Spilomenina); and Pemphredonina + (Ammoplanina + Stigmina + Spilomenina). Recently, two additional tribes of Pemphredoninae have been described: Palangini from Eocene Baltic amber and Rasnitsynapini in Turonian amber of New Jersey (Antropov, 2011). Whether these new tribes render any of the prior lineages paraphyletic remains untested, although Antropov (2011) presented a speculative and fully-resolved topology based on intuition whereby all genera, subtribes, and tribes are monophyletic. His topology reflected putative relationships of ((Spilomenina + Ammoplanina) + Rasnitsynapini) + (Palangini + (Psenini + (Pemphredonina + Stigmina))). Several of these groupings are possibly based on plesiomorphic features.

Here we report the discovery of a new genus and species of wasp in Late Cretaceous amber from northwestern France. The genus intermingles many features of the Pemphredonini and cannot be assigned to any of the presently defined subtribes with ease, although there are several traits reminiscent of the Spilomenina. Given that the genus is likely representative of a stem-group to one or more of the clades within the Pemphredonini, it has been classified as subtribe incertae sedis rather than to potentially render one of the groups paraphyletic (if it is basal to a sister-group pairing of two or more subtribes) or to establish a monogeneric subtribe that serves no classificatory value in the absence of a cladistic analysis.

MATERIAL AND METHODS

The amber that entombed the newly discovered specimen was collected in 2002 by Fanny Dupé from a deposit that was briefly exposed during works along road D32 between La Garnache and Challans, in the department of Vendée, northwestern France. The exact age of the amber-bearing stratum is uncertain within the Middle Cenomanian to Early Santonian interval (Late Cretaceous, 97–85 Ma), as discussed by Perrichot and Néraudeau (2014: 10A in this volume).

The specimen is contained in a tiny piece of clear orange amber that is 6.7 mm in length and was polished to remove the weathered opaque surface. Photomicrographs were taken with a Canon 5D Mark II digital camera attached to a Leica MZ APO stereomicroscope, and HeliconFocus 4.45 software (Helicon Soft, Ltd) was used to produce a multifocus z-stack so as to achieve sharp focus throughout the images. Metrics were taken with an ocular micrometer set on an Olympus SZX-12 stereomicroscope. Classification of the fossil follows characters and categories as outlined by Prentice (1998) while the morphological terminology is generally that of Bohart and Menke (1976).

SYSTEMATIC PALEONTOLOGY

Family CRABRONIDAE Latreille, 1802
Subfamily PEMPHREDONINAE Dahlbom, 1835
Tribe PEMPHREDONINI Dahlbom, 1835
MENOPSILA new genus

Type species.—*Menopsila dupeae* new species, by original designation.

Diagnosis.—The fossil can be recognized as a member of the crabronid subfamily Pemphredoninae by the combination of its small size; normal ocelli; simple mandible exteroventrally; sub-parallel inner orbits of the compound eyes; and single mesotibial spur. It is placed in Pemphredonini on the basis of the antennal toruli set low, adjacent to the clypeal margin; low and broad pronotal collar; and two forewing submarginal cells. Placement within the tribe is less certain; it can be excluded from all subtribes based on available character evidence and these features, along with the aforementioned, serve to diagnose the genus. It is excluded from the Pemphredonina by its two ‘discoidal’ cells (sensu Bohart & Menke, 1976, whereby in their chapter on Pemphredoninae they consider the subdiscoidal cell as one of the discoidal cells; in broader Hymenoptera terminology there is in this wing a single discoidal and single subdiscoidal, or, in the system of apoid wing cells of Engel, 2001, the second cubital cell is present and there is a single medial cell), relatively narrow gena, fairly large pterostigma, lack of facial fovea on frontal area, mesepisternal sulcus not positioned anteriorly, sessile metasoma, and hind wing cu-a interstitial; from Ammoplanina by the orthognathous head, longer marginal cell, less reduced venation of the forewing (and likely hind wing), and presence of an omaulus; from the Stigmina by the presence of a definitive mesepisternal sulcus descending ventrally from the subalar fossa, absence of a hypersternaulus, and by the lack of both a long maxillary palpus and long petiole; from the Spilomenina by its six-segmented maxillary palpus (rather than five), relatively narrow mandible, mesepisternal sulcus strong and not positioned anteriorly; from Spilomenina other than *Arpactophilus* by the presence of an occipital carina.

Etymology.—The new genus-group name is an anagram of the crabronid genera *Spilomena*, *Psilomena*, and *Lisponema*. The name is treated as feminine.

Remarks.—Inclusion in Crabronidae is easily established by the aforementioned suite of pemphredonine traits (e.g., single mesotibial spur, unmodified ocelli, simple mandible, sub-parallel inner orbits of the compound eyes) as well as the combination of a simple compact mesosoma with a well-differentiated pronotal lobe and fully-developed wings, simple pretarsal claws, and sessile metasoma (Prentice, 1998).

Given that the new genus clearly belongs to the Pemphredonini, yet can be excluded from its constituent subtribes, it is here considered a stem-group lineage to the tribe or one of its constituent clades. Placing the fossil in a newly erected genus within Pemphredonini lacking subtribal designation is logically consistent with all possibilities of its phylogenetic position and permits the greatest taxonomic flexibility for the future when, hopefully, more complete material will be available, including perhaps females.

Although ambiguity remains as to which subtribe(s) the new genus is most closely allied, the majority of available evidence suggests it may be most closely related to the Spilomenina. This is indicated by the combination of a forewing with a fairly large pterostigma, elongate, closed marginal cell, single discoidal cell (i.e., single medial cell with 2 m-cu is absent: Bohart & Menke, 1976, refer to this as two discoidal cells in their system of Pemphredoninae); sessile metasoma; and lack of tarsal plantulae. In Menke’s (1988) revision to Bohart and Menke’s (1976) key to the genera of Pemphredonini, the specimen runs to the couplet separating *Spilomena* and *Arpactophilus*. In

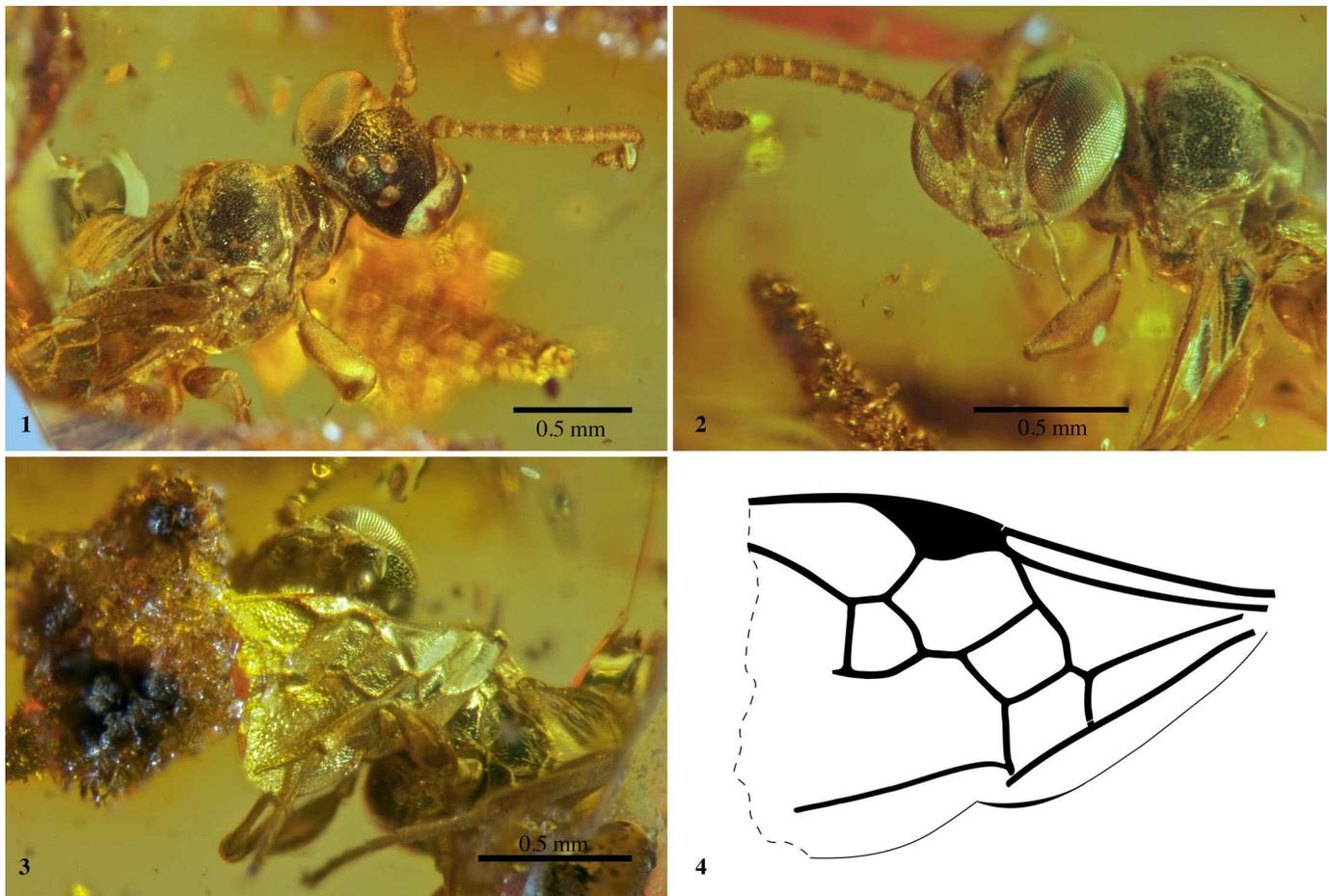


Figure 11. *Menopsila dupeae* n. gen. and sp., in Late Cretaceous amber of Vendée, NW France, holotype male IGR.GAR-50; 1, habitus in dorsal view; 2, head and pronotum in frontolateral view; 3, head and forewing in ventral view; 4, line drawing of the forewing.

Antropov's (2011) key to tribes and subtribes of Pemphebroninae, the new genus will run to the subtribe Spilomenina.

MENOPSILA DUPEAE new species
Figure 11

Type material.—Holotype male, IGR.GAR-50 (ex coll. Dupé), in Late Cretaceous (Middle Cenomanian to Early Santonian, 97–85 Ma) Vendean amber; deposited in the Geological Department and Museum of the University Rennes 1, France.

Type locality.—La Robinière, departmental road D32, about 2.5 km south-west of La Garnache, Vendée, France.

Etymology.—The specific epithet is a matronym honoring Fanny Dupé for her generosity in permitting us to study the holotype and many other spectacular inclusions that she collected from the Vendean amber locality.

Diagnosis.—As for the genus (see above).

Description.—Measurements: Total length as preserved ca. 1.85 mm; head length 0.65 mm, width 0.78 mm; mesosoma length 1.35 mm; forewing length as preserved 1.10 mm (wing torn transversely at about marginal cell midlength with wing apex missing). Dorsal part of head and mesosoma (other than pale tegulae) evenly dark but not black; face completely pale in ventral half and along inner orbits nearly to level of median ocellus; flagellum pale, scape slightly darker; fore and midlegs mostly pale, becoming brown on basal part

of profemur; hind leg more or less brown throughout; wings hyaline; integument generally imbricate throughout.

Head (Fig. 11.1, 11.2) orthognathous; face rather spherical in frontal view; integument finely sculptured; compound eyes slightly converging at about their lower third, not converging above; lateral ocelli separated from median ocellus by one ocellar diameter, separated from each other by 1.5 ocellar diameter; ocular-ocular distance 1.2x median ocellar diameter; toruli positioned low on face, against clypeal margin, separated from each other by about one torular diameter; clypeus nearly as tall as broad, clypeal margin undulate, with a low, rounded tooth adjacent to midline; without a scapal basin; with a small tubercle between upper margin of toruli; scape ovoid, 1.4x longer than wide; flagellomeres slightly longer than wide, roughly similar in shape and size, apical four strongly curved such that apex faces towards base [likely an artifact]; mandible with two subequal apical teeth; labrum not protruding beyond clypeus or covered by mandible (likely the former); palpal formula 6-4; gena behind compound eye very narrow, roughly one-fifth compound eye width; malar space very short anteriorly, a little longer posteriorly; occipital carina complete, continuous ventrally, near hypostomal carina, removed from it by about half basal breadth of mandible.

Pronotum short, with a low, transverse carina dorsally; mesonotum finely punctate, punctures separated by 1–2x a puncture width,

grooved along lateral margins but not coarsely pitted; notauli weak; mesopleural sulcus fairly strong; mesopleuron with omaulus present but weak, acetabular carina, scrobal sulcus, and hypersternaulus all absent; episternal sulcus descending from subalar fossa more or less directly ventral, weak dorsally, becoming strong and coarsely pitted ventrally; midventral line not carinate or flanked by grooves but with a pair of submedian pits; precoxal groove coarsely pitted; metapostnotum and propodeum coarsely areolate, with cells large, carina in posterolateral angle raised to form low lamella; legs simple, without modifications, without notable spines or bristles; mesocoxae narrowly separated; without pretarsal rake setae; metatibia without spines; pretarsal claws and metafemoral apex simple, plantulae absent; forewing (Fig. 11.3, 11.4) with two submarginal cells, second about half size of first; apex missing but marginal cell likely closed, preserved portion larger than pterostigma; pterostigma large, about as long as, and nearly as broad as, first discoidal cell (= first medial cell sensu Engel, 2001), significantly smaller than marginal cell; 2m-cu absent; all veins rather straight, none arched; hind wing media seemingly diverging at cu-a (though an ideal view is not possible and many hind wing details are obscured).

Metasoma absent, not encompassed by resin, edge of the piece is along hind margin of propodeum, with impression in resin from first metasomal segment, impression demonstrates that metasoma definitively sessile, without even a short petiole.

DISCUSSION

Pemphredonines comprise the majority of apoid wasps known from amber (Evans, 1973; Sorg, 1986; Budrys, 1993; Antropov, 2000a, 2000b; Bennett & Engel, 2006; Antropov & Perkovsky, 2009; Ohl & Bennett, 2009; Antropov, 2011), and several Cretaceous fossils demonstrate the antiquity of their lineage. It is further notable that the twig-nesting habit (inferred by particular body structures [Evans, 1969; Antropov, 2011]) was in place by the end of the Cretaceous. Several of these fossils have been placed in the modern genus *Passaloecus* (Sorg, 1986; Budrys, 1993) but most defy classification below tribe (Evans, 1969, 1973; Antropov, 2000a, 2000b). Such is to be expected given the preponderance of stem-group taxa, the often unknown phylogenetic arrangement of subtaxa, and the unknown polarity of informative characters. Nonetheless, in some cases arguments have been made regarding the affinities of fossil pemphredonines to modern taxa. Evans (1969) regarded the Cretaceous *Lisponema singularis* Evans as closely related to modern *Spilomena* based on similar wing venation, but Antropov (2000a) argued that such a conclusion was not warranted given the missing character data (the fossil lacked a head). Evans (1973) noted that another poorly preserved fossil, *Pittoecus pauper* Evans, bears similarities to both *Passaloecus* and *Arpactophilus*. Ohl and Bennett (2006) classified *Palarpactophilus saxonicus* Ohl & Bennett as incertae sedis within Pemphredonini but highlighted its similarities to Spilomenina, particularly *Arpactophilus*. Antropov (2011), however, considered the genus to belong to Pemphredonina. Clearly much speculation has taken place and continues to take place regarding relationships. Despite this healthy debate, much remains to be done regarding relationships among living and fossil Pemphredoninae and extensive cladistic analyses with numerous exemplars across the full diversity of the subfamily is greatly needed. Assuredly, many of the

Cretaceous fossils, including *Menopsila*, will be vital for resolving early divergences among the principal lineages and revising our understanding of pemphredonine diversification and biogeography. Critical to such work will be the continued discovery and description of further taxa from fossil deposits throughout the world. While there are a number of fossil species (e.g., refer to tables in Bennett & Engel, 2006; Antropov, 2011), our available material is obviously the merest fraction of what existed and even of what is potentially to be found. Indeed, prolific amber deposits such as those of Myanmar, Spain, France, and elsewhere remain to be thoroughly explored and future fossil pemphredonines, complete with as of yet unsuspected character combinations, are assured.

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