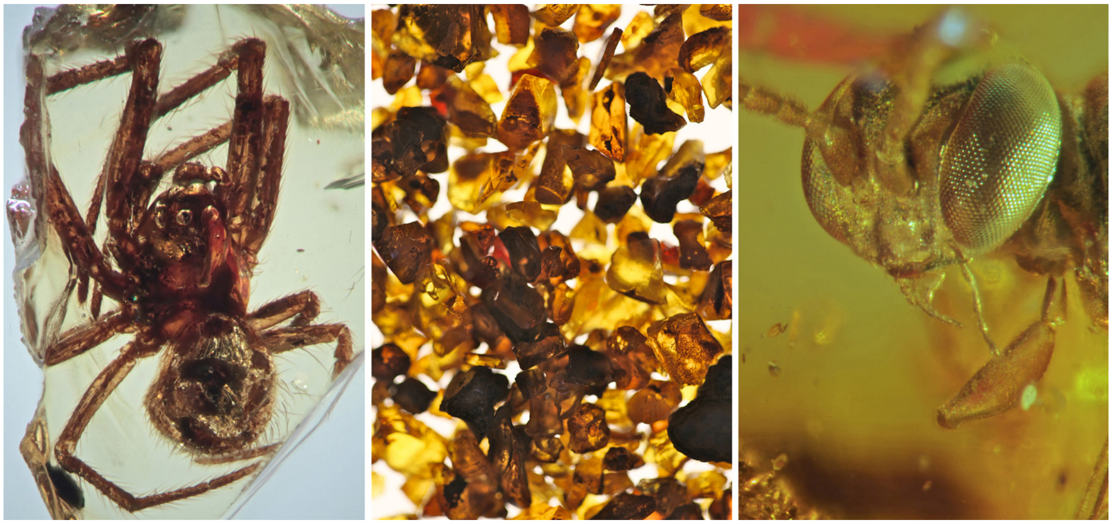
Paleontological Contributions

Number 10

Fossil arthropods in Late Cretaceous Vendean amber (northwestern France)

Vincent Perrichot, Editor



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Paleontological Contributions

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INTRODUCTION TO THEMATIC VOLUME “FOSSIL ARTHROPODS IN LATE CRETACEOUS VENDEAN AMBER (NORTHWESTERN FRANCE)”

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There is growing knowledge of the insect and arachnid Cretaceous diversity worldwide, most notably as a result of the discovery, in the past twenty years, of numerous Konservat-Lagerstätten (highly fossiliferous deposits) that provide a plethora of fossil arthropods (Wang & Szwedo, 2014). Early Cretaceous (Berriasian–Aptian) insects are known primarily from imprints in rocks, while fossiliferous amber yielding arthropod inclusions range mostly from the Albian to the Campanian – the sole exception being Hauterivian-Barremian amber of Lebanon and Jordan.

In France, only few (14) Cretaceous insect deposits are known, with their study still in a very nascent stage. Indeed, the first taxonomic descriptions of Cretaceous French insects did not appear before the 1970s, with 39 species recorded from amber of two Early Cenomanian localities in Anjou (Kühne, Kubig, & Schlüter, 1973; Schlüter, 1978, 1983; see detailed list of taxa in Perrichot & others, 2007: tab. 1). Investigations for additional paleoentomological material have been launched since the early 2000s, that have led to the discovery of twelve further localities (Fig. A1). Insect imprints are remarkably scarce, known only from two Early Cenomanian outcrops, and consisting of few wings or elytra of various Odonata and indeterminate Blattaria, Coleoptera, and Neuroptera, as well as one case of Trichoptera and coprolites of Isoptera (Nel & others, 2008, 2015; Colin & others, 2011; Vullo, Néraudeau, & Dépré, 2013). A significantly larger amount of data have been provided by amber inclusions from ten further localities, most of which from around the Early–Late Cretaceous boundary (Albian–Cenomanian), a crucial period in the evolution of insects (Szwedo & Nel, 2014). A single locality was found from later in the Cretaceous (Santonian), that has yielded relatively few insects (Choufani & others, 2013). All together, more than 2000 fossils of arthropods (arachnids, myriapods, hexapods, and crustaceans) are currently recorded from these outcrops, but mostly from Albian-Cenomanian Charentese amber, in southwestern France (Perrichot & others, 2007; Perrichot & Néraudeau, 2009; Perrichot, Néraudeau, & Tafforeau, 2010; Girard & others, 2013).

The present volume introduces systematic studies on fossil arthropods from a new amber deposit discovered in the early Late Cretaceous (Middle Cenomanian to Early Santonian, 97–85 Ma) of Vendée, a department in northwestern France (Fig. A1), and hereafter referred to as Vendean amber. The outcrop was accessible only briefly during work for enlargement of a road that took place between 2002 and 2005. The precise age of the amber is difficult to assess because the regional geology is rather complex: some boreholes around the outcrop have revealed three Cretaceous lignitic strata dated by palynological analyses as Middle–Late Cenomanian, Early Turonian, and Early Santonian, that sometimes lie unconformably on each other (Ters & Viaud, 1983; Legrand & others, 2006). Unfortunately, the sediment associated with amber yielded only few, poorly preserved palynomorphs without marker species, and the outcrop is currently unaccessible, preventing any stratigraphic correlation. Resolving this issue is still work in progress, and more details on the regional geology, chemical and taphonomical characteristics of the amber, the associated plant remains, and the plant source of the resin will be discussed elsewhere (Néraudeau & others, in prep.).

All the material (5700 pieces of amber totaling 305 grams only) was provided to us by private collectors who discovered and exploited

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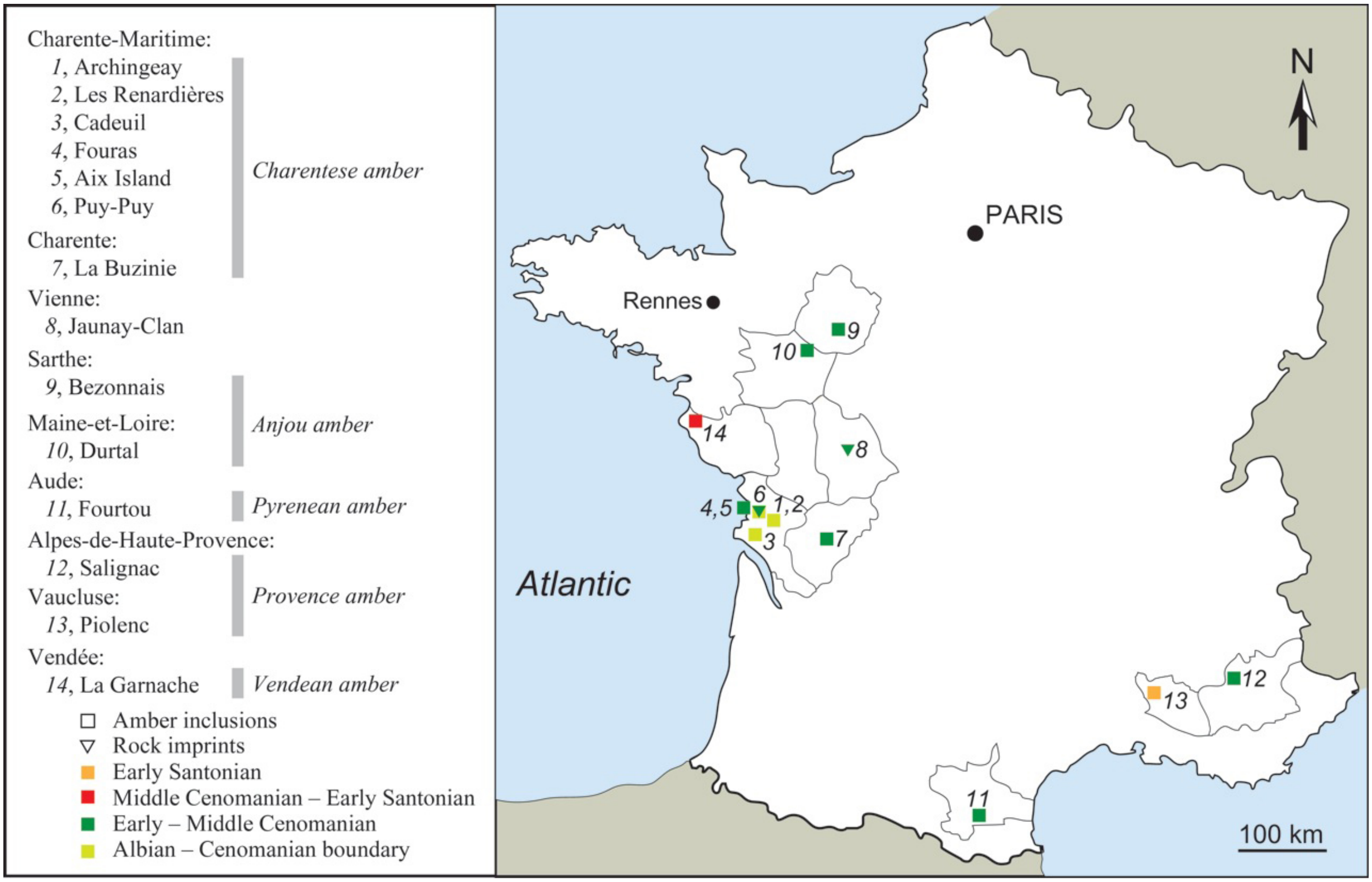

Figure A1. Location of the Vendean amber deposit and other known Cretaceous insect localities from France.

the outcrop before it was sealed by the construction of a paved road. Most of the pieces are 3 to 10 mm in size, but rare larger pieces up to 35 mm were also found (Fig. A2). Amber grains are clear yellow to orange in colour, with only a thin weathered surface, and biological inclusions are generally exquisitely preserved, with only few distortion or alteration. Despite the small amount of amber, investigation for its fossiliferous content revealed a high biotic diversity, with 171 arthropod inclusions recorded (Table A1) together with various microinclusions such as spider webs (Saint Martin & others, 2014), bacterial filaments, fungal hyphae, sponge spines, fern spores, and diatoms (Saint Martin & others, 2015). Vendean amber is therefore exceptionally rich in arthropod inclusions compared to similar amber deposits with a majority of small-sized pieces. Ambers from the Triassic of Italy and the Santonian of southeastern France, for example, are very similar in aspect but contain only a handful of arthropods each (Schmidt & others, 2012; Choufani & others, 2013).

Contributions in this volume provide new insights on the taxonomic diversity of Cretaceous insects and spiders, their morphological disparity, paleoecology, paleobiogeographical distribution, and their relationships with modern lineages. It also enlightens the entomofauna from the Late Cretaceous of western Europe which is otherwise poorly known. Newly described taxa include one species of spider (Penney, 2014: 10B in this volume) and six genera and eleven species of various insects – barklice (Azar, Nel, & Perrichot, 2014: 10C in this volume); earwigs (Engel & Perrichot, 2014a: 10D in this volume); termites (Engel, 2014: 10E in this volume); dustywings (Perrichot & others, 2014: 10F in this volume); flies and midges (Choufani & others, 2014: 10H in this volume; Perrichot & Engel, 2014: 10G in this volume); and wasps (Bennett, Perrichot, & Engel, 2014: 10I in this volume; Engel & Perrichot, 2014b: 10J in this volume).

All specimens described in this volume or to be described elsewhere were kindly donated to the Geological Department of Rennes University by private collectors. We are grateful to all of them: Fanny Dupé who first discovered the Vendean amber, as well as Arlette Boulo, Thérèse Corgnet, Dominique Doyen, Anne-Marie Guèdes, Gérard Guérineau, Alain Guillet and brothers, Didier Graves, Luc Lucas, and Magali Weigandt. This special volume is dedicated to the late André Dupé who also participated in amber collection with his wife Fanny, and sadly passed away before we could publish this work; André and Fanny have long provided tireless efforts and tremendous interest for this fossil deposit. We are also grateful to the Conseil Général de Vendée and the Agence Routière Départementale de Challans for assistance during field work; to colleagues and friends who contributed the different papers or identification of all fossil inclusions; to the many referees for the critical reviews of the manuscripts; and to the chief and technical editors of this volume, Prof. Paul Selden and Denise Mayse for great support in editing of this work.

Figure A2. A sample of Vendean amber showing the size and color of various pieces.

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Class Order	Suborder/Family	Number of specimens
Crustacea		
Isopoda	indet.	28
Tanaidacea	Alavatanaidae	1
Diplopoda		
Polyxenida	Polyxenidae	1
Arachnida		
Acari	Mesostigmata	2
	Prostigmata	8
	'Hydracarina'?	1
	indet.	17
Araneae	Theridiosomatidae*	1
	indet.	8
Opiliones	indet.	1
Entognatha		
Collembola	indet.	1
Insecta		
Blattaria	indet.	1
Coleoptera	Ptinidae	2
	indet.	2
Dermaptera	Neodermaptera*	1
Diptera	Cecidomyiidae	4
	Ceratopogonidae*	10
	Chironomidae	5
	Dolichopodidae*	1
	Anisopodidae	3
	indet.	9
Hemiptera	Eriococcidae	1
	Fulgoromorpha	2
	indet.	2
Hymenoptera	Crabronidae*	1
	Megaspilidae	1
	Mymaridae	4
	Mymarommatidae	5
	Platygastridae	8
	Serphitidae*	2
	indet.	3
Isoptera	'*Meiatermes*-grade'*	1
Neuroptera	Berothidae	1
	Coniopterygidae*	1
Orthoptera	Grylloidea	1
Psocodea	Archaeatropidae*	3
	Amphientometae*	1
	Mesopsocidae*	2
	indet.	3
Thysanoptera	Merothripidae	1
	indet.	1
Indet.		14
Arthropoda	indet.	6
	Total Arthropods	**171**

Table A1. Arthropod taxa recorded from Vendean amber (*denotes taxa described in the present volume)

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A FOSSIL RAY SPIDER (ARANEAE: THERIDIOSOMATIDAE) IN CRETACEOUS AMBER FROM VENDÉE, FRANCE

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ABSTRACT

A new species of fossil ray spider, *Baalzebub*? *mesozoicum* n. sp. (Araneae: Theridiosomatidae), is described from Mesozoic amber from the Cretaceous (Middle Cenomanian to Early Santonian) deposits of La Garnache, Vendée, NW France. The palpal structures, especially the highly sclerotized claw-shaped retrolateral 'paracymbium' originating as an outgrowth of the cymbium basally and the basal cymbial lamella, are considered sufficient to make a tentative placement of the new fossil species in the extant genus *Baalzebub* Coddington, 1986.

Key words: Arachnida, spider, Mesozoic, Late Cretaceous, France

RÉSUMÉ

Une nouvelle espèce d'araignée fossile, *Baalzebub? mesozoicum* n. sp. (Araneae: Theridiosomatidae), est décrite de l'ambre mésozoïque des dépôts crétacés (Cénomanien moyen à Santonien inférieur) de La Garnache, Vendée, nord-ouest de la France. Les structures des palpes, en particulier le 'paracymbium' rétrolatéral en forme de griffe et fortement sclérotisé, issu d'une excroissance basal du cymbium, et la lamelle cymbiale basale, sont considérées comme suffisantes pour un placement possible de la nouvelle espèce fossile dans le genre moderne *Baalzebub* Coddington, 1986.

Mots-clés: Arachnide, araignée, Mésozoïque, Crétacé supérieur, France

INTRODUCTION

The fossil record of spiders is diverse (Penney, Dunlop, & Marusik, 2012; Dunlop, Penney, & Jekel, 2013), particularly in Tertiary ambers. Within the last few decades, however, an increasing number of species have been described from the Mesozoic (Selden & Penney, 2010; Penney & Selden, 2011; Wunderlich, 2008, 2012; Penney, 2013). France has a diverse fossil spider fauna in both amber and rock (briefly summarized by Penney, 2004), including the oldest known fossil spider species (Selden, 1996). Amber spiders have been formally described and named from Tertiary deposits of Oise (Micropholcommatidae: Penney & others, 2007; Pholcidae: Penney, 2007a; Oonopidae: Penney, 2007b; see Nel & Brasero (2010) for a summary of this deposit) and Cretaceous Charentes amber (Mecysmaucheniidae: Saupe & Selden, 2009; see Perrichot, Néraudeau, & Tafforeau (2010) for a summary of this deposit).

Ray spiders (family Theridiosomatidae) are minute orb-web weaving spiders with a worldwide distribution today. They are usually found in shady, humid places and are represented by 106 extant species in 18 genera (Platnick, 2013). In addition, fossil species have been described from Tertiary amber deposits: Dominican Republic (Wunderlich, 1988) (but note that the species described as *Theridiosoma incompletum* Wunderlich, 1988 is probably misplaced in that genus, see Penney (2006, 2008); Bitterfeld and Baltic (Wunderlich, 2004); Cretaceous amber from Myanmar (Wunderlich, 2012); and a single species, based on several specimens, has been described in rocks from the Cretaceous of Baissa, Transbaikalia (Selden, 2010). Here, a new species of ray spider is described from the newly discovered amber deposits of La Garnache, Vendée, France, possibly representing the only extant theridiosomatid genus known from the fossil record.

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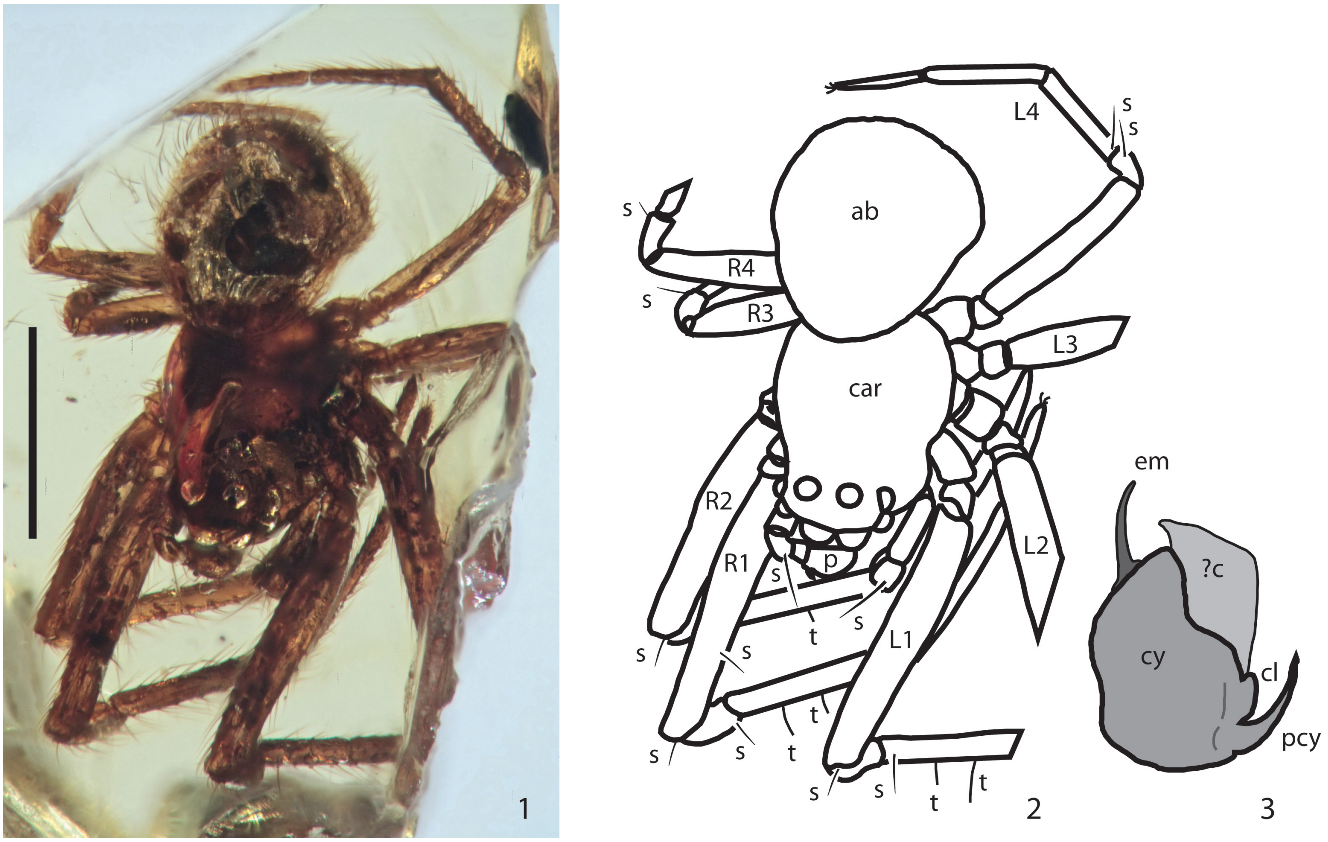

Figure B1. *Baalzebub? mesozoicum* n. sp. in Late Cretaceous amber from Vendée, France: *1*, holotype male (IGR.GAR-91), scale bar = 0.5 cm; *2*, explanatory drawing of *1*; *3*, right pedipalp in quasi-dorsal view.

GEOLOGICAL SETTING

The amber originates from deposits of early Late Cretaceous age, either Middle Cenomanian, Turonian, or Early Santonian. The regional geology is rather complex, resulting in difficulties obtaining a precise age, and resolving this issue is still work in progress. For further details see the foreword paper in this volume (Perrichot & Néraudeau, 2014: 10A).

MATERIAL AND METHODS

One specimen, coll. Fanny Dupé (IGR.GAR-91) held in the collections of the Geological Institute and Museum of the University Rennes 1, Rennes, France. The fossil spider is preserved in a tiny sliver of amber which, prior to receipt by the author, was embedded in clear synthetic resin; total dimensions of the resin matrix: 6 × 3 × 0.5 mm. There are no syninclusions. Abbreviations used in the text and figures are as follows: ab = abdomen; AME = anterior median eyes; c = conductor; car = carapace; cl = cymbial lamella; cy = cymbium; em = embolus; L/R1–4 = left and right walking legs 1–4; p = pedipalp; pcy = paracymbium; PME = posterior median eyes; s = spine; t = trichobothrium.

SYSTEMATIC PALAEONTOLOGY

ARANEAE Clerck, 1757
OPISTHOTHELAE Pocock, 1892
ARANEOMORPHAE Smith, 1902
THERIDIOSOMATIDAE Simon, 1881
BAALZEBUB Coddington, 1986

Type species.—Baalzebub baubo Coddington, 1986 by original designation.

Included species.—B. albonotatus (Petrunkevitch, 1930) (Puerto Rico), *B. baubo* Coddington, 1986 (Costa Rica, Panama, Brazil); *B. brauni* (Wunderlich, 1976) (Australia); *B. nemesis* Miller, Griswold, & Yin, 2009 (China); *B. rastrarius* Zhao & Li, 2012 (China); *B. youyiensis* Zhao & Li, 2012 (China). Coddington (1986) referred to 10–20 additional undescribed species, including additional geographic records from Mexico, Guatemala, Colombia, South Africa, Malaysia, New Guinea and New Zealand.

BAALZEBUB? MESOZOICUM n. sp.

Figure B1

Etymology.—The specific epithet relates to the Mesozoic Era, from which the fossil originates.

Material.—Holotype male (IGR.GAR-91) held in the collections of Geological Institute and Museum of the University Rennes 1, Rennes, France. The only known specimen.

Diagnosis.—Pedipalp of male with claw-shaped retrolateral 'paracymbium' fused to the cymbium basally and with a basal cymbial lamella; 'conductor' large and embolus extending distally beyond the cymbium. The palpal structure is similar to *B. albonotatus* (Petrunkevitch, 1930) but differs in having the embolus directed anteriorly rather than laterally.

Description.—Tiny spider, total body length approximately 1 mm. Carapace approximately 0.6 mm, not distinctly raised in the ocular area, and with a low clypeus. Eight eyes in two rows, anterior row recurved, posterior row straight. AME largest, contiguous, remaining eyes subequal, laterals contiguous, PME separated by slightly less than their diameter (Fig. B1). Sternum with promarginal sternal pits characteristic of the family, shield-shaped, as broad as long and extending between fourth coxae. Labium and maxillae broader than long. Leg formula (longest first) 1243, lacking unusual modifications. Femur 1 with distinct prolateral spine in distal half (Fig. B1); patellae 1 and 2 with both proximal and distal spine; patellae 3 and 4 with only distal spine. Tibia 1 and 4 with single dorsal spine close to patella; absence of similar spines on legs 2 and 3 cannot be confirmed with absolute certainty. Trichobothria difficult to see, but visible as follows: two on tibia 1, one on tibia 2, one on tibia 4. Tarsus with three claws; paired claws without teeth.

Abdomen lacking scuta, approximately 0.6 mm, damaged but was probably subspherical in life and overlapping carapace slightly; adorned with short setae. Spinnerets not clear, but appear short, compact and unmodified.

Pedipalp (Fig. B1) with highly sclerotized claw-shaped retrolateral 'paracymbium' fused to cymbium basally and with a basal cymbial lamella; 'conductor' large and embolus extending distally beyond cymbium. Palpal patella with single, long spine distally.

DISCUSSION

Theridiosomatidae is a poorly known or understood, exotic, cosmostropical family of tiny spiders, usually less than 2 mm in total body length (Coddington, 1986) with a relatively long geological history. Their true extant diversity far exceeds that which is known at present. The same is true for the constituent genera, including *Baalzebub*, considered in this paper (see previously under species included in the genus). This can make the placement of new fossil species in extant genera uncertain, especially when details of the pedipalps are obscured, and this is particularly true for older fossils from the Mesozoic.

Unfortunately, the bulbus structures are not clearly visible in the specimen described here, so it is not possible to differentiate between structures such as the tegulum, subtegulum and conductor. Nonetheless, the remaining palpal structures, especially the highly sclerotized claw-shaped retrolateral 'paracymbium' originating as an outgrowth of the cymbium basally and the basal cymbial lamella are considered sufficient to make a tentative placement of the new fossil species in the extant genus *Baalzebub*. Indeed, there are no particular characters that could be identified to exclude the fossil from this genus and to warrant the description of a new genus. Extant species of this genus prefer dark habitats and are often found in the interior of hollow logs or under large, fallen trees, a behaviour that would make them susceptible to becoming trapped in any secreted resin that may be present.

Interestingly, this Cretaceous French fossil shares features used in the diagnoses of Wunderlich's (2012) new Cretaceous genera, e.g. the presence of a single prolateral bristle on femur 1 (*Leviunguis* Wunderlich, 2012) and a very long and pointed paracymbium (*Hypotheridiosoma* Wunderlich, 2012). However, the overall palpal configuration excludes it from either of these genera. *B.*? *mesozoicum* represents the first Mesozoic fossil theridiosomatid assigned to an extant genus, suggesting a considerable antiquity for this spider lineage.

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Paleontological Contributions

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DIVERSE BARKLICE (PSOCODEA) FROM LATE CRETACEOUS VENDEAN AMBER

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ABSTRACT

The fossil psocodeans from Late Cretaceous (Cenomanian to Santonian) amber of Vendée, in northwestern France, are studied. Two new genera and three new species are described and illustrated, as *Proprionoglaris axioperierga* n. sp. (Archaeatropidae), *Scocompus atelisus* n. gen. and sp. (uncertain family within the Amphientometae), and *Mesopsocoides dupei* n. gen. and sp. (earliest fossil record of the Mesopsocidae). The new fossils are distinguished from their congeners, and their respective systematic placement is discussed. Other fragmentary fossil psocodeans from the same outcrop are illustrated and discussed.

Keywords: Insecta, Psocoptera, Trogiomorpha, Troctomorpha, Psocomorpha, Cretaceous

RÉSUMÉ

Les psoques fossilisés dans l'ambre crétacé supérieur (Cénomanien à Santonien) de Vendée, dans le nord-ouest de la France, sont étudiés. Deux nouveaux genres et trois nouvelles espèces sont décrits et illustrés: *Proprionoglaris axioperierga* n. sp. (Archaeatropidae), *Scocompus atelisus* n. gen. et sp. (famille incertaine au sein des Amphioentometae), et *Mesopsocoides dupei* n. gen. et sp. (plus ancien Mesopscocidae fossile). Ces nouveaux taxons sont comparés à leurs congénères, et leur position systématique respective est discutée. D'autres psoques fossiles fragmentaires issus du même gisement sont discutés.

Mots-clés: Insectes, Psocoptères, Trogiomorphes, Troctomorphes, Psocomorphes, Crétacé

INTRODUCTION

The Psocodea (Psocoptera + Phthiraptera) is an insect order comprising about 10,000 modern species. The earliest fossil that could be assigned to psocodeans (*Westphalopsocus pumilio* Azar & others, in Nel & others, 2013) is a forewing imprint from the Moscovian (= Westphalian; Pennsylvanian, Late Carboniferous) of France. The group's fossil record has significantly increased in the last decade with the further discoveries of insectiferous amber and lacustrine deposits over the world. Psocodean taxa fossilized in amber are usually well preserved enough for precise comparison with their modern congeners.

Here, we present some new psocids recently discovered in Late Cretaceous amber of Vendée, in northwestern France. Eight out of the 171 arthropod inclusions found in this amber deposit belong to Psocodea, but only four of them are complete or visible enough to permit a thorough study reaching to the specific level. Two new genera and three new species are described and illustrated, which significantly represent a new record of the trogiomorphan genus *Proprionoglaris* Perrichot & others, 2003, the record of an Amphientometae sharing affinities with both the superfamilies Amphientomoidea and Electrentomoidea, and the earliest record of the psocomorphan family Mesopscocidae, respectively. The remains of four additional but poorly preserved specimens from the same deposit are also figured and briefly discussed.

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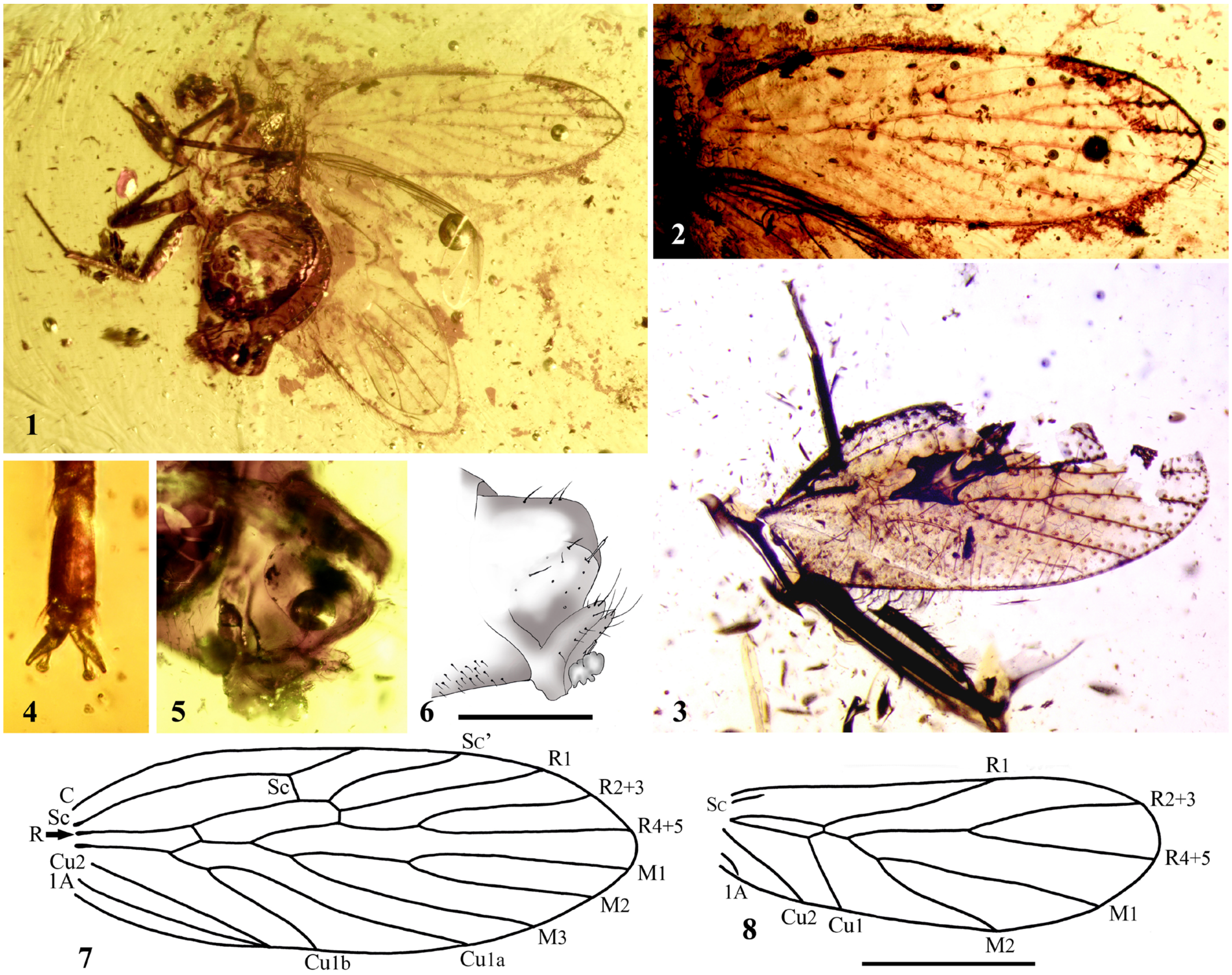

Figure C1. *Proprionoglaris axioperierga* n. sp., in Late Cretaceous Vendean amber. (*1–2, 4–8*: holotype female IGR.GAR-69; *3*: paratype IGR.GAR-39). *1*, habitus in ventral view; *2*, forewing; *3,* specimen as preserved, with forewing and fragments of legs; *4,* detail of tarsal claw; *5–6,* female genitalia, scale bar = 0.3 mm; *7–8,* drawings of forewing and hind wing, scale bar = 0.5 mm.

MATERIAL AND METHODS

The amber material was excavated in 2002 by private collectors from a deposit that briefly cropped out during construction along the D32 road between La Garnache and Challans, in the department of the Vendée, northwestern France. The absence of current outcrop and the few available palynological data (Legrand & others, 2006), which are contradictory with the regional geological map (Ters & Viaud, 1983), make the exact dating of the amber-bearing stratum difficult, and a conservative Middle Cenomanian–Early Santonian interval (97–85 Ma) is provisionally considered (see Perrichot & Néraudeau, 2014: 10A in this volume). The amber pieces containing the specimens were cut, polished, and prepared between two microscopic coverslips with epoxy medium. The study was done under incident and transmitted light using a Nikon SMZ 1500 stereomicroscope and a Leitz Wetzlar compound microscope, both equipped with a digital camera for photographs, and camera lucida for line drawings. The studied material is housed in the amber collection of the Geological Department and Museum of the University Rennes 1, France.

We follow the wing venation nomenclature and body structures of Smithers (1972), and keys of Smithers (1990), Mockford (1967, 1993), Lienhard (1998), and Badonnel and Lienhard (1988).

SYSTEMATIC PALEONTOLOGY

Suborder TROGIOMORPHA Roesler, 1944
Family ARCHAEATROPIDAE Baz & Ortuño, 2000

Genus PROPRIONOGLARIS Perrichot & others, 2003

Type species.—*Proprionoglaris guyoti* Perrichot, Azar, Néraudeau & Nel, 2003.

Remarks.—Perrichot and others (2003) left this genus unplaced in the suborder Trogiomorpha, either in Prionoglarididae or Archaeatropidae. In a recent reassessment of all Cretaceous amber Psocoptera, Mockford, Lienhard, and Yoshizawa (2013) excluded an assignment to the Prionoglarididae, and instead argued for a placement in the

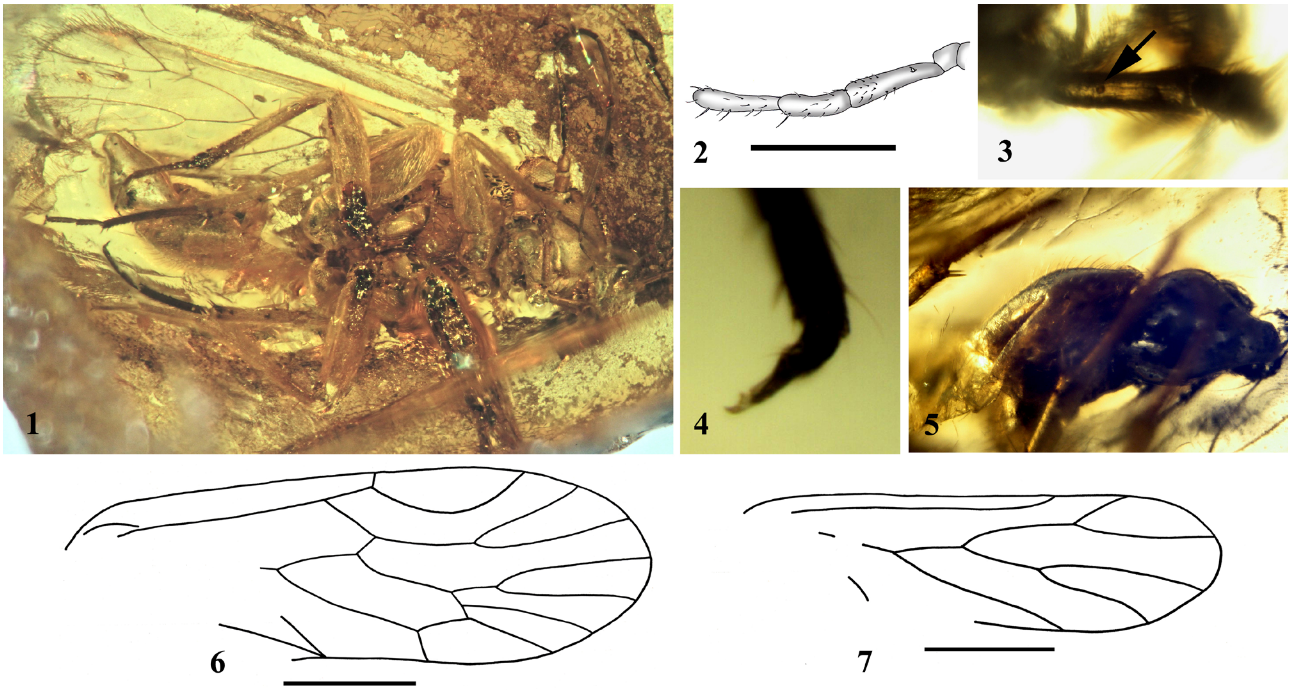

Figure C2. *Scocompus atelisus* n. gen. and sp., holotype female IGR.GAR-40, in Late Cretaceous Vendean amber. *1*, habitus in ventral view; *2*, drawing of maxillary palps, scale bar = 0.3 mm; *3*, second maxillary palp, with conical sensillum indicated by arrow; *4*, detail of tarsal claw; *5*, detail of genitalia; *6–7*, forewing and hindwing, scale bars = 0.5 mm.

Archaeatropidae. This placement is provisionally followed herein, although Mockford, Lienhard, and Yoshizawa (2013) did not examine the material and their assumption still requires a stronger support.

PROPRIONOGLARIS AXIOPERIERGA, new species

Figure C1

Type material.—Holotype female IGR.GAR-69 (ex coll. Dupé), a poorly preserved specimen lacking most of head and part of dorsum (Fig. C1.1); paratype IGR.GAR-39 (ex coll. Dupé), sex unknown, preserved only by a forewing and parts of legs (Fig. C1.3); both in Late Cretaceous (Middle Cenomanian to Early Santonian, 97–85 Ma) Vendean amber. Both specimens are 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 derived from the Greek αξιοπεϱίεϱγος (axioperiergos) = particular; the gender of the genus, which was not staked in the original description, is feminine.

Diagnosis.—Very similar to *Proprionoglaris guyoti* but smaller (forewing length 1.64 mm, as opposed to 3.0 mm in *P. guyoti*); with forewing setae arranged in two rows, one on each side of veins (as opposed to a single row on the dorsal side of veins of *P. guyoti*); fork of R2+3 and R4+5 deeper and nearly equal in size to the fork of M1 and M2 (distinctly larger than fork of M1 and M2 in *P. guyoti*); in hind wing, fork of R2+3 and R4+5 deeper; R1 reaching costa beyond the level of radial fork (distinctly before in *P. guyoti*); median tibia with two long trichobothria, hind tibia with four long trichobothria (respectively four and three trichobothria in *P. guyoti*).

Description.—Female. Head with only labial palps and one maxillary palp preserved, the latter 4-segmented. Wings hyaline; forewing (Fig. C1.2, C1.3, C1.7) 1.64 mm long, 0.58 mm wide, with one row of long setae on each side of veins; pterostigma not sclerotized; a cross-vein between distal part of Sc and anterior wing margin, reaching C 0.83 mm from wing base; Sc curving back to reach R; common part of Sc with R 0.07 mm long; vein Sc' (*sensu* Lienhard, 1998) emerging from R1 and directed anteriad, reaching C at 1.14 mm apically; R1 reaching C 1.36 mm from wing base; radial cell closed, six-angled, elongate and narrow; fork of R2+3 and R4+5 at 1.01 mm from wing base; R2+3 and R4+5 reaching distal part of wing margin respectively at 1.51 and 1.62 mm; M with three branches; fork of M1+M2 at 0.98 mm; M1 and M2 reaching wing margin at 1.62 and 1.51 mm respectively; fork of M into M1+M2 and M3 at 0.65 mm; M3 reaching wing margin at 1.34 mm; Cu1 fork into Cu1a and Cu1b at 0.4 mm; Cu1a and Cu1b forming an elongate areola postica and reaching wing margin at 1.16 and 0.72 mm respectively; veins Cu2 and 1A meeting in a distinct nodulus on wing margin at 0.57 mm. Hind wing bare (Fig. C1.8), 1.27 mm long; Sc short; basi-radial cell four-angled; R1 reaching wing margin at 0.8 mm apically, beyond the level of fork of R2+3 and R4+5 at 0.72 mm from wing base; M forking into two terminal branches M1 and M2 at 0.44 mm. Legs with tarsi trimerous; tarsal claws simple, without preapical tooth; pulvillus present, thin elongate and wavy, ending in an inflated sphere (Fig. C1.4); median tibia with two long trichobothria; hind tibia with four long trichobothria. Female ovipositor relatively long with valvulae v3 long (0.23 mm) and narrow, with few long apical setae (Fig. C1.5, C1.6); male unknown.

Discussion.—Although incomplete, the new fossil matches with the genus *Proprionoglaris* for the following features as diagnosed by Perrichot and others (2003): sensilla on second maxillary palp 'mx2' absent; in forewing, a cross-vein between distal part of Sc and anterior wing margin; distal end of Sc (Sc' *sensu* Lienhard, 1998) emerging from R1 and directed towards wing apex; radial cell 6-angled, elongate; nodulus present; female ovipositor valvulae v3 long.

Suborder TROCTOMORPHA Roesler, 1944
Infraorder AMPHIENTOMETAE Pearman, 1936
Family INCERTAE SEDIS

Genus SCOCOMPUS, new genus

Type species.—*Scocompus atelisus* n. sp., by present designation.

Etymology.—The genus name is an anagram of *Compsocus*, type-genus of the family Compsocidae with which it shares some characters; gender masculine.

Diagnosis.—13 antennomeres each finely annulated; maxillary palps 4-segmented, with second segment bearing a conical sensillum; tarsi trimerous, pretarsal claw with preapical tooth; forewing pterostigma closed basally; areola postica linked to M3 by a cross-vein; hind wing hairy along distal margin, with first segment of Rs absent and M bifurcated.

SCOCOMPUS ATELISUS, new species

Figure C2

Type material.—Holotype female IGR.GAR-40 (ex coll. Dupé) (Fig. C2.1), 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 derived from the Greek ατελής (atelis) = incomplete, for the incomplete state of the fossil.

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

Description.—Female specimen with dorsum and wings badly preserved, 2.18 mm long. Head 0.75 mm wide, with subspherical compound eyes; antenna 2.44 mm long, with 13 segments; each antennomere with very fine secondary annulations; length of antennomeres (in mm) I: 0.08, II: 0.08, III: 0.32, IV: 0.29, V: 0.29, VI: 0.24, VII: 0.21, VIII: 0.19, IX: 0.16, X: 0.16, XI: 0.16, XII: 0.13, XIII: 0.13; maxillary palps 4-segmented (Fig. C2.2), 0.57 mm long; length of segment I (im mm): 0.05, II: 0.2, III: 0.15, IV: 0.17; second maxillary segment with conical sensillum in its basal third (Fig. C2.2, C2.3). Wings hyaline, forewing (Fig. C2.1, C2.6) hairy, exposed to amber surface so its base difficult to observe, 2.25 mm long, 0.74 mm wide; pterostigma not thickened; Sc curving toward base of R1; R1 reaching C at 1.75 mm apically; fork of R2+3 and R4+5 at 1.54 mm from wing base; R2+3 and R4+5 reaching distal part of wing margin at 1.95 and 2.14 mm, respectively; fork of M1+M2 at 1.64 mm; M1 and M2 reaching wing margin at 2.25 and 2.14 mm, respectively; fork of M into M1+M2 and M3 at 1.46 mm; M3 reaching wing margin at 2 mm; a cross-vein linking M3 to Cu1a; Cu1 forking into Cu1a and Cu1b and forming a linked areola postica; the two latter veins reaching wing margin at 1.83 and 1.35 mm, respectively; veins Cu2 and 1A meeting in a nodulus at level of wing margin; remaining basal part of the forewing missing. Hind wing (Fig. C2.1, C2.7) with setose margin, 1.84 mm long; first segment of Rs absent; R1 reaching wing margin at 1.21 mm apically; R2+3 and R4+5 reaching costal margin at 1.48 and 1.82 mm; M bifurcating into M1 and M2 at 1.13 mm and the two latter veins reaching wing margin at 1.75 and 1.56 mm, respectively; Cu1 reaching posterior margin at 1.48 mm apically. Legs with tarsi trimerous; tarsal claws with distinct preapical tooth (Fig. C2.4); female subgenital plate with dense setation (Fig. C2.5). Male unknown.

Discussion.—In Smithers's (1990) keys to families of Psocoptera, the fossil would match with the Compsocidae or the Prionoglarididae for the following features: macropterous; tarsi 3-segmented; body and wings without flattened scales; wing venation not reduced to two parallel veins; pterostigmal area not more opaque than rest of wing membrane; forewing with nodulus. The lack of information on the number of anal veins in the forewing forbids us to choose between these two families, even if the surface between the nodulus and the wing base is nearly the third of the forewing length which makes a place for a possible presence of a second anal vein. *Scocompus* n. gen. would share with some Prionoglarididae the presence of a conical sensillum on the second segment of the maxillary palp, a character absent in Compsocidae. The hind wing M forked is a character present in both families. But the forewing venation of *Scocompus* n. gen. better fits with those of the Compsocidae rather than to the Prionoglarididae. The number of antennal segments and the wing venation definitely assign it to infraorder Amphientometae, rather than to the trogiomorphan Prionoglarididae.

Nevertheless, the wing hairs present in *Scocompus* n. gen., do not occur in any known electrentomoids (the group that comprises the Compsocidae, Electrentomidae, Proctoctopsocidae, Troctopsocidae, and Musapsocidae). Also, the first hind tarsomere in all known electrentomoids is at least twice as long as the second and third together, while in *Scocompus* n. gen. it is less than twice as long. The sensillum of the second maxillary palpal segment is extremely rare in the electrentomoids in general, being known only in the lower Cretaceous genus *Libanomphientomum* Choufani, Azar, & Nel, 2011 with a single species (Choufani, Azar, & Nel, 2011). These characters could be viewed as plesiomorphies within the infraorder (with caution because of the lack of a phylogenetic analysis of this clade based on morphology), suggesting that this genus may represent a sister group to both superfamilies Amphientomoidea (with wing hairs and wing scales) and Electrentomoidea (with bare wings). Because of the incomplete state of preservation of the type specimen of *Scocompus* n. gen., we prefer to assign it to the infraorder Amphientometae, family incertae sedis.

Suborder PSOCOMORPHA Roesler, 1944
Family MESOPSOCIDAE Enderlein, 1903

Genus MESOPSOCOIDES, new genus

Type species.—*Mesopsocoides dupei* Azar, Nel, & Perrichot, n. sp., by present designation.

Etymology.—The genus name refers to the strong resemblance with the genus *Mesopsocus*; gender masculine.

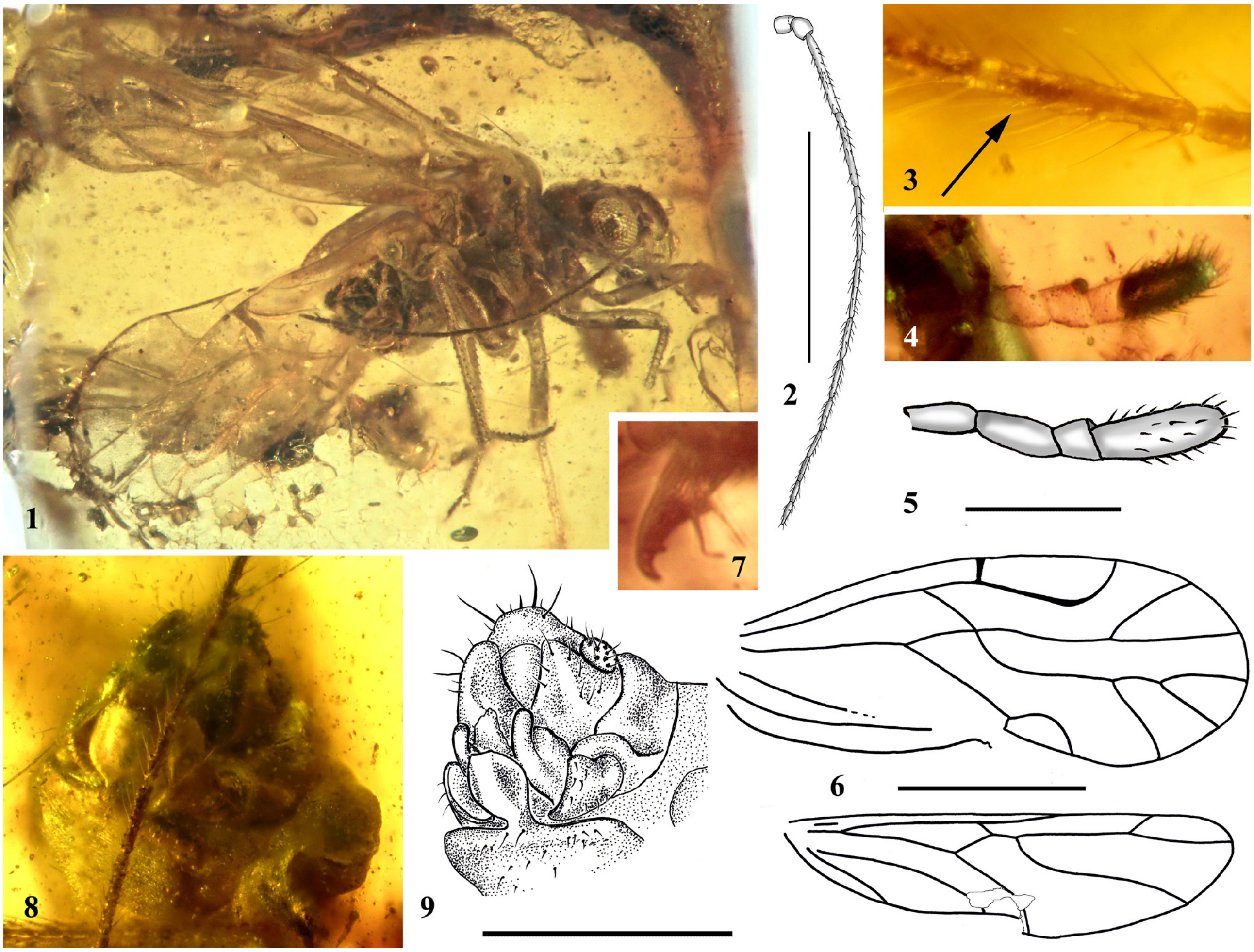

Figure C3. *Mesopsocoides dupei* n. sp., holotype female IGR.GAR-46, in Late Cretaceous Vendean amber. *1*, habitus in profile view; *2*, drawing of antenna, scale bar = 0.5 mm; *3*, detail of 6th antennal flagellomere, with subapical placoid sensillum indicated by arrow; *4*, maxillary palps; *5*, drawing of maxillary palps, scale bar = 0.1 mm; *6*, drawing of forewing and hind wing, scale bar = 0.5 mm; *7*, detail of tarsal claw; *8*, female genitalia; *9*, drawing of female genitalia, scale bar = 0.3 mm.

Diagnosis.—Very similar to *Mesopsocus* but with a subapical placoid sensillum present on the sixth flagellomere.

MESOPSOCOIDES DUPEI, new species

Figure C3

Type material.—Holotype female IGR.GAR-46 (ex coll. Dupé) (Fig. C3.1), 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 patronym honoring André Dupé who greatly assisted his wife Fanny in collecting of the Vendean amber.

Diagnosis.—Antenna 13-segmented, forewing pterostigma without hind angle, bare; hind wing with veins R and M+Cu fused basally for a distance; anal vein long and curved following wing margin; legs with tarsi trimerous, tarsal claws with preapical tooth present and pulvillus setiform, slightly wavy, with apex somewhat enlarged; female subgenital plate with distinct isthmus-like neck; external valves ovoid; ventral valves without dense setation.

Description.—Female. Head with subspherical compound eyes not pedunculate, longest diameter 0.15 mm, smaller diameter 0.13 mm; antenna with 13 segments (Fig. C3.2), 1.17 mm long; length of antennomeres (in mm) I: 0.038, II: 0.044, III: 0.177, IV: 0.161, V: 0.161, VI: 0.127, VII: 0.094, VIII: 0.083, IX: 0.072, X: 0.061, XI: 0.055, XII: 0.044, XIII: 0.055; sixth flagellar segment with a subapical placoid sensillum (Fig. C3.3); maxillary palps 4-segmented (Fig. C3.4, C3.5), length of segments I: 0.044, II: 0.05, III: 0.027, and IV: 0.061 mm. Wings hyaline (Fig. C3.6); forewing 1.44 mm long, 0.54 mm wide; forewing veins bare; pterostigma thickened; Sc reaching C 0.75 mm from wing base; R1 reaching C at 1.1 mm apically; fork of R2+3 and R4+5 at 1.07 mm from wing base; R2+3 and R4+5 reaching distal part of wing margin at 1.29 and 1.41 mm, respectively; M with three branches; fork of M1+M2 at 1.2 mm; M1 and M2 reaching wing margin at 1.44 and 1.36 mm, respectively; fork of M into M1+M2 and M3 at 1.07 mm; M3 reaching wing margin at 1.21 mm; Cu1 forking into Cu1a and Cu1b and form-

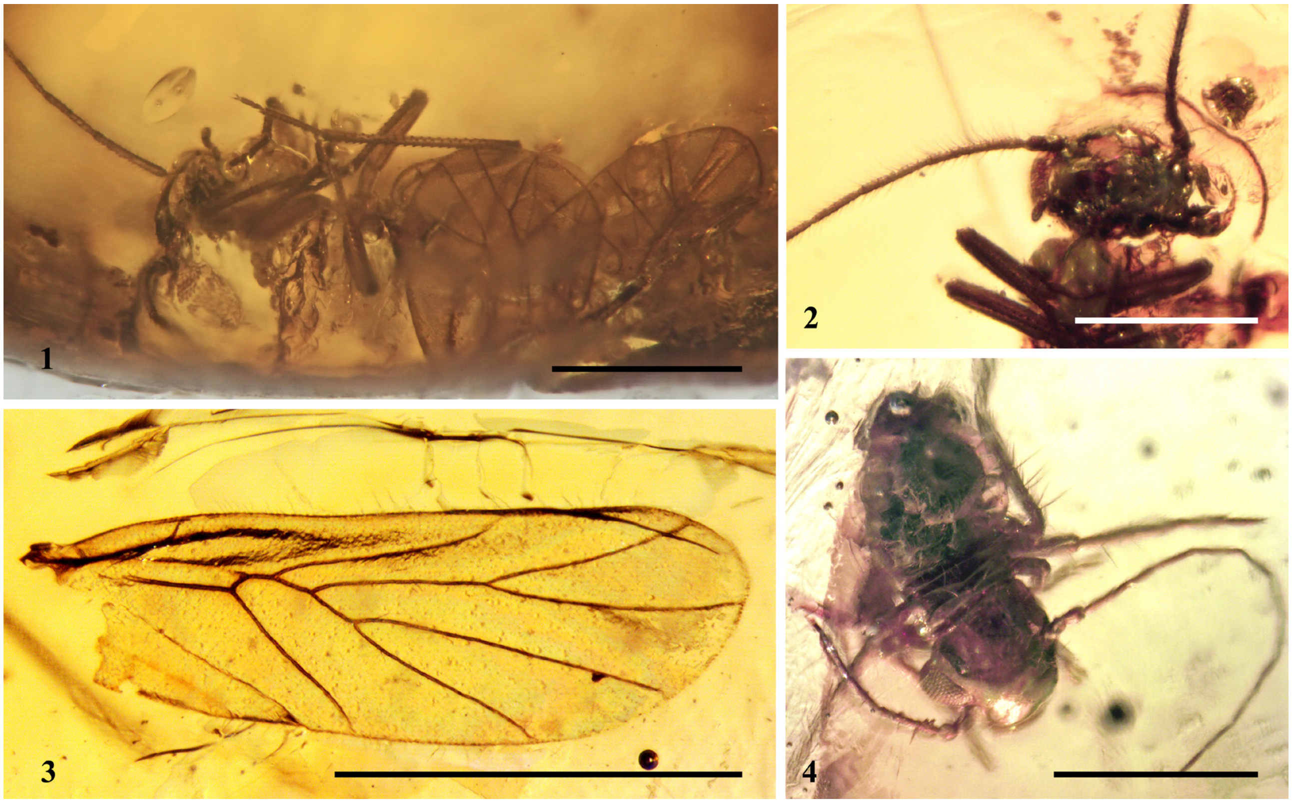

Figure C4. Partial, undetermined psocopterans in Late Cretaceous Vendean amber. 1–2, specimen IGR.GAR-81, habitus and detail of head in ventral view; 3, specimen IGR.GAR-105, hind wing of an undetermined Psocodea; 4, specimen IGR.GAR-3, an undetermined larva. All scale bars = 0.5 mm.

ing a free areola postica; the two latter veins reaching wing margin at 0.97 and 0.77 mm, respectively; veins Cu2 and 1A meeting in a nodulus on wing margin. Hind wing bare, 1.22 mm long; Sc short; basi-radial cell 4-angled; veins R and M+Cu fused basally for 0.16 mm; R1 reaching wing margin at 0.75 mm apically, well before the level of fork of R2+3 and R4+5; these two veins reaching costal margin at 0.99 and 1.21 mm; M simple, reaching wing margin at 1.1 mm; anal vein long and curved following wing margin. Legs with tarsi 3-segmented; tarsal claws with distinct preapical tooth; pulvilus present, thin elongate and slightly wavy, with apex somewhat enlarged (Fig. C3.7); female subgenital plate with distinct isthmus-like neck; external valves ovoid; ventral valves without dense setation (Fig. C3.8, C3.9). Male unknown.

Discussion.— In Smithers's (1990) keys to families of Psocoptera, the fossil matches with the Mesopscocidae for the following features: adult macropterous, tarsi trimerous, body and wings without flattened scales, forewing venation complex (i.e. not reduced to two veins), pterostigma thicker than rest of wing membrane, head not elongate and labrum without two ridges from base to anterior margin, areola postica free, Cu1a and Cu1b separate near wing margin, forewing margin and veins glabrous. It matches similarly with Mesopsocidae using Lienhard's (1998) keys, for it is macropterous, with tarsi trimerous, areola postica free, and wings glabrous. In Badonnel and Lienhard's (1988) keys of Mesopsocidae, the fossil would run to the genus Mesopsocus for its hind wing with anal vein long and curved following wing margin, with veins R and M+Cu fused basally for a distance, the pulvillus setiform, and ventral valve in female without dense setation. Our fossil remarkably differs from *Mesopsocus*, however, in having a subapical placoid sensillum on the sixth flagellomere. The absence of placoid sensillum on this segment is determinant for the genus *Mesopsocus*, and is interpreted as a putative apomorphy by Badonnel and Lienhard (1988). Affinities with the more recently described genus *Idatenopsocus* Yoshizawa and Lienhard, 1997, are excluded for the absence of a hind angle in pterostigma (Yoshizawa & Lienhard, 1997). *Mesopsocoides dupei* n. gen. and sp., constitutes the oldest record of the family Mesopsocidae. It is noteworthy, however, that a fossil taxon from the Middle Jurassic of north China (*Mesopsocus divaricatus* Hong, 1983:75) and belonging to the Thripida: Lophioneuridae Tillyard, 1921, was erroneously given the generic attribution *Mesopsocus*, this homonymy should certainly be corrected.

OTHER EXAMINED PSOCODEAN MATERIAL

The four following partial specimens assigned to psocodeans were also examined from the collection of Rennes University, but their preservation hinders an accurate determination:

- IGR.GAR-81 (ex coll. Guillet): Psocomorpha, Mesopsocidae, and possibly belonging to the genus *Mesopsocus*, but unfortunately a large part of the wings is lacking (Fig. C4.1, C4.2). Preserved features are similar to *Mesopsocoides dupei* n. gen and sp., but it differs in having more robust antennae with different dimensions, and in lacking the subapical placoid sensillum on the 6th flagellar segment.

- IGR.GAR-105 (ex coll. Weigandt): hind wing with M forked (Fig. C4.3). Features are lacking even for a placement in any suborder.

- IGR.GAR-3 (ex coll. Dupé): larva (Fig. C4.4) with 13-segmented antenna, ocelli lacking, tarsi 2-segmented with claw having a preapical tooth.

- IGR.GAR-103 (ex coll. Corgnet): psocodean preserved only by 4-segmented maxillary palps, left antenna with at least 18 segments (16 flagellomeres detached and slightly distant from pedicel), five legs with tarsi trimerous and claws without preapical tooth, and apical parts of forewings and one hind wing, with forewing setae arranged in two rows. This likely corresponds to *Proprionoglaris axioperierga* n. sp.

CONCLUSION

Cretaceous psocodeans are increasingly available thanks to the recent discovery of numerous amber outcrops around the world. Vendean amber significantly provides a new species of the genus *Proprionoglaris*, the earliest representative of the family Mesopsocidae, and a genus in the Amphientometae that may represent a taxon ancestral to both superfamilies Amphientomoidea and Electrentomoidea. These discoveries increase our knowledge of the paleobiodiversity and help in understanding the evolutionary history of the Psocodea group.

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Paleontological Contributions

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AN EARWIG IN LATE CRETACEOUS VENDEAN AMBER (DERMAPTERA)

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ABSTRACT

A new fossil earwig nymph is described and figured from the Late Cretaceous (Cenomanian to Santonian) amber of Vendée, northwestern France. *Vendeenympha gravesi* n. gen. and sp., is distinguished from previously recorded nymphs in other French fossil deposits and compared to modern lineages. This is the third record of earwig nymphs in French Cretaceous ambers.

Keywords: Insecta, Neodermaptera, Labiduridae, Cretaceous, France

RÉSUMÉ

Une nouvelle nymphe fossile de perce-oreilles est décrite et illustrée de l'ambre crétacé supérieur (Cénomanien à Santonien) de Vendée, dans le nord-ouest de la France. *Vendeenympha gravesi* n. gen. et sp., est comparée aux nymphes précédemment décrites d'autres gisements fossiles français et est également comparée aux lignées modernes. Il s'agit de la troisième occurrence de nymphes de perce-oreilles dans les ambres crétacés de France.

Mots-clés: Insecte, Néodermaptère, Labiduridae, Crétacé, France

INTRODUCTION

Earwigs are, unfortunately, one of the understudied lineages among insect diversity. The group is undoubtedly monophyletic and modest in their species diversity, with about 2000 described species. However, they are behaviorally and morphologically rich, with intricate systems of parental care, complicated parent-offspring interactions, and varied in their ecology (Costa, 2006). In addition, their general affinities among the other orders of polyneopteran insects remain unresolved and rather controversial (Grimaldi & Engel, 2005; Jarvis, Haas, & Whiting, 2005; Wan & others, 2012). It is exactly for this reason that a full understanding of their fossil history is vital, with those species from the Mesozoic potentially permitting a revised understanding of the timing of origin for particular dermapteran traits and reconstructing a meaningful groundplan for the order as we understand it and linking those earliest stem members to Late Paleozoic or other Triassic lineages among the Polyneoptera (e.g., Zhao & others, 2010). In this light, the discovery and documentation of fossil Dermaptera is an integral component of resolving long-standing debates pertaining to their origins and thereby the origination and evolution of their various biologies.

Whether preserved as inclusions in amber or compressions, earwigs are typically uncommon to rare in most deposits throughout the world. Naturally, there are isolated exceptions to this pattern but overall, Dermaptera have a remarkably sparse record despite the fact that the lineage is undoubtedly ancient, with records going back to the Triassic (e.g., Wappler, Engel, & Haas, 2005; Grimaldi & Engel, 2005). Jurassic earwigs are restricted to few fossils remarkably preserved as impressions in sedimentary rocks (e.g., Zhao & others, 2010). In amber, most records have come from those rich deposits of the Baltic region or Dominican Republic (Wappler, Engel, & Haas, 2005; Engel, unpubl. data), both from the Tertiary, while in the Cretaceous the most diverse fauna is that of the Albian-Cenomanian amber from Myanmar (e.g., Engel & Grimaldi, 2004; Engel, 2011,

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unpubl. data). For all other Cretaceous amber deposits, earwigs are represented by usually one or a few individuals (Engel, 2009; Engel, Ortega-Blanco, & Azar, 2011; Perrichot & others, 2011), not all of which are sufficiently preserved for meaningful study (e.g., those presently in Turonian amber from New Jersey: Engel, pers. obs.). Here is reported the third record of Dermaptera from the Cretaceous ambers of France. The new specimen is represented by an isolated nymph and is compared with the older specimens from Archingeay (Engel, 2009; Perrichot & others, 2011), as well as other living and fossil Dermaptera.

MATERIAL AND METHODS

The nymph was entombed within a small piece of clear yellow amber generally free of debris (Fig. D1.1, D1.2), with one biting midge (Diptera: Ceratopogonidae – described by Choufani & others, 2014: 10H in this volume) and one scelionine wasp (Hymenoptera: Scelionidae) as syninclusions. The piece was cut into three parts to obtain an optimal view of each inclusion. The specimen is missing most of its dorsum but preserves many important diagnostic features. The posterior border of the head is missing, although the lateral surfaces are complete back to the posterolateral corners, and the posterior dorsal portion of the head integument is similarly absent, with small bubbles trapped within the emptied head capsule. The dorsal sclerites of the thorax are missing and the prosternum is absent, the latter more likely having become greatly cleared and dissolved as the setae are still in place demarcating where it and some of the other ventral sclerites once were. Much of the dorsum of the abdomen is gone, although for some segments lateral extremities of the terga remain. The cerci are complete, although a fracture through the amber piece does cut across them, but does not deter from their examination and study. Much of the integument is cleared and permits a wonderful view of fine details of sculpturing. A sizeable bubble is preserved alongside the specimen's venter but does not obscure any details (Fig. D1.1).

The amber was collected in 2002 by Didier Graves from a deposit which was temporarily exposed during construction along the highway D32 between La Garnache and Challans, department of Vendée, northwestern France. The exact dating of the amber remains uncertain within the Middle Cenomanian–Early Santonian interval (97–85 Ma). More details on the geology will be provided elsewhere (see Perrichot & Néraudeau, 2014: 10A in this volume)

Photographs were prepared with a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens and also with a Canon 5D Mark II attached to a Leica MZ APO stereomicroscope, while measurements were taken with an ocular micrometer on an Olympus SZX-12 stereomicroscope. Morphological terminology generally follows that used elsewhere for Dermaptera (e.g., Giles, 1963; Günther & Herter, 1974; Engel, 2009, 2011; Engel, Ortega-Blanco, & Azar, 2011; Perrichot & others, 2011), while the classification followed herein is that of Engel and Haas (2007).

SYSTEMATIC PALEONTOLOGY

Suborder NEODERMAPTERA Engel, 2003

Genus VENDEENYMPHA new genus

Type species.—*Vendeenympha gravesi* n. sp.

Diagnosis.—Small individual, ca. 4.6 mm in total length (excluding antennae); body as preserved apparently not compressed dorsoventrally (*cf.* with the more compressed body of *G. walleri*: Perrichot & others, 2011), with sparsely scattered fine setae, not chaetulose; integument where evident matt and imbricate. Head prognathous, apparently slightly broader than long, preserved portions of posterior angles rounded, not acute. Maxillary palpus with five palpomeres, sparsely and finely setose, apicalmost palpomere and penultimate palpomere of approximately equal length, apicalmost palpomere not distinctly larger (Fig. D1.3). Compound eyes small, not prominent, near to antennal base, separated from posterior border of gena by length more than compound eye diameter; post-ocular ridge absent; ocelli apparently absent (posterior dorsum of head is damaged and missing but surface where ocelli should be is preserved and there is no evidence of them). Antenna with scattered, ultrafine setae; scape short and thick, shorter than distance between antennal bases, length slightly less than twice width; pedicel short, about as long as wide; six flagellomeres present (based on form of apex of flagellomere VI antenna appears to be complete); flagellomere I elongate and longest of flagellomeres, length approximately 5 times width, slightly thicker than remaining flagellomeres; flagellomeres II–VI, longer than wide, individual lengths three-quarters that of flagellomere I and nearly 4 times as long as wide. Genal carina absent; coronal line apparently absent (again, dorsum of head is damaged posteriorly but anteriorly there is no line present). Prosternum not preserved but setae remain, position of such setae (particularly the prominent erect setae usually associated with the margins) serve to demarcate its relative position and boundaries (given the uncertainty involved with this portions deduced from setal positions are placed in braces); apparently subquadrate with lateral margins weakly converging posteriorly between procoxae; small, fine setae anterior to this and very near medioanterior margin of prosternum suggest that the posterior ventral cervical sclerite was touching prosternum (as is typical in the "forficuloid neck"). Mesosternum subtrapezoidal, with lateral margins converging posteriorly; anterior margin slightly convex, posterior margin slightly convex (somewhat similar to the more distinctly convex condition found in Anisolabidinae); with prominent, erect, stiff setae anteriorly near or on margin, two particularly elongate prominent seta on lateral margin just anterior to mesocoxae; mesocoxae articulating in posterior, near mesosternum-metasternum juncture). Metasternum large, anteriorly wider than posteriorly, laterally slightly constricted in posterior half at metacoxae, with a couple of prominent, erect, stiff setae anterolaterally and a single prominent seta in posterolateral corner, corners rounded; anterior margin slightly convex, posterior margin straight. Legs not elongate; procoxae near posterior margin of prosternum (although prosternum is not preserved, the setae from the surface of the cervical sclerites and prosternum are still present to demarcate its area roughly; this combined with the position of the procoxae and mesosternum serve to determine their position in life); femora not compressed and not carinate or keeled, ventral surface flattened but not depressed; profemur more swollen than other femora; tibiae not greatly elongate but longer than tarsi, particularly so for metatibia; tarsi trimerous, second tarsomere greatly reduced, not widened apically and not greatly projecting beneath base of third tarsomere (Fig. D1.4), apex of second tarsomere truncate and slightly slanted such that ventral length is slightly more than dorsal

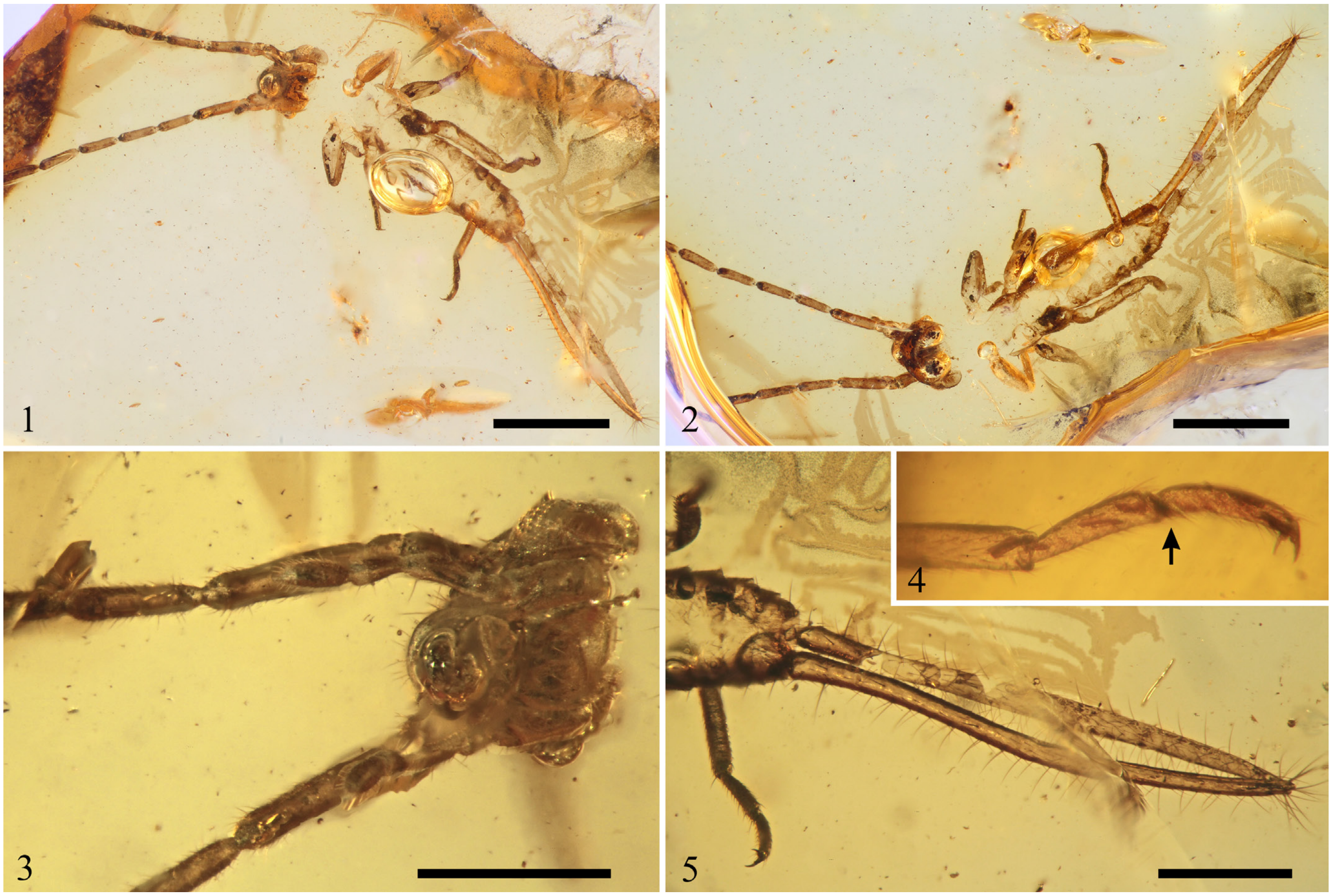

Figure D1. *Vendeenympha gravesi* n. gen. and sp., holotype nymph, IGR.GAR-72.2, in early Late Cretaceous Vendean amber, NW France; *1*, habitus in ventral view; *2*, habitus in dorsal view; *3*, head in ventral view; *4*, left metatarsomeres, with indication of the reduced second tarsomere (arrow); *5*, right hind leg and cerci in ventral view (scale bars: 1, 2 = 1 mm; 3, 5 = 0.25 mm).

length; pretarsal ungues simple except for minute bump near base, arolium absent. Abdominal segments apparently transverse, wider than long; penultimate segment not modified or distinct from preceding segments; where tergal and sternal integument is preserved surface is finely imbricate; cerci formed of a single cercomere, greatly elongate, nearly twice length of abdomen and only slightly shorter than combined lengths of abdomen and thorax; bases of cercal forceps nearly touching, cerci somewhat tubular and simple over entire length, slightly curved in apical half such that apices come together and partially overlap, cercal apex acutely rounded, surface with numerous, erect, stiff, and somewhat elongate setae, such setae particularly numerous at apex (Fig. D1.5).

Etymology.—The new genus-group name is a combination of Vendée, the department from which the amber originate, and *nympha* (Latin, meaning "young woman"). The name is feminine.

VENDEENYMPHA GRAVESI, new species
Figure D1

Type material.—Holotype nymph (sex indeterminate), IGR.GAR-72.2 (ex coll. Graves), 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 patronym honoring Didier Graves, the specimen's collector.

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

Description.—Nymph. As described for the genus, with the following minor additions: Total body length 4.6 mm (as preserved, excluding antennae), head width across compound eyes 0.64 mm; integument brown to light brown (coloration in most parts largely artifact of degree of postmortem clearing that has taken place); flagellomere I length 0.43 mm, maximum width 0.086 mm; integument of head more finely and weakly imbricate than elsewhere, with a few erect, stiff setae near compound eye, antennal base, and frontoclypeal margin. Thoracic length 1.01 mm; preserved portions of pleural distinctly imbricate, similar to sculpturing present on legs. Abdomen of moderate length, length 1.14 mm as preserved, 0.45 maximum width as preserved; integument imbricate, with scattered fine setae, more apical segments with some sparse prominent, erect setae laterally and/or apically; from preserved portions of cleared sterna abdominal segments transverse, with straight posterior margins on sterna. Cerci elongate tubular, length 1.92 mm, basal width

0.08 mm, basal separation between cerci 0.026 mm, individual cerci longer than abdomen, without dentition, crenulations, or serrations, slightly curved, of relatively uniform width over most of length, tapering slightly and gently apical to acutely rounded apex; apex with dense elongate, stiff, erect setae, such setae sometimes more than three times cercal diameter.

DISCUSSION

The holotype of *V. gravesi* is likely a first-instar nymph for largely the same reasons provided for staging the material discussed by Engel (2009). Most notably the elongate meriston is suggestive of an early instar, as is the long form of the succeeding flagellomeres and the reduced number of total flagellomeres (in this case merely six) (Günther & Herter, 1974). Familial placement is rather questionable. Certainly the species belongs to the Neodermaptera owing to the trimerous tarsi and absence of ocelli, and can be excluded from the Diplatyidae and Karschiellidae by the non-annulated cerci, and from the Forficulidae and Chelisochidae by the unmodified second tarsomere. The fossil may also be excluded from the epizoic families Arixeniidae and Hemimeridae by the absence of their large suite of peculiar modifications associated with living on bats and rats, respectively (Günther & Herter, 1974). Placement within Pygidicranidae seems unlikely given the absence of carinate or keeled femora and, if the assertions regarding the ventral cervical sclerites are correct, the presence of a "forficuloid neck". The pygidium and other critical features are unfortunately not preserved and so refining the placement beyond this is impossible other than to note that the significantly elongate form of the cerci in such a young instar is suggestive of the family Labiduridae, and the form of the preserved thoracic sterna do not outright contradict such an assignment. Moreover, labidurids are well known from the Cretaceous and so there is no contradiction with the limited phylogenetic-stratigraphic correlations available for lineages of earwigs (e.g., Grimaldi & Engel, 2005).

Among the three forms of immature earwigs preserved in French Cretaceous ambers, *Vendeenympha* can be distinguished quickly from the previously known taxa. *Vendeenympha* differs most noticeably from *Gallinympha* Perrichot & Engel (in Perrichot & others, 2011) in the form and number of the antennal segments (six flagellomeres, each much longer than wide and finely setose in *V. gravesi versus* 10 flagellomeres, the basal ones being distinctly compact and more densely setose in *Gallinympha*), body not noticeably dorsoventrally compressed (distinctly compressed in *Gallinympha*), ventral surfaces of femora not depressed (distinctly depressed in *Gallinympha*), cervix presumably of "forficuloid" type (definitely of "blattoid" type in *Gallinympha*), and the form of the thoracic sterna (refer above to those for *V. gravesi* and to Perrichot & others, 2011, for *Gallinympha*). From the nymphs described by Engel (2009) as ARC-240, *V. gravesi* differs in the absence of the coronal line (present in ARC-240), compound eyes separated from posterior corner of temples by length greater than eye diameter (separated by compound eye diameter in ARC-240), longer flagellomeres II and III relative to length of meriston (shorter in ARC-240 and if all of the same instar, then likely informative), more noticeably dense patch of elongate setae at apex of cerci (not so in ARC-240), and close basal approximation of the cerci (more widely separated in ARC-240). As outlined briefly here, there are now at least three diagnosable groups of earwigs present in the paleontologically rich French Cretaceous ambers. It is greatly hoped that continued exploration will bring further material and ideally complete adults from which to elucidate more clearly the relationships of these taxa.

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Paleontological Contributions

December 1, 2014 Number 10E

A TERMITE (ISOPTERA) IN LATE CRETACEOUS AMBER FROM VENDÉE, NORTHWESTERN FRANCE

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ABSTRACT

A new genus and species of primitive termite is described and figured from the remains of an alate in Late Cretaceous (Cenomanian to Santonian) amber from the Department of Vendée in northwestern France. *Termitotron vendeense* n. gen. and sp. is distinguished on the basis of its head and wing morphology and exhibits unique features in the mouthparts relative to other Cretaceous termite genera. Brief comments are made on its possible affinities among the "*Meiatermes* grade" of Euisoptera.

Keywords: Insecta, Isoptera, Cretaceous, amber, France, Dictyoptera

RÉSUMÉ

Un nouveau genre et une nouvelle espèce de termite primitif sont décrits et figurés d'après les restes d'un individu ailé préservés dans l'ambre crétacé supérieur (Cénomanien à Santonien) de Vendée, nord-ouest de la France. *Termitotron vendeense* n. gen et sp. se distingue par sa morphologie de la tête et des ailes, et ses pièces buccales présentent des caractères uniques par rapport aux autres genres de termites crétacés. Ses affinités possibles au sein du "grade *Meiatermes*" des Euisoptères sont brièvement commentées.

Mots-clés: Insecte, Isoptère, Crétacé, ambre, France, Dictyoptère

INTRODUCTION

Today, termites (Isoptera) are a ubiquitous feature of virtually all temperate and tropical ecosystems, particularly numerous in tropical forests and savannahs, and among the most critical of all detritivores. The majority of living species, belonging to the derived families Rhinotermitidae and Termitidae, live in frequently large, perennial colonies, can be relatively dense in numbers, and serve as the principal recyclers of plant material (Grimaldi & Engel, 2005). Isoptera extend back to the earliest stages of the Cretaceous (Engel, Grimaldi, & Krishna, 2007a), although until the mid-Tertiary the lineage did not exhibit the ecological dominance and abundance for which they are so famous today, although they were certainly eusocial already by that time (Engel, Grimaldi, & Krishna, 2009). During the Mesozoic the termites were represented by a grade of primitive groups whose survivors today frequently live in relatively small colonies (although *Mastotermes darwiniensis* Froggatt is a notable exception), feeding on felled and decomposing logs or grasses (e.g., Archotermopsidae and Hodotermitidae). It is fascinating to imagine how lignocellulose was broken down and nutrients recycled in an epoch in which termites were such a minor component of the fauna. An intimate understanding of the early fossil history of termites is needed in order better to elucidate isopteran diversification and their eventual rise to become the pre-eminent recyclers of the modern era.

The number of Cretaceous termites has risen remarkably during the last 15 years, with more species discovered and described during that period than all other works prior (Krishna & others, 2013). Herein is documented a fragmentary termite in Late Cretaceous (Middle Cenomanian to Early Santonian) amber from northwestern France. This is the first termite from the Late Cretaceous of Europe and the only record from the amber-bearing strata of the department of Vendée. Although the specimen is fragmentary within the amber piece, there is a remarkable amount of information available from

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the observed character details. A brief description is provided and a few comments made on its affinities.

MATERIAL AND METHODS

The unique specimen is fossilized in a piece of clear yellow amber that was collected in 2002 by Fanny Dupé from a deposit exposed briefly during work for the enlargement of the road D32 between La Garnache and Challans, in the department of the Vendée, northwestern France. The exact dating of the amber-bearing stratum remains uncertain within the Middle Cenomanian–Early Santonian interval (97–85 Ma), and resolving this issue is still work in progress (see Perrichot & Néraudeau, 2014: 10A in this volume). The original amber piece split into four smaller fragments during the polishing of its surface due to internal fracture planes, but this did not affect the integrity of the fossil since it was already fragmentary when entombed in the resin flow. The specimen comprises an isolated head capsule and the shed fore and hind wings of an alate. The head is situated along an internal fracture plane within the amber flow and this obscures a direct dorsal view. Nonetheless, a beautifully detailed ventral and slightly oblique view is possible and shows clearly several important details such as the presence of a preoccipital sulcus and the form of the labium. In addition, the compound eyes are clear as is the associated integument along their upper boundary curving onto the dorsum of the head and into the fracture plane. Unfortunately, neither antenna is complete beyond the basalmost antennomeres. The wings are preserved in two other fragments of what was originally the single piece of amber. The piece split along the plane of the wings such that, in the larger piece, a complete pair of wings is preserved along with a relatively complete forewing and fragments of the second hindwing. From one side the wings are seen through and within the resin, while from the other side they are exposed and appear as impressions in the amber surface. The opposing and smaller piece of amber preserves the reverse of this impression. Together, the two pieces give a rather complete perspective on the venation. The most complete wings are preserved beyond the wing scales, the others are partially preserved and only parts well beyond the scales are present, and are presumed to have been shed at the time of entrapment.

Photomicrographs were prepared using a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens and illuminated by both reflected and transmitted light from a timed Xenon flash. Measurements were taken with an ocular micrometer on an Olympus SZX-12 stereomicroscope. Morphological terminology follows that of Krishna and others (2013) and the format of the description is generally based on those of Engel, Grimaldi, and Krishna (2007a, 2007b, Engel & others, 2011), Engel and Gross (2009), and Engel and Delclòs (2010). The classification adopted is that of Engel, Grimaldi, and Krishna (2009) as augmented by Krishna and others (2013).

SYSTEMATIC PALEONTOLOGY

Infraorder ISOPTERA Brullé, 1832
Family *incertae sedis*

‘MEIATERMES-GRADE’
Genus TERMITOTRON new genus

Figure E1. Photomicrograph of head of holotype of *Termitotron vendeense* n. gen. and sp.

Type species.—*Termitotron vendeense*, new species.

Diagnosis.—Imago. Head rounded, lateral and posterior margins gently rounded; basal part of antenna moniliform (scape, pedicel, and first flagellomere); compound eyes circular, relatively small; ocelli apparently absent (somewhat uncertain); occipital carina present; subgenal sulcus present; occipital foramen rounded (as in *Mastotermes*); maxillary palpus pentamerous, characteristically compact, with basal three palpomeres reduced and transverse, fourth palpomere longer than wide, about as long as combined length of basal three palpomeres, apical palpomere longer than wide, subequal in length to fourth palpomere, entire palpus scarcely surpassing apex of labrum (in most termites the maxillary palpomeres are more elongate in shape). Forewing with membrane highly reticulate and relatively rounded apex; all veins apparently originating inside wing scale; Sc terminating at about wing midlength; R1 simple for most of length, with short superior twig near apex, terminating just anterior of wing apex; Rs encompassing wing apex, without superior branches, at least two primary inferior branches, proximal-most branch forking near wing apex; M running about midway between Rs and CuA, branching in apical half of wing; CuA encompassing posterior margin of wing to about four-fifths of wing length, with numerous branches, most simple, although more apical branches forking near wing margin; hind wing without anal lobe (unlike Mastotermitidae).

Etymology.—The new genus-group name is a combination of *Termes*, meaning, “termite”, and *thronion*, neuter diminutive meaning “throne” (as in the archangel Metatron). The gender of the name is considered neuter.

TERMITOTRON VENDEENSE new species
Figures E1–E2

Type material.—Holotype alate (sex indeterminate), IGR.GAR-30 (ex coll. F. 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 southwest of La Garnache, Vendée, France.

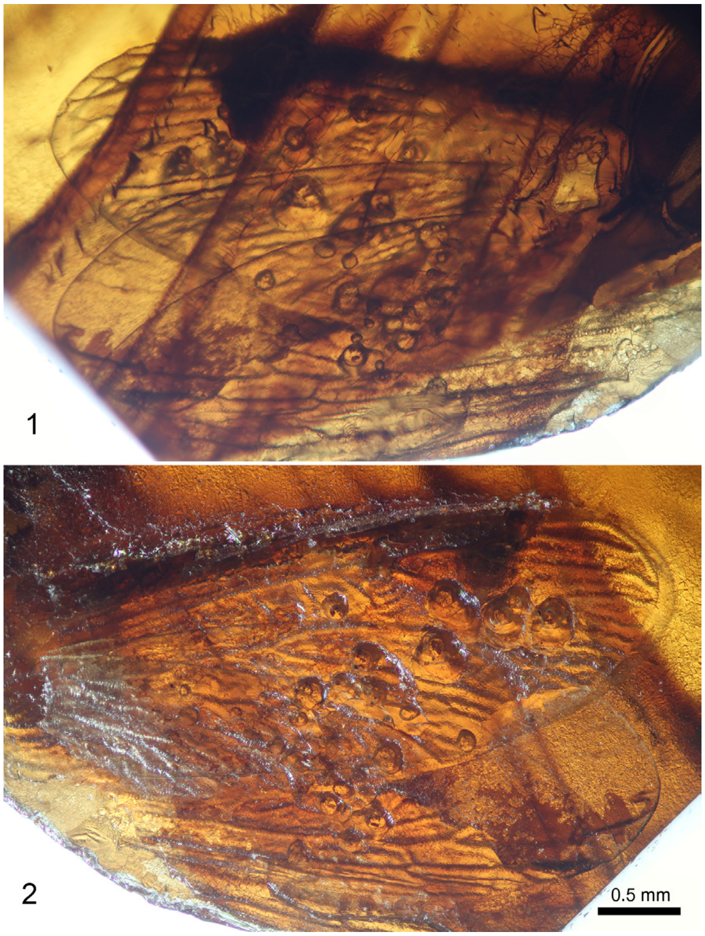

Figure E2. Photomicrographs of wings of holotype of *Termitotron vendeense* n. gen. and sp. *1*, Wings as viewed through the amber piece; *2*, Wings preserved at the surface of the amber piece.

Etymology.—The specific epithet refers to the Department of Vendée where the amber originates.

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

Description.—Imago. Head brown, matte, legs brown; wing apparently hyaline; head with sparse suberect, short setae, more elongate setae present on labium, maxilla, and labrum; wing apparently bare, without nodules or seta, membrane reticulate (Fig. E2.1). Head generally round, apparently slightly longer than wide (direct measure of width not possible; compound eye round, moderately convex, relatively small, separated from posterior border of head by more than compound eye diameter, integument bordering upper tangent of compound eye without evident ocelloid; mandibles partly visible but dentition not entirely discernable; basal portion of antenna moniliform, 3 antennal articles preserved, first slightly thicker than pedicel and first flagellomere; submentum quadrate, mentum short and relatively transverse, labial palpus trimerous, palpomeres short, only slightly longer than wide; maxillary palpus pentamerous, basal palpomeres greatly compact, combined length of basal three palpomeres about equal to length of fourth palpomere, apical palpomere subequal to fourth palpomere, with blunt apex, fourth and fifth palpomeres with a few long, suberect setae. Forewing Sc simple, running close to anterior wing margin, terminating near wing midlength; R1 running near anterior wing margin, simple for majority of length, a single superior branch near termination anterior to wing apex; radial field relatively broad and expanding slightly apically (plesiomorphy), such that Rs encompasses wing apex; Rs with at least two strong branches present, basalmost forked near wing margin and terminating just behind wing apex, apicalmost branch terminating at wing apex; M separated from R prior to basal suture such that M is already a free vein, M branching at about wing midlength, with at least two distinct branches, at least apicalmost forking near wing margin; CuA well-developed, with at least 8 posterior branches, covering main part of posterior wing margin, more apical branches forking near margin. Length of head 1.17 mm; diameter of compound eye 0.29 mm, temple length (posterior of compound eye to posterior of head) 0.42 mm; length of forewing from suture 4.73 mm, width of forewing 1.87 mm.

DISCUSSION

Naturally, it is unfortunate that the present specimen is so fragmentary, represented only by the wings and an isolated head. The entirety of the thorax and abdomen are missing and were presumably in another shard of the amber which was not recovered. Important information regarding the pronotum, tarsal formula, leg spination, cerci, styli, and other characters remains to be discovered. Nonetheless, it is possible to make some simple statements concerning the identity and affinity of the present species. The broad radial area with multiple branches of Rs excludes affinities with the Icoisoptera (=Neoisoptera + Kalotermitidae). The possession of notable plesiomorphies such as the occipital carina and reticulate wing membranes is indicative of the primitive grade of Cretaceous termites known generally as the "*Meiatermes* grade", basal among the Euisoptera. The wing venation is generally like many of the genera in this grade, including some other groups from the Cretaceous of France such as *Santonitermes* Engel, Nel & Perrichot and *Syagriotermes* Engel, Nel & Perrichot (Engel & others, 2011). The venation of *Termitotron* is most similar to *Santonitermes*, although the form of R1 and Sc are unknown for the latter, but the distinctive, compressed form of the palpi in the former can readily distinguish it. From *Syagriotermes*, the new genus can be distinguished by the more elongate Sc and Rs encompassing the wing apex. It is greatly hoped that more complete material may be recovered in the future and the distinctive apomorphy of the maxillary palpus should make future identification of conspecifics relatively simple.

ACKNOWLEDGEMENTS

I am grateful to Dr. Vincent Perrichot for bringing the specimen to my attention, permitting its study, and providing a French translation of my abstract; to Fanny Dupé (Arthon-en-Retz) who collected the amber pieces and donated them to the University Rennes 1; and to Dr. Ismael A. Hinojosa-Díaz for assistance with photomicrography as supported by the Engel Illustration Fund of the University of Kansas College of Liberal Arts and Sciences. Work on the Vendean amber was partly supported by CNRS-INSU grant (research project Interrvie NOVAMBRE 2 to D. Néraudeau, University Rennes 1) and French National Research Agency grant nº BLAN07-1-184190 (project AMBRACE to D. Néraudeau). This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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Paleontological Contributions

December 1, 2014 Number 10F

A NEW GENUS OF DUSTYWINGS (NEUROPTERA: CONIOPTERYGIDAE) IN LATE CRETACEOUS VENDEAN AMBER

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ABSTRACT

A new genus and species of Coniopterygidae is described from a female preserved in Late Cretaceous (Cenomanian to Santonian) amber of Vendée, in northwestern France. *Garnaconis dupeorum* Perrichot & Nel, n. gen. and sp., displays intermixing features between Aleuropteryginae and Coniopteryginae as currently defined, making its accurate phylogenetic placement difficult. It is tentatively placed in the Aleuropteryginae. A new practical key to the Mesozoic genera of dustywings is proposed.

Keywords: Insecta, Neuropterida, Aleuropteryginae, Mesozoic, France

RÉSUMÉ

Un nouveau genre et une nouvelle espèce de Coniopterygidae sont décrits d'après une femelle préservée dans l'ambre du Crétacé supérieur (Cénomanien à Santonien) de Vendée, nord-ouest de la France. *Garnaconis dupeorum* Perrichot & Nel n. gen. et sp., montre une mosaïque de caractères des deux sous-familles Aleuropteryginae et Coniopteryginae telles que définies actuellement, rendant sa position phylogénétique relativement incertaine. Il est ainsi provisoirement placé au sein des Aleuroteryginae. Une nouvelle clé des genres de Coniopterygidae mésozoïques est proposée.

Mots-clés: Insecte, Neuropterida, Aleuropteryginae, Mésozoïque, France

INTRODUCTION

Fossil dustywings are almost exclusively found in amber, with 24 species known in 15 genera (10 extinct) from the Neogene Dominican and Mexican ambers, the Palaeogene Baltic, Ukrainian, Indian, and Parisian ambers, and the Cretaceous ambers from Siberia, New Jersey, France, Myanmar, and Lebanon (see the detailed list in Engel & Grimaldi, 2008: appendix 1; and updates in Kupryjanowicz & Makarkin, 2008, Engel, 2010, and Grimaldi & others, 2013). Only two additional, monotypic genera are known as compression fossils, from the Oligocene of France (Nel, 1991) and the Jurassic of Kazakhstan (Meinander, 1975). Two subfossil species were also described from African copal (Meunier, 1910a, 1910b) but are likely synonymous with extant species (Engel, 2004). Finally, several specimens have been reported from Campanian Canadian amber (McKellar & others, 2008) and Albian Spanish amber (Pérez-de la Fuente, 2012), but have yet to be described.

Cretaceous dustywings mostly belong in the Aleuropteryginae, with ten species known in four genera. The Coniopteryginae are known by only two monotypic genera (see the key to Cretaceous genera below).

Herein we report the discovery of a new Coniopterygidae from the Mesozoic, based on a fossil inclusion from Late Cretaceous amber of France.

MATERIAL AND METHODS

The specimen is entombed in a piece of Vendean amber, which derives from a deposit that briefly outcroped between 2002 and 2005

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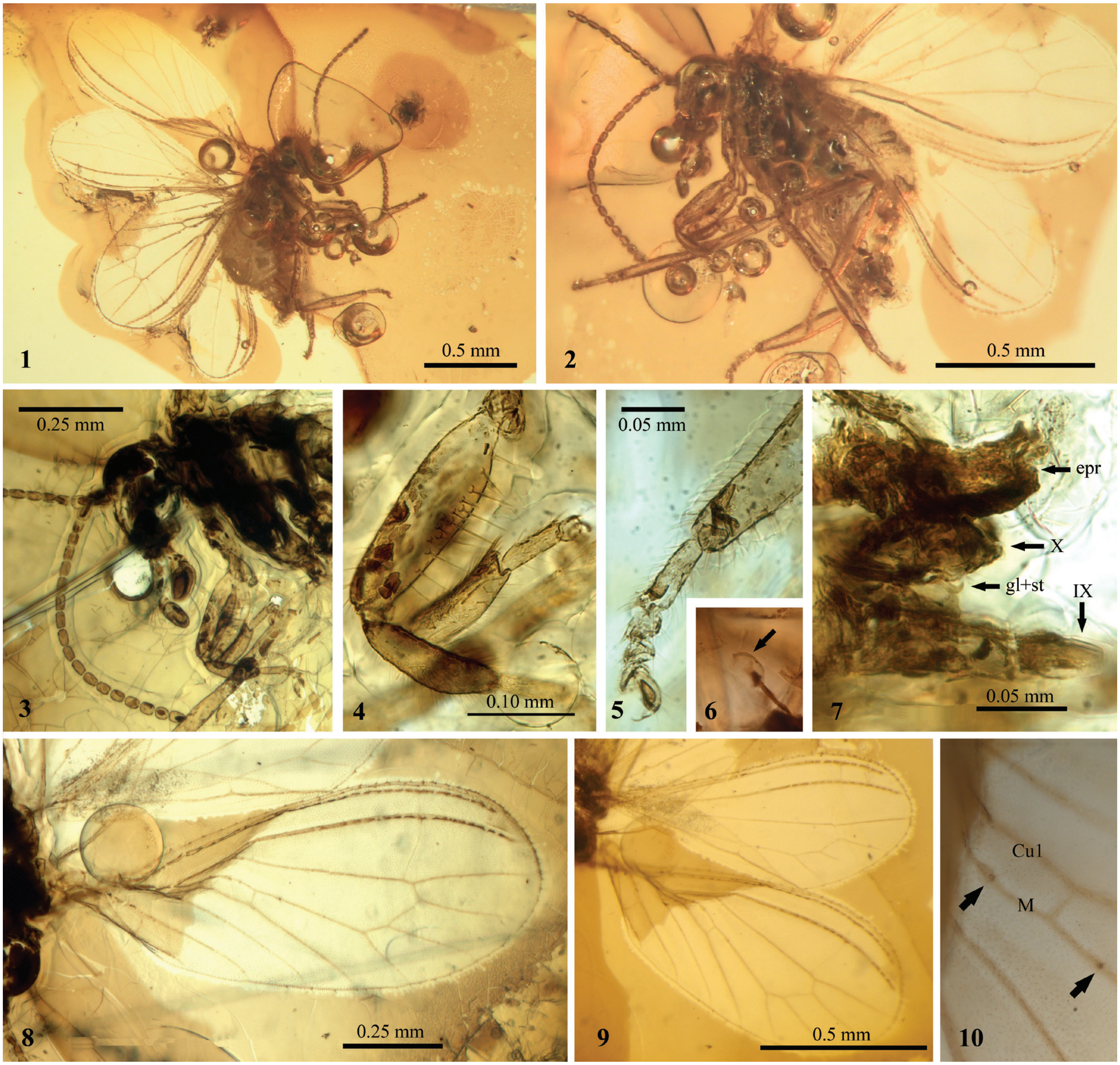

Figure F1. Photomicrographs of *Garnaconis dupeorum* Perrichot & Nel, n. gen. and sp., holotype female IGR.GAR-2, in Late Cretaceous Vendean amber. *1, 2,* profile views; *3,* head and mesosoma in left profile view, as preserved after embedding in Canada balsam; *4,* fore femur; *5,* hind tarsi; *6,* plicature on fourth abdominal segment (arrow); *7,* genitalia with indication of the 9th segment (IX), ectoproct (epr), 10th sternite (X), and gonapophyses laterales with two curved setae visible (gl+st); *8,* left forewing; *9,* left hindwing (above) and forewing (below); *10,* forewing median area with indication of the two stiff setae.

during construction along the D32 road between La Garnache and Challans, in the department of Vendée, northwestern France. The exact dating of the amber-bearing stratum remains uncertain within the Middle Cenomanian–Early Santonian interval (97–85 Ma), and a discussion with more details on the geology and paleoenvironment of this deposit will be provided elsewhere (see preliminary account in Perrichot & Néraudeau, 2014: 10A in this volume).

The clear yellow amber sliver containing the specimen was originally 7×5×4 mm in size and was polished to maximize close views; polishing used emery papers at different grits (1200 and 2500) on a water-fed grinder. Because some structures were still hidden by large air bubbles, a razor blade was used to remove precise portions with bubbles and the remaining piece was included in Canada balsam between cover glasses; unfortunately the balsam diffused within the amber matrix and caused irreversible damages (lightening and/or blurring) to the inclusion cuticle (e.g., Fig. F1.3, F1.7), so embedding of fossiliferous Vendean amber in this natural medium must be strictly avoided and instead, epoxy-embedding should be preferred. Photographs were taken with a Canon 5D Mark II camera attached to Leica microscopes, and HeliconFocus 4.45 software was used to produce multifocus z-stacks so as to achieve sharp focus throughout the images.

We use the morphological terminology proposed by Meinander (1972).

SYSTEMATIC PALEONTOLOGY

Family CONIOPTERYGIDAE Burmeister, 1839
Subfamily ALEUROPTERYGINAE Enderlein, 1905
Genus GARNACONIS Perrichot & Nel, new genus

Type species.—*Garnaconis dupeorum*, new species, by original and monotypic designation.

Etymology.—The new genus-group name is a combination of the name Garnache (the town near which the amber deposit originates) and the Greek *konis* (meaning dust), a common suffix for dustywing genera.

Diagnosis.—Female. Antenna with 17 flagellomeres. Forewing entirely fuscous, without any clouds over crossveins; crossveins sc-r and r-rs aligned, r-rs meeting Rs distinctly basad fork of R_{2+3}–R_{4+5} (i.e., r-rs connected to Rs); no crossvein between Rs and M (i.e., only distal crossvein r-m between R_{4+5} and M_{1+2}), about 2.5× as long as basal abscissa of R_{4+5}; medial vein with two branches, with thickened setigerous spot on each side of m-cu; Cu2 with one thickened setigerous spot distal to crossvein cua-cua2. Small plicatures visible at least on third and fourth abdominal segments. Abdominal segment 9 very long.

GARNACONIS DUPEORUM, Perrichot & Nel, new species
Figures F1–F2

Type material.—Holotype female IGR.GAR-2, in Late Cretaceous (Middle Cenomanian to Late 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 patronym honoring Fanny and André Dupé who collected this and most of the Vendean amber material.

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

Description.—Body length ca. 0.8 mm (measured from tip of the head to tip of genitalia). Head (Fig. F1.2, F1.3) hypognathous, elongate, ca. 0.24 mm long. Compound eyes well developed and oval, smallest diameter 0.07 mm, largest diameter 0.09 mm. Interocular distance equal to smallest eye diameter. Antenna 0.74 mm long, with all articles bearing scattered sensilla (Fig. F1.3); flagellomeres cylindrical, f1-f13 about twice as long as broad, f14-f17 about 1.6 × as long as broad; f1 and f2 not distinctly longer than following flagellomeres, f1 0.02 mm long, 0.01 mm wide. Maxillary palps five-segmented, about 0.19 mm long; third segment slightly longer than first, second, and fourth; fifth segment particularly swollen basally, distinctly larger than others, 0.07 mm long and 0.02 mm wide. Galea and lacinia obscured. Labial palps three-segmented, with third segment very large, 0.1 mm long, distinctly larger than first two segments. Thorax 0.27 mm long. Prothorax short, 0.12 mm long. Mesothorax 0.1 mm long, bearing two prominent tubercles dorsally, and two distinct lateral shoulders basad forewings. Metathorax 0.05 mm long. Forewing (Figs. F1.8–F1.10, F2) 1.1 mm long, 0.48 mm wide; Sc_1 long and parallel to costal margin in its basal two thirds; fork Sc_1 and Sc_2 (or sc-r) at 0.82 mm from wing base; sc-r 0.85 mm long, aligned with r-rs at 0.26 mm from wing apex; R branching off from R+M at 0.2 mm from wing base, then bifurcating into R_1 and Rs after a distance of 0.17 mm; Rs 0.41 mm long before its fork; R_{2+3} 0.27 mm long; crossvein r-rs slightly sinuate, 0.15 mm long, basal to fork of R_{2+3}–R_{4+5}; distance between base of R_{4+5} and its apex 0.26 mm; M 0.48 mm long before its fork into M_{1+2} and M_{3+4}; M_{1+2} curved; crossvein rs-m connected to M_{1+2} 0.05 mm distally of fork of M_{1+2}–M_{3+4}; M setae approximately equidistant on each side of m-cu (Fig. F1.10); M_{3+4} weakly curved, 0.15 mm long; Cu bifurcating into Cu_1 and Cu_2 0.12 mm from wing base; Cu_1 curved, reaching wing margin 0.74 mm from wing base; Cu_2 curved, distal half nearly parallel to Cu_1, reaching wing margin 0.63 mm from wing base; no visible crossvein between Cu_1 and Cu_2; crossveins cua-cu_2 and cua nebulous. Hind wing (Fig. F1.9) slightly shorter than forewing, 0.98 mm long, 0.41 mm wide; Sc_1 rather long and parallel to costal margin, approaching costal margin 0.95 mm from wing base; fork of R_1– Rs not clearly visible but in a very basal position, just distal base of M; Rs bifurcating into R_{2+3} and R_{4+5} 0.79 mm from wing base; R_{2+3} slightly curved, 0.19 mm long; r-rs 0.13 mm long, basad fork of Rs; distance between base of R_{4+5} and tip of R_{4+5} 0.16 mm; M (0.5 mm long before its fork) branching off from R+M very basally; M and Cu distinctly separated, not touching; M_{1+2} slightly curved; crossvein between R_{4+5} and M_{1+2} 0.07 mm from base of M_{1+2}; M_{3+4} 0.11 mm long; Cu bifurcating into Cu_1 and Cu_2 very basally; Cu_1 curved; a crossvein m-cu present; Cu_2 curved, nearly parallel to Cu_1. Legs slender and densely covered by microtrichiae; fore femur with 13–14 stiff erect setae on posterior surface (Fig. F1.4); tibiae rather long, covered with regular rows of regularly spaced setae; tarsi five-segmented, covered with setae (Fig. F1.5); first tarsomere long, slightly shorter than remaining tarsomeres; second and third tarsomeres nearly equal in length; fourth tarsomere shorter than others, broad and dorsally hollowed around base of fifth tarsomere; fifth tarsomere

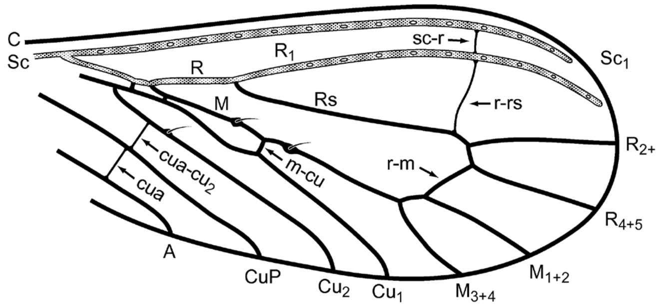

Figure F2. Forewing of *Garnaconis dupeorum* Perrichot & Nel, n. gen. and sp., holotype female IGR.GAR-2, in Late Cretaceous Vendean amber.

elongated. Abdomen flattened and probably deformed by air bubbles, 0.46 mm long, 0.23 mm wide, including genitalia; a plicature visible at least on the third and fourth abdominal segments (Fig. F1.6), with a dark spot inside abdomen corresponding to each of them. Genitalia (Fig. F1.7) partly obscured and delicate to interpret because these organs are much internalized in the Coniopterygidae, male or female. Nevertheless, it seems most likely that they correspond to female genitalia for their striking similarities with those of a female *Coniocompsa* (see Meinander, 1972: fig. 45 C); the main diagnostic character is the very elongate segment 9 (s9) that extends far beyond the gonapophyses laterales (gl) which bear strongly curved setae; other genital structures are hidden inside abdomen.

Key to Cretaceous genera of Coniopterygidae (modified from Engel, 2004)

1. Media in forewing with three branches 2
   Media in forewing with two branches 4
2. Forewing without stiff setae proximally on media 3
   Forewing with two stiff setae situated on thickenings of media (Late Cretaceous) .... *Apoglaesoconis* Grimaldi
3. Antennae with 25 or more flagellomeres (25–30 where known); R_{4+5} distinctly angling anteriorly at distalmost rs-m crossvein; media branching strongly distad of basal r-m crossvein (Early–Late Cretaceous) .... *Glaesoconis* Meinander
   Antennae with less than 20 flagellomeres; R_{4+5} not angling anteriorly at distalmost r-m crossvein, instead continuing straight to wing margin; media branching at basal r-m crossvein (Early–Late Cretaceous) .... *Libanoconis* Engel
4. Forewing crossveins r-rs, r-m, and cu_1-cu_2 absent; R_{4+5} not connected to M_{1+2}; m-cu_1 near bifurcation of M .... *Phtanoconis* Engel
   Forewing crossveins r-rs, r-m present, cu_1-cu_2 present or absent; R_{4+5} connected to M_{1+2}; m-cu_1 strongly basad bifurcation of M 5
5. Forewing crossvein r-rs meeting bifurcation of Rs; 2r-m subequal to basal abscissa of R_{4+5}; cu_1-cu_2 present; 24 flagellomeres (Early Cretaceous) .... *Libanosemidalis* Azar, Nel, & Solignac
   Forewing crossvein r-rs not meeting Rs at bifurcation R_{2+3}–R_{4+5}; antennae with 20 or less flagellomeres 6
6. Forewing crossvein r-rs meeting Rs distinctly basad bifurcation R_{2+3}–R_{4+5} (i.e., connected to Rs); only one crossvein between Rs and M; cu_1-cu_2 absent; 17 flagellomeres (Late Cretaceous) .... *Garnaconis* n. gen.
   Forewing crossvein r-rs meeting R_s strongly distad bifurcation R_{2+3}–R_{4+5} (i.e., connected to R_{2+3}); two crossveins between Rs and M; cu_1-cu_2 absent; 20 flagellomeres (Early Cretaceous) .... *Alboconis* Nel, Perrichot & Azar

DISCUSSION

Until now there has been no clear phylogenetic analysis of the Coniopterygidae, except for the preliminary proposal of Meinander (1972). *Garnaconis* n. gen. has only one radio-medial crossvein on forewing, a character currently considered as proper to Coniopteryginae (Meinander, 1972). Nevertheless, *Garnaconis* n. gen. has the hind wing base of Rs very close to that of M, which is a character present in Aleuropteryginae and in *Flintoconis* Sziráki, second brucheiserine genus, while *Brucheiser* Navás, has highly modified fore and hind wing venation delicate to interpret (Riek, 1975). The polarity of this character remains controversial because even the sister-group relationships of Coniopterygidae within the Neuroptera remain debatable: Aspöck, Plant, and Nemeschkal (2001) supported a 'Coniopterygidae + Sisyridae' clade, while Haring and Aspöck (2004) and Aspöck and Aspöck (2008) supported a 'Coniopterygidae + dilarid clade' (see summary in Aspöck & Aspöck, 2007); Winterton, Hardy, and Wiegmann (2010) found Coniopterygidae as sister group of all other Neuroptera; Beutel, Friedrich, and Aspöck (2010) considered that the position of this family remains uncertain; Zimmermann and others (2011) considered them as sister group to the clade (Mantispidae + (Dilaridae + (Rhachiberothidae + Berothidae))); while Aspöck, Haring, & Aspöck (2012) proposed them as sister group of the (Dilaridae + (Mantispidae + (Rhachiberothidae + Berothidae))). Note that this last hypothesis, as for the sisyrid or dilarid hypotheses, is congruent with a basal position of Rs as a plesiomorphy for the Coniopterygidae.

Garnaconis n. gen. also shows a plicature at least on the third and fourth abdominal segments (see Fig. F1.5). Meinander (1972) considered the presence of abdominal plicatures as a potential synapomorphy of the Aleuropteryginae. They are also present in Brucheiserinae. But Zimmermann, Klepal, and Aspöck (2009) hypothesized the following relationships between the three subfamilies: (Brucheiserinae + Coniopteryginae) + Aleuropteryginae, on the basis of potential synapomorphies in the larvae. They concluded that the presence of abdominal plicatures could rather be a plesiomorphy. *Garnaconis* n. gen. also has the two stiff setae on median vein, a character considered by Meinander (1972:17-18) as an apomorphy of the Aleuropteryginae, absent in Coniopteryginae. Note that *Flintoconis* has no 'outstanding setae of M', but 'somewhat stronger bristle at about the basal third of M' that could correspond to a 'remnant of one of these stiff setae (Sziráki, 2007), while *Brucheiser* seems to have no clear specialized setae on M. The genital apppendages of *Garnaconis* n. gen., although showing similarities with those of the females *Coniocompsa* (Aleuropteryginae), are too obscured to be safely used because many diagnostic features (Aspöck & Aspöck, 2008; Zimmermann, Klepal, & Aspöck 2009) are not visible. Consequently, *Garnaconis* n. gen. could be attributed to the Aleuropteryginae in the basis of the set of characters considered by Meinander (1972) as apomorphic to this subfamily. Nevertheless the polarity of these characters remains debatable because of the lack of a more recent phylogenetic analysis of the family. The present attribution to the Aleuropteryginae is tentative and will need verification when such analysis will become available.

Among the Cretaceous Coniopteryginae, *Libanosemidalis* shares with *Garnaconis* the hind wing with vein Rs branching from R very near the wing base, but *Libanosemidalis* has no stiff setae on M and no plicature. The second Mesozoic coniopterygine genus *Phthanoconis* has a hind wing Rs branching far from wing base, as in modern representatives of the subfamily. *Garnaconis* n. gen. also differs from other Cretaceous dustywings except *Libanosemidalis*, *Phtanoconis*, and *Alboconis*, by the presence of only two (as opposed to three) terminal branches of the media on the forewing. It differs from *Libanosemidalis* and *Alboconis* by the number of antennal flagellomeres, which is 17 in *Garnaconis*, as opposed to 24 in *Libanosemidalis*, and 20 in *Alboconis* – erroneously mentioned with 18 flagellomeres in the original description by Nel, Perrichot, & Azar (2005); the vertex not prominent; and the forewing with Rs branching into R_{2+3} and R_{4+5} distally of crossvein r-rs.

The new fossil adds significantly to the scant geological record of dustywings, and it displays intermingled features of both Aleuropteryginae and Coniopteryginae as currently defined, such that it might help to refine the limits of both subfamilies once incorporated in a phylogenetic analysis.

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Paleontological Contributions

December 1, 2014 Number 10G

YOUNGEST OCCURRENCE OF THE GENUS *MICROPHORITES* (DIPTERA: DOLICHOPODIDAE): A NEW SPECIES IN LATE CRETACEOUS VENDEAN AMBER

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ABSTRACT

A new species of the extinct genus *Microphorites* Hennig (Dolichopodidae: Microphorinae) is described from a single male preserved in Late Cretaceous (Cenomanian to Santonian) Vendean amber (NW France). *Microphorites magaliae* n. sp., is mostly characterized by large compound eyes, flagellomere I with base bulbous and abruptly tapering to slender apex, thorax strongly hump-backed, with numerous acrostichal and dorsocentral setae, including a pair of elongate posterior setae on the mesoscutum, mesoscutellum with two long strong setae, wing vein C terminating just beyond R_{4+5}, and R_{4+5} approximately equidistant between R_{2+3} and M_1 along wing margin. It is the latest occurrence of the genus which is otherwise known exclusively from Early to mid-Cretaceous amber of Lebanon, Spain, and southwestern France. The existing key to all species of *Microphorites* is modified to include the new species.

Keywords: Insecta, Empidoidea, Microphorinae, Cretaceous, France

RÉSUMÉ

Une nouvelle espèce du genre fossile *Microphorites* Hennig (Dolichopodidae: Microphorinae) est décrite à partir d'un mâle fossilisé dans l'ambre crétacé supérieur (Cénomanien à Santonien) de Vendée (nord-ouest de la France). *Microphorites magaliae* n. sp., est caractérisé par de grands yeux composés, le flagellomère I bulbeux à sa base et se rétrécissant brusquement vers l'apex, le thorax fortement bosselé, avec de nombreuses soies acrostichales et dorsocentrales, y compris une paire de soies postérieures allongées sur le mésoscutum, le mésoscutellum avec deux soies épaisses et longues, l'aile avec la nervure C se terminant juste au-delà de R_{4+5}, et R_{4+5} approximativement équidistante de R_{2+3} et M_1 le long de la marge de l'aile. Il s'agit de la plus récente occurrence du genre connu autrement des ambres du Crétacé inférieur et moyen du Liban, d'Espagne, et du sud-ouest de la France. La clé des espèces de *Microphorites* est modifiée pour inclure la nouvelle espèce.

Mots-clés: Insecte, Empidoidea, Microphorinae, Crétacé, France

INTRODUCTION

The family Dolichopodidae, or long-legged flies, is the world's fourth largest dipteran family and one of five major lineages within the superfamily Empidoidea. The traditional concept of the family comprises 15 subfamilies and is referred to as Dolichopodidae *s. str.* This concept was expanded to Dolichopodidae *s.lat.* to include Microphorinae and Parathalassiinae (Sinclair & Cumming, 2006), two small subfamilies for a time placed in Empididae (Negrobov, 1978; Evenhuis, 1994), but also considered at family rank by some authors (Chvála, 1983; Moulton & Wiegmann, 2004) or left unplaced as sister to Dolichopodidae (Hennig, 1971; Moulton & Wiegmann, 2007). Indeed, both clades have dolichopodid characteristics such as the Rs vein originating at or near the level of crossvein h, crossvein r-m situated in the basal fourth of the wing, and the male

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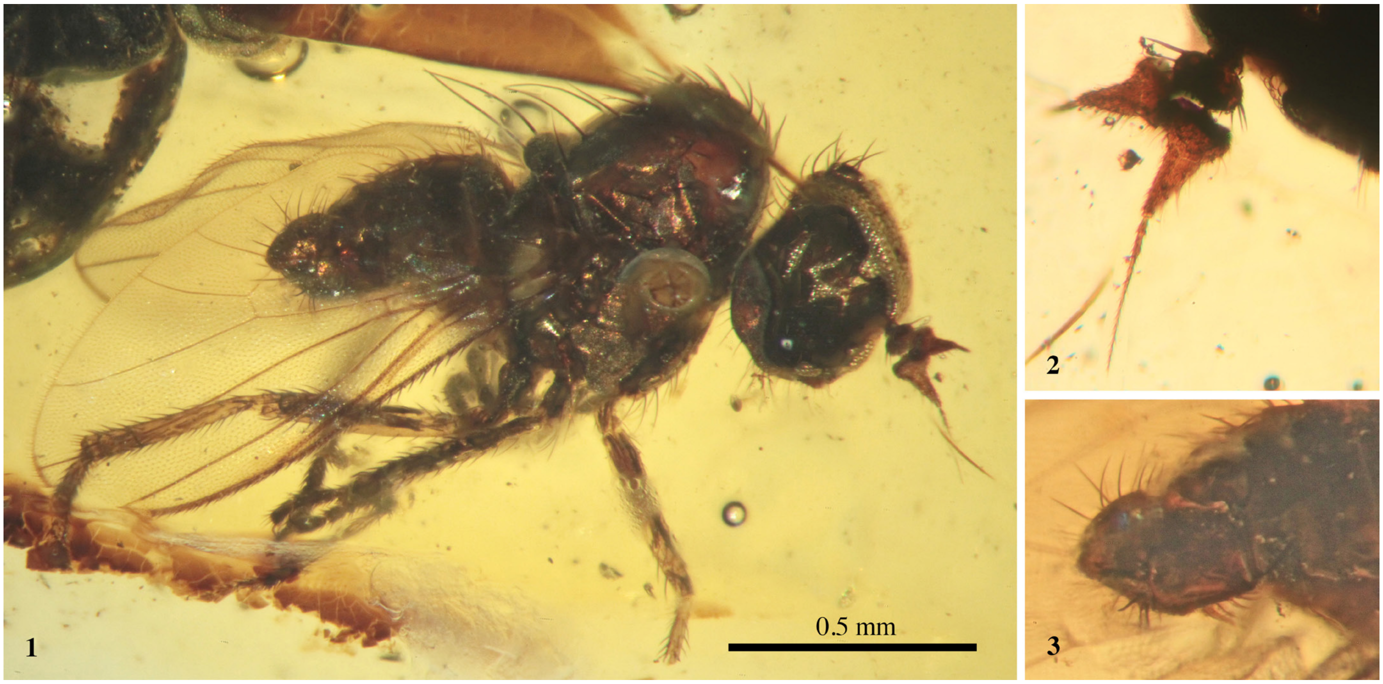

Figure G1. *Microphorites magaliae* n. sp., holotype male IGR.GAR-106a, in Late Cretaceous amber of Vendée, NW France. *1*, habitus in right lateral view; *2*, detail of antennae; *3*, detail of the genitalia.

terminalia rotated forward beneath the preceding segments of the abdomen (Wiegmann, Mitter, & Thompson, 1993). Microphorinae and Parathalassiinae are distinguished from other dolichopodids by the presence of an additional basal crossvein (bm-cu) and crossvein dm-cu connected to the base of M_2. Recent molecular analyses even suggest that Parathalassiinae are part of Dolichopodidae *s.str.*, with Microphorinae as sister group to the latter (Germann & others, 2011).

The subfamily Microphorinae is comprised of the modern genera *Microphor* Macquart and *Schistostoma* Becker and the extinct genera *Avenaphora* Grimaldi & Cumming and *Microphorites* Hennig, with the fossil record extending back to the Early Cretaceous. *Microphorites* is the most speciose one of the extinct genera and is known exclusively from the Cretaceous. The new fossil described here is the sixth species of *Microphorites*, and the latest occurrence of the genus which was otherwise known exclusively from Early to mid-Cretaceous amber of Lebanon, France, and Spain (Hennig, 1971; Grimaldi & Cumming, 1999; Nel & others, 2004; Arillo, Peñalver, & Delclòs, 2008).

MATERIAL AND METHODS

The material is comprised of one specimen preserved in a small sliver of clear yellow amber with one Hymenoptera (Serphitidae: *Serphites fannyae* Engel & Perrichot, 2014: 10J in this volume) as a syninclusion. The specimen is almost complete, missing only the tibia and tarsomeres of the right foreleg. It exhibits a minor taphonomic collapse of the compound eyes (Fig. G1.1). The amber was collected in 2002 by Magali Weigandt and Fanny Dupé from a deposit which was temporarily exposed during works along the D32 road between La Garnache and Challans, in the department of Vendée, northwestern France. The exact age of the amber-bearing stratum remains 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 piece of amber was slightly polished on all sides to remove the weathered opaque surface and to facilitate the examination of the inclusions. Drawings were carried out under both incident and transmitted light with a camera lucida attached to a Leica MZ APO stereomicroscope. Photographs were taken with a Canon 5D Mark II camera attached to the stereomicroscope, and image stacks were merged using HeliconFocus 5.3 software (Helicon Soft Ltd.). Measurements were taken with an ocular graticule. The piece of amber was eventually embedded in a block of epoxy resin which was in turn polished on all sides.

SYSTEMATIC PALEONTOLOGY

Family DOLICHOPODIDAE Latreille, 1809
Subfamily MICROPHORINAE Collin, 1960
Genus MICROPHORITES Hennig, 1971

Type species.—Microphorites extinctus Hennig, 1971, p. 16, figs. 2, 3, 19–25.

Included species.—Microphorites deploegi Nel & others, 2004, *M. extinctus* Hennig, 1971, *M. magaliae* Perrichot & Engel, n. sp., *M. oculeus* Grimaldi & Cumming, 1999, *M. similis* Grimaldi & Cumming, 1999, *M. utrillensis* Peñalver in Arillo, Peñalver, & Delclós, 2008.

The generic diagnosis by Grimaldi and Cumming (1999), with supplements by Nel and others (2004), is followed.

MICROPHORITES MAGALIAE new species

Figures G1–G2

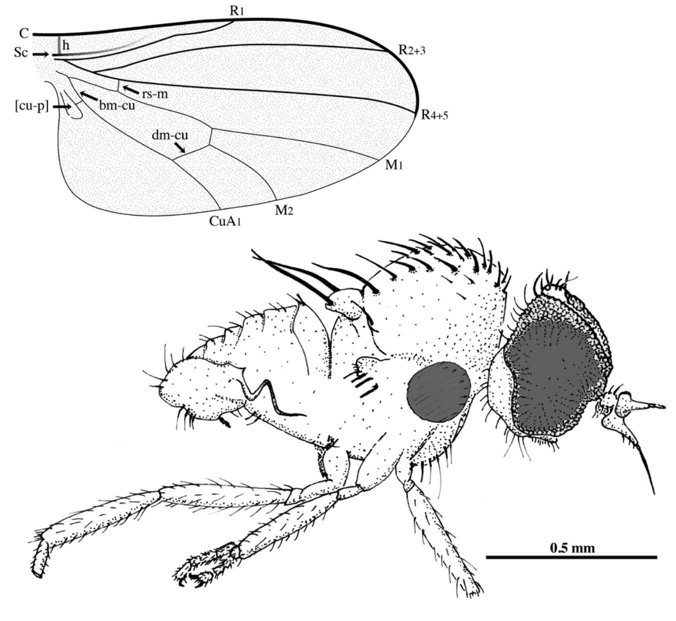

Figure G2. *Microphorites magaliae* n. sp., holotype male IGR.GAR-106a, in Late Cretaceous amber of Vendée, NW France; wing venational nomenclature and lateral habitus with no wings to show the typical male genitalia.

Type material.—Holotype male, IGR.GAR-106a (ex coll. Weigandt), 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 Magali Weigandt who collected the amber piece containing the specimen.

Diagnosis.—The new species has the following unique combination of characters within the genus: compound eyes encompassing most of head, touching each other along inner margins, bare; flagellomere I with bulbous base and abruptly tapering to slender apex; thorax strongly hump-backed; mesoscutum with pair of elongate posterior setae; mesoscutellum with two strong, elongate setae; wing vein C terminating just beyond R_{4+5}; and R_{4+5} approximately equidistant between R_{2+3} and M_1 along wing margin.

Description.—Male. Total body length 1.30 mm; wing length 1.23 mm, maximum width 0.51 mm; flagellomere I length 0.11 mm, maximum width (basally) 0.70 mm; arista length 0.16 mm, basal aristomere length 0.01 mm.

Head large, spherical (Fig. G1.1); compound eyes holoptic (dorsal and ventral facets not differentiated), with inner margins touching for most distance anteriorly to ocellar triangle; gena present only by narrow strip. Antenna aristate, with fine microtrichiae; pedicel cup-like, with apical marginal ring of fine setae; flagellomere I long, with bulbous base, then abruptly tapered, apical portion long, slender, almost tubular by apex (Fig. G1.2); arista two-segmented, basal aristomere very short, apical aristomere elongate. Ocellar triangle prominent, with pair of moderately elongate setae anteriorly, two pairs of short setae posteriorly. Dorsal row of 16 postocular setae progressively decreasing in size laterally: median pair long, stiff and curved; lateralmost setae short, fine and straight. Six elongate, fine setae posteroventrally on each side of mouthparts. Proboscis either retracted or reduced, not visible.

Thorax. Notum strongly hump-backed, with two median rows of 6–7 fairly long acrostichal setae, two rows of 6–7 dorsocentral setae, two posteriormost setae elongate; anterior face of notum with pair of short, stiff setae directed forward; postpronotal lobe with long, upright seta; row of 3 long notopleural setae; mesoscutellum prominent, with one pair of elongate (0.27 mm long) stiff setae. Legs long, slender, bristly; each coxa with a ventral row of 4–5 long setae; hind femur with dorsal longitudinal row of erect setae, proximal setae longest; tibiae, particularly metatibiae, densely covered by erect setae.

Wing broadly rounded at apex (Fig. G2); vein C terminating just beyond R_{4+5}; Sc curved posteriorly towards R_1, not contacting R_1 along length but closely parallel, apically nebulous such that it appears to terminate before C; Rs originating just immediately beyond tangent with crossvein h (= c-sc); R_{2+3} slightly shorter than R_{4+5}, the latter reaching to wing apex and near midpoint between R_{2+3} and M_1; rs-m in basal quarter of forewing, about 1.75x its length from R_{2+3}-R_{4+5} fork; M_1 straight; M_2 present; bm separated from dm by distinct and complete bm-cu; CuA_1 straight; CuA_2 arched posteriorly, joining A_1 and creating small basal cell [cu-p]; short A_2 present as nebulous furrow; anal lobe rounded.

Abdomen short, less than 0.5x wing length. First five pregenital segments each with 6–8 erect setae dorsally. Hypopygium large, rounded, rotated and lateroflexed to right (Fig. G1.3, G2); posterior half strongly setose; left lamella with rounded dorsal lobe, apex of lobe with hooked tooth; right lamella with small dorsal flange; phallus long, curled.

DISCUSSION

Placement of this species within *Microphorites* is easily established owing to the bare compound eyes, wing with complete crossvein bm-cu, and antenna with two-segmented arista. Given the discovery of a species of *Microphorites* in Cenomanian–Santonian amber, thereby pushing the lineage into the Late Cretaceous, the genus should be sought in other deposits of similar age. For example, it seems possible that the genus may be discovered eventually in the Campanian amber of Canada or Turonian of New Jersey, both rich sources of Late Cretaceous insect inclusions and in close paleogeographic proximity to those Eurasia localities. The mid-Cretaceous amber of Myanmar and Santonian amber of Siberia are also strong candidates to eventually reveal species of *Microphorites*, unless, of course, the genus had a more restricted distribution which confined species to the western archipelagos and landmasses of Eurasia during this period. Hopefully, continued paleoentomological investigation will give us a greater understanding of the biogeography and phylogenetic relationships of the genus.

The following key, updated from that of Arillo, Peñalver, and Delclòs (2008), will permit recognition of *M. magaliae* from its congeners. It applies to both males and females although all but one species (*M. deploegi*) are known by a single gender only. The size of the compound eye relative to the head, as proposed in Arillo's key, was removed because it appears to vary between male and female of a same species, i.e. males have larger eyes than females.

Key to species of *Microphorites*

1. Basal flagellomere abruptly tapered, with base bulbous and tubular apex 2
 Basal flagellomere more evenly tapering from base to apex 3
2. Wing vein C terminating at R_{4+5}; R_{4+5} closer to M_1 than to R_{2+3} along wing margin; mesoscutum without posterior pair of strong, elongate setae [Barremian; Lebanon] .... *M. oculeus* Grimaldi & Cumming
 Wing vein C terminating just beyond R_{4+5}; R_{4+5} approximately equidistant between R_{2+3} and M_1 along wing margin; mesoscutum with posterior pair of strong, elongate setae [Cenomanian–Santonian; France] .... *M. magaliae* Perrichot & Engel n. sp.
3. Wing vein C terminating beyond R_{4+5} 4
 Wing vein C terminating at R_{4+5} [Barremian; Lebanon] .... *M. similis* Grimaldi & Cumming
4. Antennal arista long, around twice basal flagellomere length; forewing vein R_{2+3} barely shorter than R_{4+5} 5
 Antennal arista short, as long as basal flagellomere; forewing vein R_{2+3} clearly shorter than R_{4+5} [Lower Albian, Spain] .... *M. utrillensis* Peñalver in Arillo & others
5. Four strong setae on mesoscutellum [Barremian; Lebanon] ....*M. extinctus* Hennig
 Two strong setae on mesoscutellum [Upper Albian; France] .... *M. deploegi* Nel & others

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Paleontological Contributions

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NEW BITING MIDGES (DIPTERA: CERATOPOGONIDAE) IN LATE CRETACEOUS VENDEAN AMBER

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ABSTRACT

The ceratopogonids from Late Cretaceous (Cenomanian to Santonian) amber of Vendée, in northwestern France, are studied. The new species *Leptoconops* (*Leptoconops*) *gravesi* n. sp., *Leptoconops* species undetermined, and *Culicoides doyeni* n. sp., are described, illustrated, and compared with other fossil species known for these two genera.

Keywords. Insecta, Leptoconopinae, Ceratopogoninae, France, Cretaceous

RÉSUMÉ

Les Cératopogonides fossilisés dans l'ambre crétacé supérieur (Cénomanien à Santonien) de Vendée, dans le nord-ouest de la France, sont étudiés. Les nouvelles espèces *Leptoconops* (*Leptoconops*) *gravesi* n. sp., *Leptoconops* espèce indéterminée, et *Culicoides doyeni* n. sp., sont décrites, illustrées, et comparées aux autres espèces fossiles connues pour ces deux genres.

Mots-clés: Insectes, Leptoconopinae, Ceratopogoninae, France, Crétacé

INTRODUCTION

The first fossil Ceratopogonidae from Cretaceous French amber were illustrated by Schlüter (1978) based upon four individuals that he found in Cenomanian amber of Anjou, in northwestern France. These were formally described by Szadziewski and Schlüter (1992) as *Atriculicoides cenomanensis*, *A. incompletus*, *Austroconops borkenti*, and *Leptoconops* sp. New studies were recently initiated after the discovery of several Cretaceous amber deposits in other regions of France, that revealed an abundant new material of biting midges. The Albian-Cenomanian amber of Charentes, in southwestern France, contains about 4% of ceratopogonids (62 specimens out of 1500 arthropod inclusions), with *Leptoconops daugeroni* Choufani, Azar & Nel, as the first and only described species (Choufani & others, 2011). The Santonian amber of Provence, in southeastern France, is poorly fossiliferous but remarkably contains up to 15% of ceratopogonids (2 specimens out of 13 arthropods) representing two species: *Devalquia brisaci* Choufani & Nel, and *Metahelea roggeroi* Choufani & Nel (in Choufani & others, 2013). The present study aims to describe and illustrate the diversity of biting midges most recently discovered from Late Cretaceous (Cenomanian to Santonian) amber of Vendée, in northwestern France. Ten out of the 171 arthropod inclusions found in this amber deposit are assignable to Ceratopogonidae, but only three of them are complete or visible enough for the present study, which represent three different species.

MATERIAL AND METHODS

The three specimens are preserved in separate pieces of amber that were respectively collected in 2002 by Fanny Dupé, Dominique Doyen, and Didier Graves from a deposit exposed briefly during construction along the D32 road between La Garnache and Challans, in the department of Vendée, northwestern France. The exact age of the amber-bearing stratum remains uncertain within the Middle

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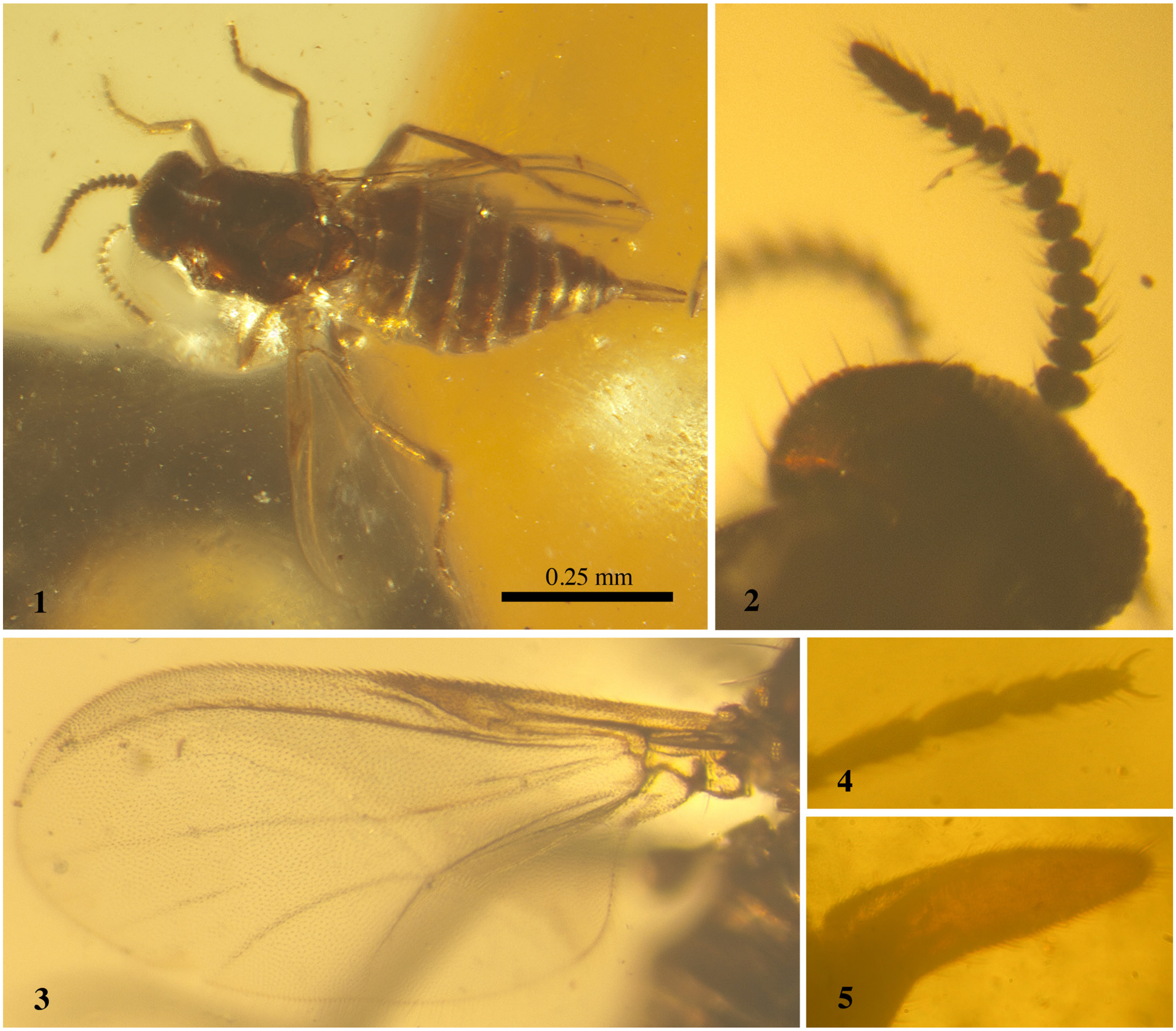

Figure H1. *Leptoconops gravesi* n. sp., holotype female IGR.GAR-72.1. *1*, habitus in dorsal view; *2*, detail of head and antenna; *3*, wing; *4*, tarsal claws; *5*, cerci.

Cenomanian to Early Santonian interval (Late Cretaceous, 97–85 Ma), as discussed by Perrichot and Néraudeau (2014: 10A in this volume). The specimens were each contained in a piece of clear yellow to orange amber, and two of the three pieces contained other syninclusions rendering their observation difficult (see detailed list in the material sections of the descriptions below). These pieces were divided and the resulting fragments polished to optimize the dorsal, profile, and frontal views whenever possible. The study was done under incident and transmitted light using an Olympus SZ9 stereomicroscope and an Olympus inverted microscope, both equipped with a digital camera for photographs and an ocular micrometer for measurements. Each amber piece was ultimately embedded in a block of epoxy resin for preservation and easier manipulation. The material is now housed in the amber collection of the Geological Department and Museum of the University Rennes 1, France.

SYSTEMATIC PALEONTOLOGY

Family CERATOPOGONIDAE Newman, 1834
Subfamily LEPTOCONOPINAE Noè, 1907
Genus LEPTOCONOPS Skuse, 1889

Subgenus LEPTOCONOPS Skuse, 1889
LEPTOCONOPS (LEPTOCONOPS) GRAVESI, new species

Figure H1

Type material.—Holotype female IGR.GAR-72.1 (ex coll. Graves), originally preserved with a scelionine wasp and an earwig nymph (the latter described by Engel & Perrichot, 2014: 10J in this volume) in Late Cretaceous (Middle Cenomanian to Early Santonian, 97–85 Ma) Vendean amber, France; 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 patronym for Didier Graves, the specimen's collector.

Diagnosis.—Female. Antenna with 12 flagellomeres, flagellomeres 2-5 transverse, flagellomeres 6-11 spherical, terminal flagellomere as long as the three preceding ones combined; wing with costa prolonged beyond R3; tarsal claw with small denticle at its base and no setae; cerci much elongate, not triangular, with two long apical setae; ratio body length /wing length = 1.38.

Description.—Body stout, total length (without cerci) 0.68 mm. Head with seven setae on vertex but no pair of setae on frons; eyes bare, separated dorsomedially and large, largest diameter (D) 110 µm, small diameter (d) 55 µm; antenna with flagellum 223 µm long; flagellomeres 2-5 transverse, 6-11 spherical, each 16.7 µm in diameter; terminal flagellomere 36.2 µm long, 2.2× as long as flagellomeres 11 or 10 alone, and as long as preceding three flagellomeres combined; palpus four-segmented; third palpal segment 30.6 µm long, 12.5 µm wide; fourth palpal segment slender, 27.8 µm long.

Thorax: 0.21 mm µm long, 0.17 mm µm wide; scutum not prolonged beyond head with around 10 setae; scutellum with rounded margin and two median setae.

Wing 0.49 mm long, 0.17 mm wide; radial cells short, R1 and R3 joining costa in a thickened pterostigma; costa prolonged beyond R3; crossvein r-m absent; vein R4+5 reaching wing apex; median branches reaching wing margin; intercal vein not running close to M.

Legs slender, hairy; length of profemur 0.12 mm, protibia 0.097 mm, protarsi 0.21 mm; mesofemur 0.13 mm, mesotibia 0.097 mm, mesotarsi 0.167 mm; metafemur 0.14 mm, metatibia 0.167 mm, metatarsi 0.194 mm; protibial spur thickened; apex of metatibia with comb of four major spines and a row of smaller spines; metatibial spur not very thick; all basitarsomeres with row of dense setae; fourth tarsomere cylindrical; fifth tarsomere more elongate than fourth; claws sharp, of medium size, equal on all legs, with a small basal tooth and a bristle on each claw; empodia present, small.

Abdomen 0.39 mm long (without cerci), 0.22 mm wide; cerci lamellar, elongate, 0.10 mm long, 41.75 µm wide, with dorsal and ventral margins parallel within anterior half of length, tapering to rounded apex for posterior half of length, dorsally and ventrally with a series of small setae, and apically with two longer setae.

Comments.—According to the phylogenetic analysis proposed by Borkent and Craig (2004), *Leptoconops gravesi* n. sp. has two synapomorphies supporting its placement within the clade (*Leptoconops* + *Minyohelea*), i.e. 'radial cells very short' and 'female wing with R1 and R3 joining costa in a thickened pterostigma'. It also has the following synapomorphies of *Leptoconops*: 1) 'wing without r-m', a character that Borkent and Craig (2004) indicated as 'unique within at least the Culicomorpha'; 2) 'female cerci elongate and laterally compressed'.

Within the genus *Leptoconops*, the female cerci elongate and laterally compressed is the synapomorphy of the group of subgenera (*Holoconops* Kieffer + (*Megaconops* Wirth & Ashley + *Leptoconops* s. str. + *Proleptoconops* Clastrier)) as defined by Borkent (1995), thus excluding affinities of *L. gravesi* n. sp. with the other subgenera *Styloconops* Kieffer and *Brachyconops* Wirth & Ashley, which have short female cerci, a reversal to the plesiomorphic condition according to Borkent and Craig (2004). Following the key of Sontag and Szadziewski (2011), *L. gravesi* would fall in the extinct subgenus *Palaeoconops* Borkent (type species *L. amplificatus* Borkent), because of its costa prolonged beyond R3. Species of this last subgenus have also elongate cerci, as our fossil. Nevertheless, *Palaeoconops* differs from our fossil by having 13 flagellomeres instead of 12 and thick spines on first tarsomere of all legs. Affinities with *Holoconops* can be also excluded by the presence of 12 flagellomeres in our fossil, as opposed to 10–11 flagellomeres in *Holoconops* (Wirth & Atchley, 1973; Szadziewski & Arillo, 2003). Following the key of Downes and Wirth (1981), *L. gravesi* falls in the subgenus *Leptoconops* rather than *Megaconops* Wirth & Atchley on the basis of the absence of a pair of setae on frons and the presence of a basal tooth and bristle on the female claw.

We compare *L. gravesi* with other fossil *Leptoconops* described by Szadziewski (1988, 1996, 2004), Kalugina (1991), Borkent (1995, 1996, 1997), Szadziewski and Arillo (2003), Szadziewski and Poinar (2005), Poinar (2008), and Choufani and others (2011). Unfortunately, the *Leptoconops* species described by Szadziewski & Schluter (1992) from the Cenomanian French amber is too incompletely described for an accurate comparison. The presence of the inner tooth on claws of *L. gravesi* n. sp. excludes affinities with *L. succineus* Szadziewski, *L. burmiticus* Szadziewski, *L. rossi* Szadziewski, *L. zherikhini* Szadziewski & Arillo, *L. nosopheris* Poinar, *L. subrossicus* Szadziewski & Poinar and *L. boreus* Kalugina. *Leptoconops gravesi* has flagellomeres 2-5 transverse and 6-11 spherical, which excludes affinities with *L. daugeroni* Choufani & others (flagellomeres 2-11 spherical), *L. myanmaricus* Szadziewski (2-11 cylindrical) and *L. rovnensis* Sontag & Szadziewski (2-3 transverse, 4-11 spherical). *Leptoconops sibiricus* Szadwiewski has the costal vein very short, not extending beyond R3, the terminal flagellomere 4× as long as the preceding one (as opposed to 2.2× in *L. gravesi*), and the upper surface of claws with setae, unlike *L. gravesi*. *Leptoconops primaevus* Borkent and *L. copiosus* Borkent, do not have any long setae at apex of cerci, unlike *L. gravesi*. The small inner tooth at the base of claw of *L. gravesi* excludes affinities with *L. curvachelus* Borkent that has a large thick inner tooth. Finally, *L. gravesi* differs from *L. clava* Borkent by the absence of small empodia and absence of tibial spur on midleg.

LEPTOCONOPS species undetermined

Figure H2

Material examined.—Female IGR.GAR-31 (ex coll. Dupé), in Late Cretaceous (Middle Cenomanian to Early Santonian, 97–85 Ma) Vendean amber, France; 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.

Description.—Female. As this specimen is much damaged from head to thorax, several structures could not be examined. Total body length unknown. Head only partly visible, one eye partly visible, 117 µm in diameter, bare; at least three setae on vertex behind compound eye; antenna with 12 flagellomeres, flagellomeres 2-11 more or less spherical, all 23 µm in diameter; terminal flagellomere 53 µm long, 2.3× as long as preceding one; proboscis elongate; lacinia with at least

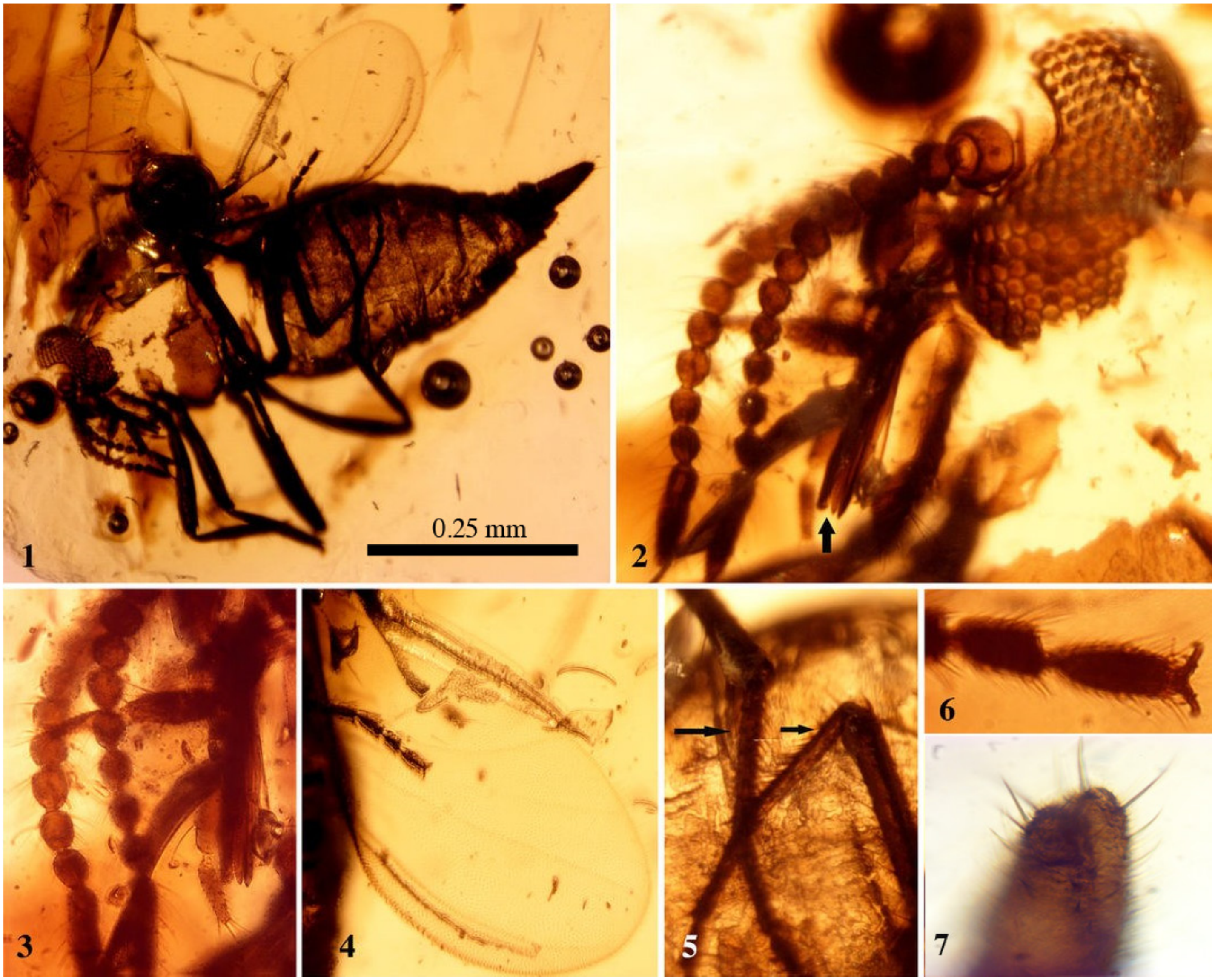

Figure H2. *Leptoconops* sp., specimen female IGR.GAR-31. *1*, Habitus in left profile view; *2*, detail of head with indication of lacinia (arrow); *3*, detail of flagellomeres 5-12 and mouthparts showing palps and lacinia with denticles; *4*, wing; *5*, metabasitarsomeres (arrows); *6*, tarsal claws; *7*, cerci.

10 denticles; palpus four-segmented, third segment ovoid, fourth segment slender with three apical setae.

Thorax damaged. Wing 0.35 mm long, 0.16 mm wide; surface covered by microtrichia, venation identical to that of *Leptoconops gravesi* (nº IGR.GAR-72.1).

Legs: length of profemur 0.26 mm, protibia 0.22 mm, protarsomeres 0.27 mm; mesofemur and metafemur 0.36 mm, slender; fourth tarsomere cylindrical, fifth tarsomere longer than fourth; foreleg tibial spur thickened; hind leg tibial comb composed of a row of five long and thick setae intermixed with smaller ones and a row of short, strong and straight setae; hind leg basitarsus with thick spines on one side and with long setae on other side; tarsal claws with a strong inner tooth in basal third; empodia absent.

Abdomen broad, 0.73 mm long, 0.4 mm wide; two visible spermathecae visible in segment 8, maybe moved from their original place by damages caused to the specimen; cerci elongate, 0.083 mm long, 33.4 µm wide, with dorsal and ventral margins converging for entire length to broadly acute apex, dorsally and ventrally with a series of small setae, and apically with two longer setae.

Comments.—The wing venation and long cerci are typical of *Leptoconops*. Similarly to *L. gravesi* n. sp. described above, the presence of inner tooth on claws of *L. gravesi* n. sp. excludes affinities with *L. succineus*, *L. burmiticus*, *L. rossi*, *L. zherikhini*, *L. nosopheris*, *L. subrossicus*, and *L. boreus*. Our fossil has flagellomeres 2-11 spherical, which excludes affinities with *L. myanmaricus* (2-11 cylindrical) and *L. rovnensis* (2-3 transverse, 4-11 spherical). The extend of costal vein beyond R3 and terminal flagellomere only 2.3× as long as preceding one, instead of 4×, exclude affinities with *L. sibiricus*. *Leptoconops primaevus* and *L. copiosus* differ from IGR.GAR-31 in the absence of the two long setae at apex of cerci. Also affinities with *L. clava* can be excluded because IGR.GAR-31 lacks the midleg tibial spur. Affinities with *L. daugeroni* can be excluded because IGR.GAR-31

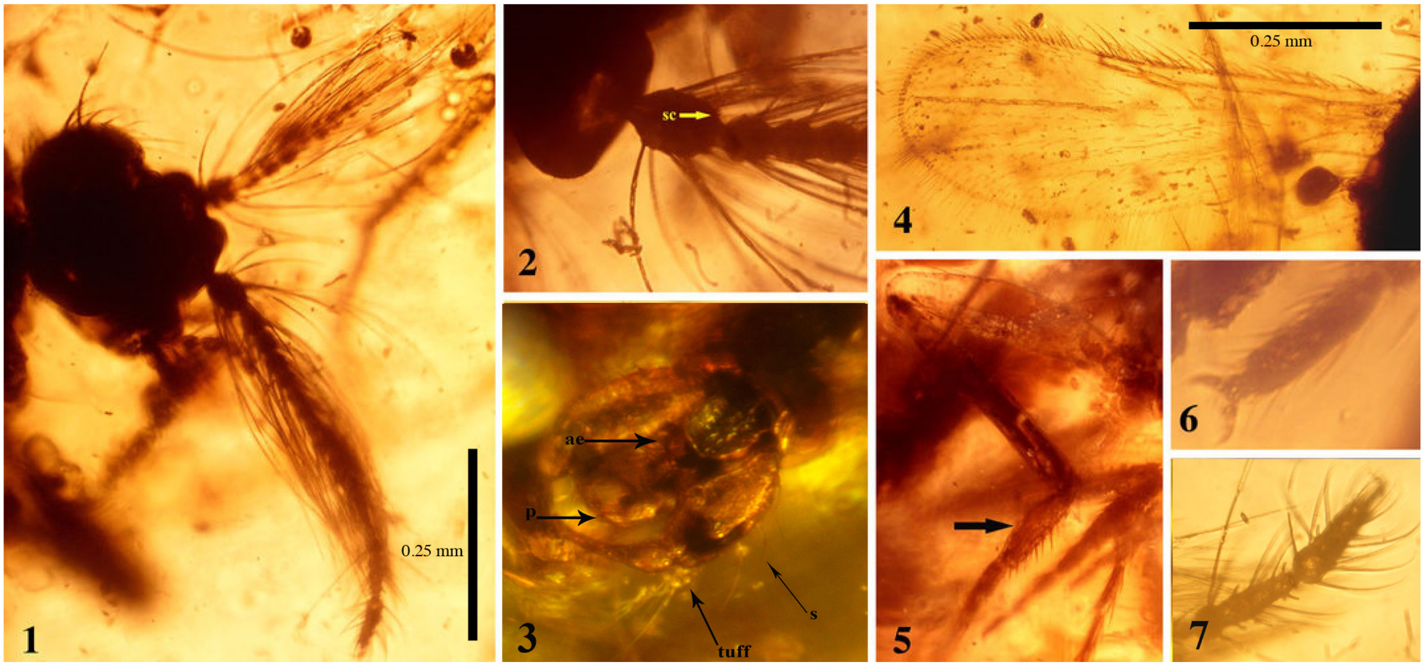

Figure H3. *Culicoides doyeni* n. sp., holotype male IGR-GAR-127.2. *1*, Head showing plumose antennae and palp; *2*, base of antenna with indication of sensilla coeloconica (sc); *3*, genitalia in ventral view (ae: aedeagus; p: parameres; s: setae; tuff: tuff of setae); *4*, wing; *5*, metabasitarsus with palisade (arrow); *6*, tarsal claws; *7*, apical two flagellomeres.

has only three apical setae on fourth palpomere, instead of six. *L. curvachelus* has thick setae on first and fifth tarsomeres of its legs and has not a pair of apical setae on cerci, unlike IGR.GAR-31, which has thick setae only on first tarsomere of hind leg and two elongated setae on apex of cerci.

Affinities with *L. gravesi* can be excluded on the basis of the shorter cerci, different proportions in leg structures, all flagellomeres rounded, not transverse, and presence of a stronger basal tooth on claws in specimen IGR.GAR-31. Therefore, it corresponds to a different, probably new species. Nevertheless we prefer not to give it a formal name because of its incomplete state of preservation, and maintain it as a *Leptoconops* species of uncertain subgenus attribution.

Subfamily CERATOPOGONINAE Newman, 1834
Tribe CULICOIDINI Kieffer, 1911
Genus CULICOIDES Latreille, 1809
CULICOIDES DOYENI new species

Figure H3

Type material.—Holotype male IGR.GAR-127.2 (ex coll. Doyen), originally preserved with a Berothidae (Neuroptera), a Thysanoptera, and a Coleoptera indeterminate; in Late Cretaceous (Middle Cenomanian to Early Santonian, 97–85 Ma) Vendean amber, France; 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 patronym for Dominique Doyen, the specimen's collector.

Diagnosis.—Wing covered with macrotrichia; costa ending at R3; vein R4+5 absent; cells r1 and r2 small to moderately large, distinctly longer than broad, touching but separated; second radial cell square ended; a single row of hairs on wing fringe; eyes narrowly separate above antennae; palpus five-segmented; antenna with 13 flagellomeres, first one with sensilla coeloconica; flagellomeres 11-13 elongate; terminal flagellomere without apical stylet-like prolongation but rounded apex; all legs having nearly similar tarsal ratios; mesobasitarsus with only slender setae, without small spines; metabasitarsus with palisade-like setae, without subbasal spine; gonostylus with a thick base tapering to pointed apex, not divided apically nor with subapical lobe.

Description.—Head: eyes bare, separated dorsomedially by two ommatidial distance; vertex with more than 12 setae; antenna with plumes directed towards apex of flagellum; pedicel 100 µm long, 140 µm large; flagellum 416 µm long; only last three flagellomeres elongate, nearly equal in length, 62 µm long, the last two flagellomeres with sensilla basiconica; first flagellomere with sensilla coeloconica, with two whorls of long setae; palpus five-segmented, third palpal segment ovoid, 24 µm long, 14 µm wide, with three long sensillae medially; fourth and fifth palpal segments slender, each 18 µm long, 12 µm wide.

Thorax: 0.4 mm long, 0.388 mm wide; scutellum rounded, with four setae; scutum very hairy; katepisternum lacking setae.

Wing 0.608 mm long, 0.24 mm wide; membrane and veins covered with short macrotrichia; radial cells small and nearly equal, almost touching, both distinctly longer than broad; second radial cell square-ended; costal vein not extending beyond R3; CR 0.65; r-m oblique; medial bifurcation not visible but most likely distal to r-m; M2 partially reduced; no patterns of dark and light spots.

Legs slender, very hairy; protibial spur with a small comb; mesotibia apparently with a spur; metatibial comb barely visible;

metabasitarsus with stout setae; fourth tarsomere cylindrical; tarsal claws simple, empodia absent.

Abdomen: tergite IX shorter than gonocoxite with small cerci; apicolateral processes not visible; gonocoxites long, with bases not contiguous, and with elongated lateral setae and a tuff of setae near the outer apical angle; gonostylus not forked, single, with thick base, gradually tapering to apex, apex not divided, with no apical tooth nor setae; aedeagus short, with short basal arms, lateral arms longer, arched, bound into slightly longer caudal arm; parameres symmetric, a little extended beyond apex of gonocoxite, with simple rounded apex directed inward.

Comments.—Following the keys of Szadziewski (1996), our fossil is distinguishable from *Lebanoculicoides* Szadziewski, by the absence of vein R4+5; from *Archiculicoides* Szadziewski, by the absence of apical stylet-like prolongation of terminal flagellomere but the presence of a rounded apex; from Leptoconopinae on the basis of the eyes narrowly separated above antennae, and the palpus five-segmented; from *Austroconops* Wirth & Lee, *Archiaustroconops* Szadziewski, and *Minyohelea* Borkent (incl. *Lebanoconops* Szadziewski), on the basis of tarsal ratios of all legs nearly similar; from *Brachycretacea* Szadziewski, by the presence of five palpal segments instead of four; from *Heleageron* Borkent, by the wing with cells r1 and r2 feebly separated; from *Protoculicoides* Boesel, by the costa ending at R3 and radial cells small to moderately large (as opposed to a costa prolonged to wing apex and very large radial cells in *Protoculicoides*); from *Washingtonhelea* Wirth & Grogan, *Ceratopogon* Meigen, *Palaeobrachypogon* Borkent, and *Peronehelea* Borkent, by the absence of sub-basal spine on metabasitarsus; and from *Atriculicoides* Remm, by its flagellomeres 11-13 elongate (as opposed to flagellomeres 10-13 in *Atriculicoides*), a situation similar to what is seen in *Culicoides*. Our fossil is also distinguishable from *Devalquia* Choufani & Nel, by the presence of a sensilla coeloconica on the first flagellomere, the presence of a single row of hairs on the wing fringe, and the second radial cell square-ended (as opposed to narrowed in *Devalquia*; see Choufani & others, 2013).

It is not possible to compare this fossil to the numerous recent species of *Culicoides*; we only compare it to other Cretaceous species. Following the keys of males proposed by Borkent (1996), *C. doyeni* n. sp. is distinguishable from *C. filipalpis* Remm, *C. tyrrelli* Boesel, and *C. bifidus* Borkent, by its gonostylus tapering to pointed apex, not divided apically nor with subbapical lobe; from *C. bullus* Borkent, and *C. succineus* Remm, by its gonostylus with a thick base, gradually tapering to apex; from *C. sphenostylus* Remm, *C. obuncus* Borkent, *C. annosus* Borkent, and *C. casei* Grogan & Szadziewski, by its wing with macrotrichia present all over the wing, and especially basal to fork of M and Cu (as opposed to a wing with macrotrichia restricted to an area distant from M and Cu in these species). It differs from *C. canadensis* (Boesel, 1937) in the radial cells weakly separated and square-ended (well separated and nearly as long as broad in *C. canadensis*); from *C. agamus* Borkent, by the second radial cell relatively thinner compared to its length, and presence of palisade-like setae on metabasitarsomere. According to the keys of Borkent (1995), *C. doyeni* n. sp. is also distinguishable from *C. kaluginae* Remm, by the mesobasitarsomere with only slender setae, without small spines.

The comparison with species of *Culicoides* known only by females is more tentative and limited to characters that are supposedly not dimorphic. *Culicoides doyeni* n. sp. is distinguishable from *C. grandibocus* Borkent, by its wing with macrotrichia not restricted to the distal half; from *C. yoosti* Borkent, by its metabasitarsomere with stout, palisade-like setae (no such setae visible in *C. yoosti)*; and from the very distinctive *C. truncatus* Borkent, by its antenna with 13 flagellomeres (as opposed to only five flagellomeres in *C. truncatus*).

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Paleontological Contributions

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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, Spheciformes, 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 Stigmina. Four genera of the Stigmina 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 externoventrally; 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

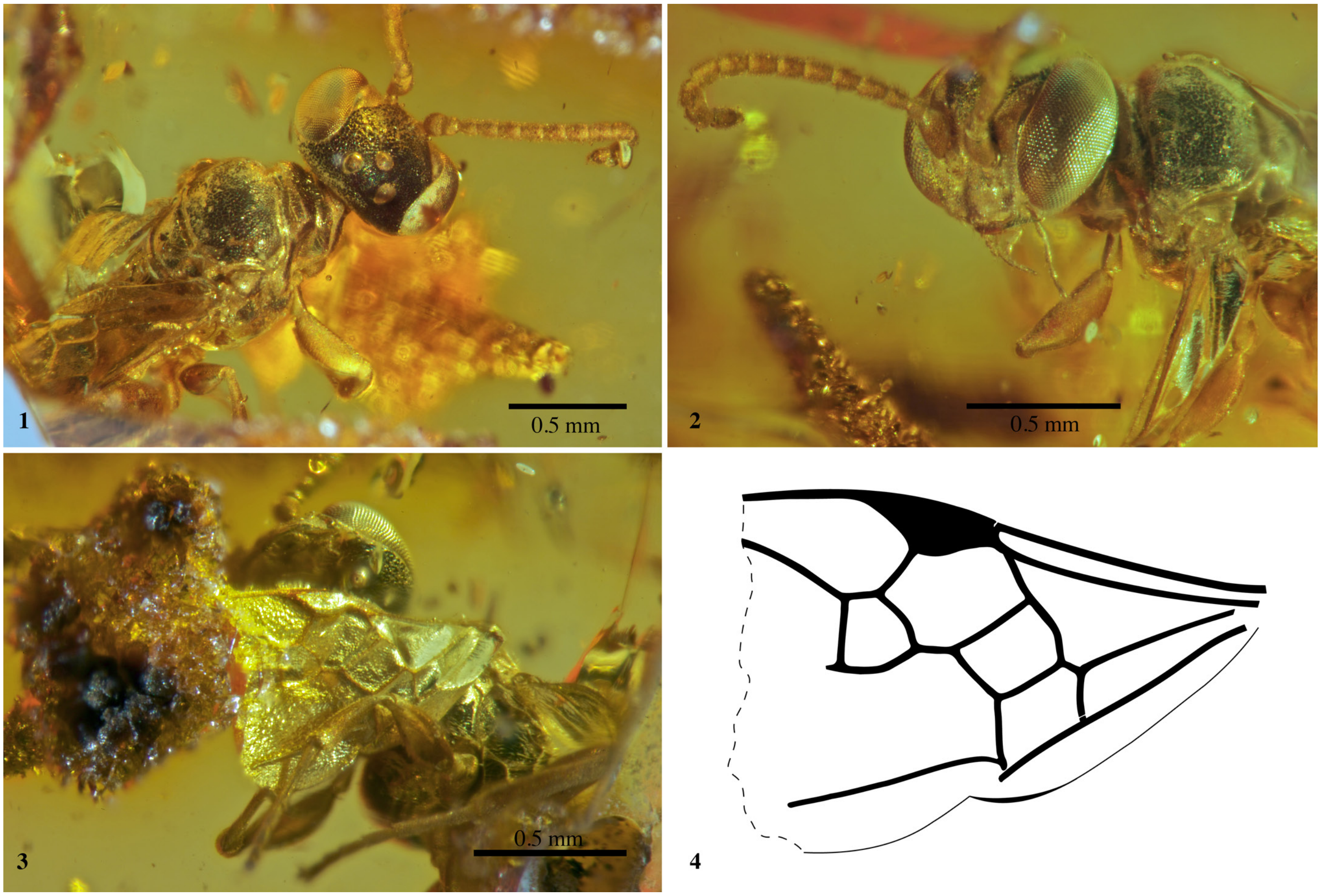

Figure I1. *Menopsila dupeae* n. gen. and sp., in Late Cretaceous amber of Vendée, NW France, holotype male IGR.GAR-50; *1*, habitus in dorsal view; *2*, head and pronotum in frontolateral view; *3*, head and forewing in ventral view; *4*, line drawing of the forewing.

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

MENOPSILA DUPEAE new species
Figure I1

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. I1.1, I1.2) 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-ocellar 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. I1.3, I1.4) 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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Paleontological Contributions

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THE EXTINCT WASP FAMILY SERPHITIDAE IN LATE CRETACEOUS VENDEAN AMBER (HYMENOPTERA)

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ABSTRACT

A new species of the extinct genus *Serphites* Brues (Proctotrupomorpha: Bipetiolarida: Serphitidae) is described from two individuals preserved in Late Cretaceous (Cenomanian to Santonian) amber from Vendée, northwestern France. *Serphites fannyae* n. sp., is distinguished from its congeners and brief comments are made on the significance of finding a serphitid wasp in Vendean amber as well as potential character polarities in the family Serphitidae.

Keywords: Insecta, Apocrita, Proctotrupomorpha, Bipetiolarida, Cretaceous, France

RÉSUMÉ

Une nouvelle espèce du genre fossile *Serphites* Brues (Proctotrupomorpha: Bipetiolarida: Serphitidae) est décrite d'après deux spécimens préservés dans l'ambre crétacé supérieur (Cénomanien à Santonien) de Vendée, dans le nord-ouest de la France. *Serphites fannyae* n. sp., est comparée à ses congénères et la présence d'un Serphitide dans l'ambre de Vendée est brièvement commentée ainsi que la possible polarité de caractères pour la famille Serphitidae.

Mots-clés: Insecta, Apocrita, Proctotrupomorpha, Bipetiolarida, Crétacé, France

INTRODUCTION

There are several families of Hymenoptera which are diagnostic for the Cretaceous. Each of these families is known almost exclusively from amber and typically ranges from the Early Cretaceous through the latter stages of the Mesozoic, and obviously none have been hitherto discovered in the Paleogene. These families include the Maimetshidae of the Trigonalyoidea (Perrichot & others, 2011), Serphitidae of the Serphitoidea (Brues, 1937; Kozlov & Rasnitsyn, 1979; McKellar & Engel, 2011a; Engel, Grimaldi, & Ortega-Blanco, 2011; Ortega-Blanco & others, 2011a), Alavarommatidae and Gallorommatidae of the Mymarommatoidea (Engel & Grimaldi, 2007; Gibson, Read, & Huber, 2007; Ortega-Blanco & others, 2011b), Stigmaphronidae and Radiophronidae of the Ceraphronoidea (Kozlov, 1975; Engel & Grimaldi, 2009; Ortega-Blanco, Rasnitsyn, & Delclòs, 2010; McKellar & Engel, 2011b; Ortega-Blanco, Delclòs, & Engel, 2011), Spathiopterygidae of the Diaprioidea (Engel & others, 2013), and Falsiformicidae of the Chrysidoidea (Rasnistyn, 1975; Perrichot & others, 2014). In all cases but Falsiformicidae, individuals are relatively small and their virtual exclusivity to amber is assuredly a representation of the suitability of this medium for preserving minute organisms with sufficient fidelity. Not surprisingly for clades of Mesozoic parasitoids, hosts of these lineages remain unknown and entirely speculative thereby hindering any conclusions as to whether the occurrence of their victims greatly influences their presence and abundance in specific deposits, although some kind of association must assuredly exist. Syninclusions have provided to date no insight into possible host taxa and all that can be surmised has come from their phylogenetic association with related lineages (e.g., Engel & Grimaldi, 2009).

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The family Serphitidae was first recognized by Brues (1937) based on a couple of male inclusions in Campanian amber from Alberta, Canada. As can be deduced from the name, Brues considered the family to be related to the Serphidae (a synonym of Proctotrupidae), although he did note several possible associations and placed particular emphasis on the two-segmented petiole, an otherwise rare feature among the Hymenoptera. Subsequent to Brues's (1937) account there remained almost no work on the family for nearly half a century. In 1979, Kozlov and Rasnitsyn described several new serphitids, including two new genera, from the Cenomanian and Santonian amber of Siberia and noted a number of traits shared between serphitids and the Mymarommatidae, particularly the form of the two-segmented petiole (later the combined clade was named Bipetiolarida). Indeed, Kozlov and Rasnitsyn (1979) suggested merging the two as subfamilies within a single family. Again, the group remained dormant until recently several additional taxa were added based on a revision of the original Canadian fauna (McKellar & Engel, 2011a) as well as material from the Albian of Spain (Ortega-Blanco & others, 2011a) and Turonian of New Jersey (Engel, Grimaldi, & Ortega-Blanco, 2011). A review of the fauna from Burmese amber is presently underway by one of us. Recently, two serphitids have been recovered in the Cenomanian–Santonian amber of Vendée in northwestern France. Herein is provided a brief account of this material.

MATERIAL AND METHODS

The material comprises two specimens. The first individual (Figs. J1.1, J2.2) is preserved in a small piece of clear yellow amber with one true fly (Diptera: Dolichopodidae: Microphorinae: *Microphorites magaliae* Perrichot & Engel – see issue 10G in this volume) as a syninclusion. The specimen is mostly complete, although the gaster is missing beyond the first gastral segment and portions of some legs are missing at the amber surface. Some areas are difficult to observe owing to deformities in the amber surface (particularly near the metasoma), a large blackened bit of debris to the specimen's right, and the position of *M. magaliae* masking the specimen's face. The second serphitid (Figs. J1.2, J2.1) is similarly preserved but rests alongside a darkened fracture plane rendering it impossible to see the specimen in dorsal-oblique view from the left. This orientation also resulted in the wings being less than ideally preserved (hind wings present, right forewing largely destroyed except for extreme base; left forewing present but mixed into fracture plane making interpretation challenging) and portions of the dorsum of the prothorax and head are obscured, including a direct facial view. Nonetheless, this is the most complete individual and because the head is twisted, gives the best view of the opened mouthparts along with antennal structure. This is also the only specimen with a complete metasoma (the sting is exposed along with the short associated styli), and it was duly selected as the holotype.

The amber pieces were slightly polished and subsequently embedded in blocks of epoxy resin which were again polished on all sides. This facilitated optimal viewing of the specimens, although the ideal vantage for particular structures was still not possible given the placement of syninclusions or other impurities with the amber. The amber was collected in 2002 by Magali Weigandt and Fanny Dupé from a deposit exposed briefly during work along the D32 road between La Garnache and Challans, in the department of Vendée, northwestern France. In a preliminary account of this amber deposit, Perrichot and others (2013) suggested a Santonian age but contradictory data have been found since then, so an uncertainty remains on the exact age and until new elements are found we cannot discriminate between Middle Cenomanian, Turonian, or Early Santonian (≈ 97–85 Ma), as discussed by Perrichot and Néraudeau (2014: 10A in this volume). Morphological terminology and the format for the description generally follows that of Engel, Grimaldi, and Ortega-Blanco (2011) and McKellar and Engel (2011a). Photographs were taken with a Canon 5D Mark II digital camera attached to a Leica MZ APO stereomicroscope, and stacks of images taken at different depths of field were merged using Helicon Focus 5.3 (HeliconSoft Ltd) to obtain sharpness throughout the entire images. Metrics were taken with an ocular micrometer set on an Olympus SZX-12 stereomicroscope.

SYSTEMATIC PALEONTOLOGY

Family SERPHITIDAE Brues, 1937
Genus SERPHITES Brues, 1937

Type species.—*Serphites paradoxus* Brues, 1937, p. 33, fig. 5A.

Included species.— Presently 12 species included in the genus (see the key below).

Comment.—The emended generic diagnosis by McKellar and Engel (2011a) is followed here and requires no modification to incorporate the present species.

Key to species of *Serphites*

1\. Pterostigma isosceles 2

Pterostigma equilateral 3

2\. Body small, 1.3 mm long in male; 1st petiolar segment twice as long as 2nd petiolar segment, the latter flattened dorsally; gaster with lateral carina between tergites and sternites [Campanian, Canada] .... *S. paradoxus* Brues

Body large, 3.0 mm long in female; 1st petiolar segment 3× as long as 2nd petiolar segment, the latter not flattened dorsally; gaster longer than mesosoma, without lateral carina [Santonian, Taimyr] .... *S. gigas* Kozlov & Rasnitsyn

3\. 1st petiolar segment longitudinally striate 4

1st petiolar segment not longitudinally striate [Cenomanian–Santonian, France] .... *S. fannyae* n. sp.

4\. 1st petiolar segment not rimmed anteriorly 5

1st petiolar segment rimmed anteriorly [Early Albian, Spain] .... *S. lamiak* Ortega-Blanco, Delclòs, Peñalver, & Engel

5\. Gaster shorter than mesosoma 6

Gaster as long as or slightly longer than mesosoma 9

6\. Metatarsus shorter than metafemur; metabasitarsus shorter than combined length of remaining tarsomeres 7

Metatarsus as long as or longer than metafemur; metabasitarsus as long as combined length of remaining tarsomeres 8

7\. Body small, female 1.10 mm long, male 1.45 mm long; forewing vein Rs not tubular, straight; 1st petiolar segment 2.7× as long as 2nd petiolar segment; 1st and 2nd gastral segments shorter than combined length of remaining segments [Turonian, New Jersey] .... *S. raritanensis* Engel & Grimaldi

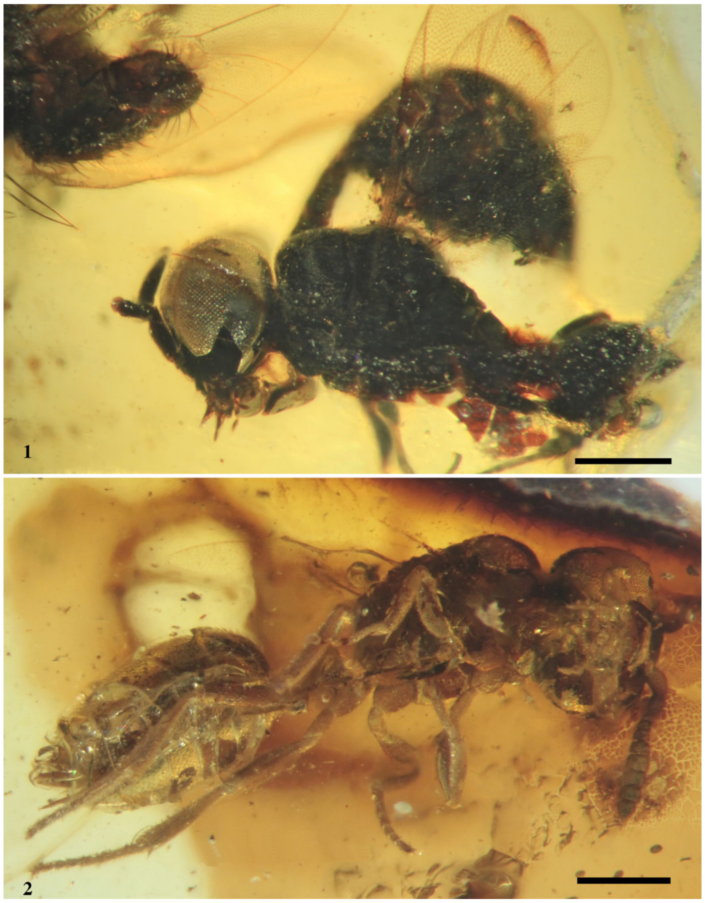

Figure J1. Photographs of *Serphites fannyae* n. sp., in Late Cretaceous (Cenomanian–Santonian) amber of Vendée, NW France; *1*, paratype male IGR.GAR-106b; *2*, holotype female IGR.GAR-26. Scale bars = 0.25 mm.

Body larger, female 2.6 mm long; forewing vein Rs tubular, curved apically; 1st petiolar segment 3× as long as 2nd petiolar segment; 1st and 2nd gastral segments longer than combined length of remaining segments [Campanian, Canada] .... *S. kuzminae* McKellar & Engel

8. Body length 2.6 mm, female with nine antennomeres; left mandible with lower tooth slightly longer than upper tooth; metatarsus longer than metafemur; 1st petiolar segment 2.5× as long as 2nd petiolar segment; 1st and 2nd gastral segments shorter than combined length of remaining segments [Turonian, New Jersey] .... *S. navesinkae* Engel & Grimaldi
Body length 2.95 mm; left mandible with lower and upper teeth equal in size; metatarsus as long as metafemur; 1st petiolar segment twice as long as 2nd petiolar segment; 1st and 2nd gastral segments longer than combined length of remaining segments [Early Albian, Spain] .... *S. silban* Ortega-Blanco, Delclòs, Peñalver, & Engel

9. Body very small, 0.9 mm long; basal flagellomere about 1/3 as long as apical one; right mandible with middle tooth longest of three teeth, left mandible with two equal teeth [Campanian, Canada .... *S. pygmaeus* McKellar & Engel
Body length at least 1.5 mm; right and left mandibles with lower tooth longest 8

10. Body length 1.5 mm; forewing vein Rs nebulous; 1st petiolar segment twice as long as 2nd petiolar segment; 1st and 2nd gastral segments shorter than combined length of remaining segments [Campanian, Canada] .... *S. hynemani* McKellar & Engel
Body length 2.0 mm; forewing vein Rs tubular; 1st petiolar segment 2.4× as long as 2nd petiolar segment; 1st and 2nd gastral segments shorter than combined length of remaining segments [Santonian, Taimyr] .... *S. dux* Kozlov & Rasnitsyn
Body length 2.1 mm; forewing vein Rs tubular; 1st petiolar segment 3× as long as 2nd petiolar segment; 1st and 2nd gastral segments longer than combined length of remaining segments [Campanian, Canada] .... *S. bruesi* McKellar & Engel

SERPHITES FANNYAE new species

Figures J1–J2

Type material.—Holotype female IGR.GAR-26 (Figs. J1.2, J2.1), ex coll. Dupé, and paratype male IGR.GAR-106b (Figs. J1.1, J2.2), ex coll. Weigandt; in Late Cretaceous (Middle Cenomanian to Early Santonian, ≈ 97–85 Ma) Vendean amber. Both specimens are 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, who collected one of the amber pieces containing the type series.

Diagnosis.—Total body length under 2 mm (differs from *S. navesinkae* at ca. 2.6 mm and *S. silban* and *S. gigas* at ca. 3 mm); trochantelli short (long in *S. lamiak*, extremely short and superficially absent in *S. gigas* and *S. dux*); metatarsus very slightly longer than metafemur (about as long as in *S. silban* and *S. gigas*); metabasitarsus distinctly shorter than combined length of remaining tarsomeres, about two-thirds length of remainder of metatarsus (as long as or nearly so in *S. lamiak* and *S. raritanensis*, about twice in *S. dux*); first petiolar segment not rimmed anteriorly (rimmed in *S. lamiak*); second petiolar segment not flattened dorsally (flattened dorsally in *S. paradoxus*); first petiolar segment not longitudinally striate (striate in most species); first petiolar segment about twice the length of second petiolar segment (more than twice, 2.7–3× as long in *S. raritanensis* and *S. kuzminae*, respectively); and gaster longer than mesosoma (shorter in *S. raritanensis*, as long as in *S. dux*).

Description.—Female. Total body length 1.63 mm; forewing length 0.82 mm. Integument apparently dark brown (although many areas with artificial metallic silver sheen owing to microscopic separation from amber causing reflections), with scattered, minute, fine setae throughout body, such setae particularly numerous on tibiae and tarsi. Head not greatly enlarged but with relatively sizeable gena, gena only slightly narrower than compound eye; antenna 10-segmented; scape barely extending half-way to vertex, with length approximately three times the greatest width (0.14 mm long); flagellum with relative lengths of articles 1.0, 0.8, 0.9, 1.2, 1.4, 1.4, 1.5, 2.0; first flagellar article chalice-like in outline, second article nearly square in outline, following articles almost rectangular in outline, broader than long, fifth article broadest flagellomere; apical flagellar article terminating in rounded acute point; right mandible tridentate, lower two teeth longest and most prominent, uppermost tooth distinctly shorter,

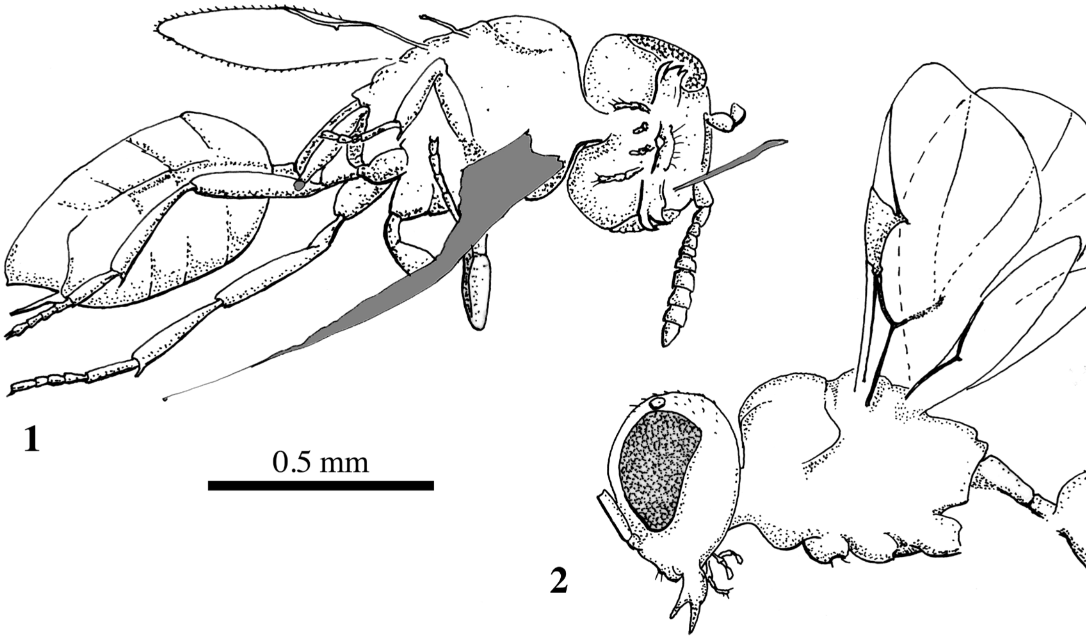

Figure J2. Line drawings of *Serphites fannyae* n. sp., Late Cretaceous (Cenomanian–Santonian) amber of Vendée, NW France. *1*, habitus of holotype female IGR.GAR-26; *2*, lateral left habitus of paratype male IGR.GAR-106b.

apparently one-half length of midtooth, lowermost tooth longest, only slightly longer than midtooth, all teeth with sharply pointed apices; left mandible bidentate, both teeth long with sharp apices, lower tooth distinctly longer than upper tooth. Mesosoma 0.53 mm in length, mostly obscured by preservation and with dorsal surface not visible. Forewing with numerous microtrichia, slightly longer setae forming continuous fringe along wing margins; venation typical for species of the genus (see McKellar & Engel, 2011a; Engel, Grimaldi, & Ortega-Blanco, 2011); C not fused to Sc+R, forming a distinct costal cell, C not pigmented (perhaps due to preservation); pterostigma massive, triangular, approximately equilateral, uniformly pigmented and sclerotized; r-rs arising from pterostigmal midlength, about as long as wide; Rs strongly pigmented, not tubular, straight, reaching wing margin; Rs+M absent; M+Cu, basal vein, and 1Cu tubular, other abscissae of Cu and M nebulose, apicalmost abscissa of M reaching wing margin, that of Cu disappearing shortly before margin; 1A tubular proximally, becoming nebulous well before 1Cu. Hind wing with numerous microtrichia, with short setae forming marginal fringe, with only C+Sc+R along anterior margin and with three hamuli apically. Legs thin, although not especially long, with scattered, minute, fine setae; trochantelli short; femora not especially swollen; meso- and metatibiae with two short, thin apical spurs (often difficult to discern from surrounding setae), single protibial spur; tarsi pentamerous; metabasitarsus two-thirds length of remaining tarsomeres combined; pretarsal claws simple and short, arolium large. Metasoma bipetiolate; first petiolar segment not rimmed anteriorly (as in *S. raritanensis*), about twice the length of second petiolar segment, petiolar segments apparently smooth and without distinct sculpturing; gaster slightly longer than mesosoma, 0.63 mm long, terga and sterna apparently smooth with minute punctures at setal bases, discs of terga and sterna with several scattered, suberect setae, sterna not concave, instead slightly convex on discs, segments generally of same size except apically larger; sting exposed, relatively short, scarcely longer than associated sheaths and only somewhat longer than an individual gastral segment (although the sting may not be fully exserted), sting simple, apparently without preapical dorsal notch.

Male. Very similar but specimen incomplete, with most of gaster missing so total length in life is unknown. Body length as preserved 1.28 mm. Forewing length 0.84 mm. Mesosomal length 0.52 mm. Antenna 9-segmented, which suggests it is a male rather than a female according to the sexual dimorphism in the number of antennomeres of *Serphites*.

DISCUSSION

The discovery of a serphitid wasp in Vendean amber, as well as a species of the microphorine genus *Microphorites* Hennig, 1971 (Perrichot & Engel, 2014: 10G in this volume), is in accordance with the Cretaceous age of this amber even though the precise layer is unknown within the Cenomanian–Santonian interval. Both *Microphorites* and, as noted above, the Serphitidae are classical Cretaceous amber taxa, and both became extinct sometime by the end of the Mesozoic. The new species can be easily assigned to *Serphites* based on the eight-segmented female flagellum (six-segmented in *Jubaserphites* McKellar & Engel, 2011), absence of distinctively elongate and numerous setae on the vertex (present in *Jubaserphites*), pronotum large and extending back to the tegula (not reaching tegula in *Microserphites* Kozlov & Rasnitsyn, 1979), pterostigma large, well defined, and sclerotized (indistinct in *Microserphites*), first petiolar segment twice length of second petiolar segment (less than twice length in *Aposerphites* Kozlov & Rasnitsyn, 1979), and lateral ocellus nearly touching compound eye (distinctly separated from compound eye margin in *Aposerphites*). *Serphites* is the most diverse and widespread of the four genera in Serphitidae and may ultimately prove to be paraphyletic with respect to one of the other genera, thereby requiring its segregation into multiple groups. For the time being serphitids remain too poorly known to speculate on relationships or to build a sufficiently rich character matrix for cladistic analysis among the various species. Some statements can possibly be made, however, about the polarity of particular characters within the family. Serphitidae are the presumed sister group to the Mymarommatoidea (Kozlov & Rasnitsyn, 1979; Grimaldi & Engel, 2005), and the putatively most plesiomorphic group within the latter is the extinct family Alavarommatidae (Ortega-Blanco & others, 2011b). If alavarommatids are employed as a possible outgroup for polarizing features within Serphitidae, then the sexually dimorphic number of antennomeres (at least in *Serphites*, with ten antennomeres in females and nine in males, with the exception of *S. navesinkae* which has nine antennomeres in female) is a striking synapomorphy of Serphitidae. The more reduced flagellum in Serphitidae (seven or eight flagellomeres in most species *versus* the ten flagellomeres in Alavarommatidae and 11 in Gallorommatidae) would be apomorphic, particularly so for the autapomorphically reduced number of flagellomeres (six) in *Jubaserphites*. Similarly, the more elongate first petiolar segment typical across all of the serphitid genera except *Aposerphites* would be considered plesiomorphic. The uniquely massive form of the pterostigma in *Jubaserphites*, *Serphites*, and *Aposerphites* may be an apomorphy relative to Mymarommatoidea and other related lineages (e.g., Ortega-Blanco & others, 2011b). The more diffuse and unsclerotized condition observed for *Microserphites* is either a primitive condition among serphitids, prior to sclerotization of the pterostigmal region, or is an autapomorphic reduction. The latter scenario seems most likely given that both of the known species of *Microserphites* are the smallest of the family (Kozlov & Rasnitsyn, 1979; Ortega-Blanco & others, 2011b). An alternative scenario would interpret the diffuse condition of *Microserphites* as a plesiomorphy as the pterostigma is absent in Mymarommatoidea and other related lineages, and could conceivably form a transformation series between the state of complete absence and the large, well-defined condition observed in other serphitid genera. Certainly a cladistic treatment of living and fossil bipetiolarid clades (Mymarommatoidea and Serphitoidea) is needed to more fully understand the complex evolutionary history of these tiny wasps.

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