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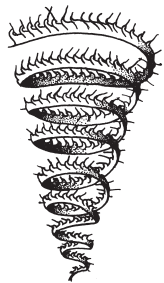
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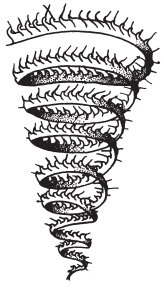
Diverse barklice (Psocodea) from Late Cretaceous Vendean amber

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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 axioperi erga* n. sp. (Archaeatropidae), *Scocompus atelisis* 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 psocodes 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 axioperi erga* n. sp. (Archaeatropidae), *Scocompus atelisis* n. gen. et sp. (famille incertaine au sein des Amphientometae), et *Mesopsocoides dupei* n. gen. et sp. (plus ancien Mesopsocidae fossile). Ces nouveaux taxons sont comparés à leurs congénères, et leur position systématique respective est discutée. D'autres psocodes 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 Mesopsocidae, respectively. The remains of four additional but poorly preserved specimens from the same deposit are also figured and briefly discussed.

*Corresponding author.

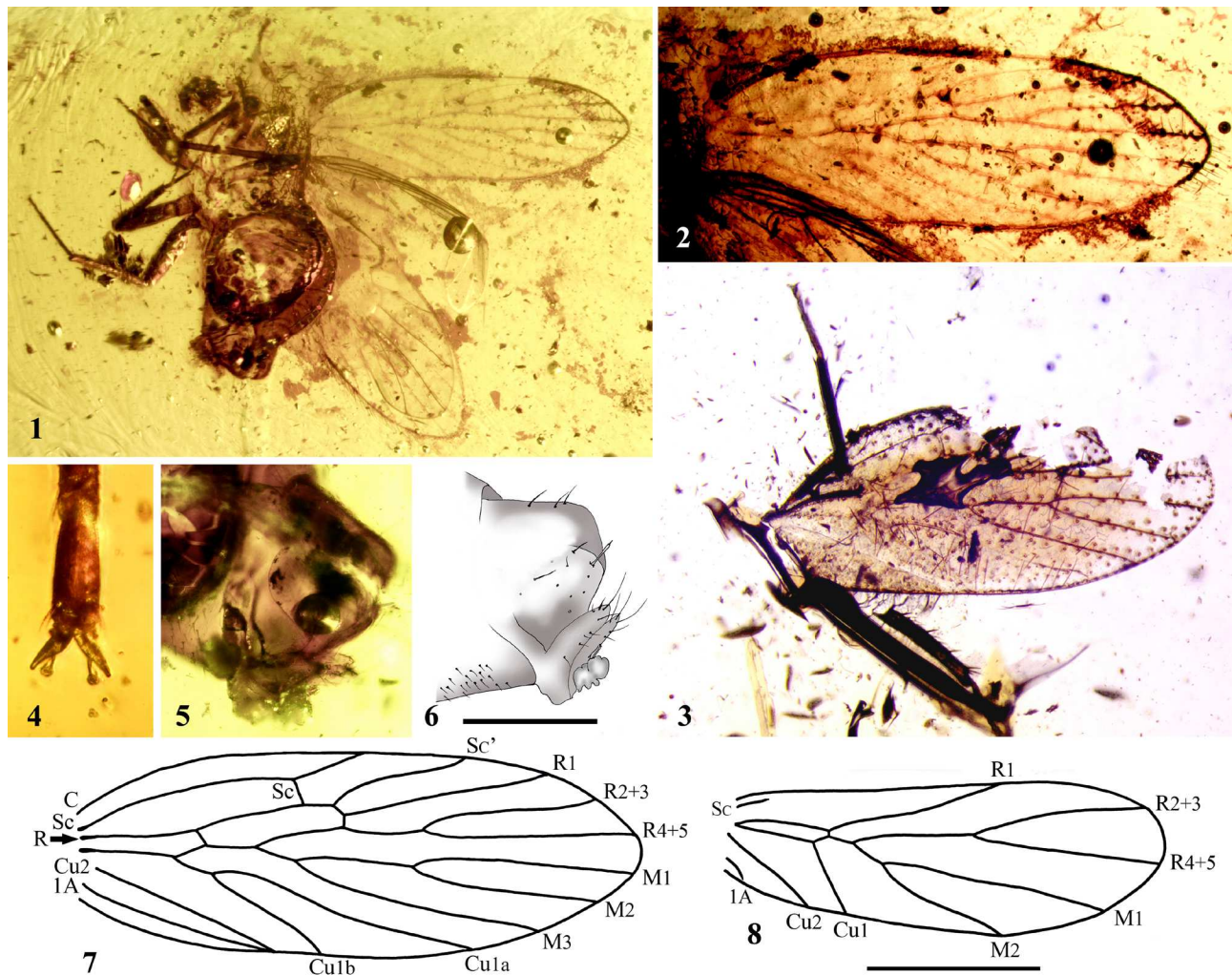


Figure C1. *Proprionoglaris axioperi erga* n. sp., in Late Cretaceous Vendean amber. (1–2, 4–8: holotype female IGR.GAR-69; 3: paratype IGR.GAR-39). 1, habitus in ventral view; 2, forewing; 3, specimen as preserved, with forewing and fragments of legs; 4, detail of tarsal claw; 5–6, female genitalia, 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 col-

lection 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

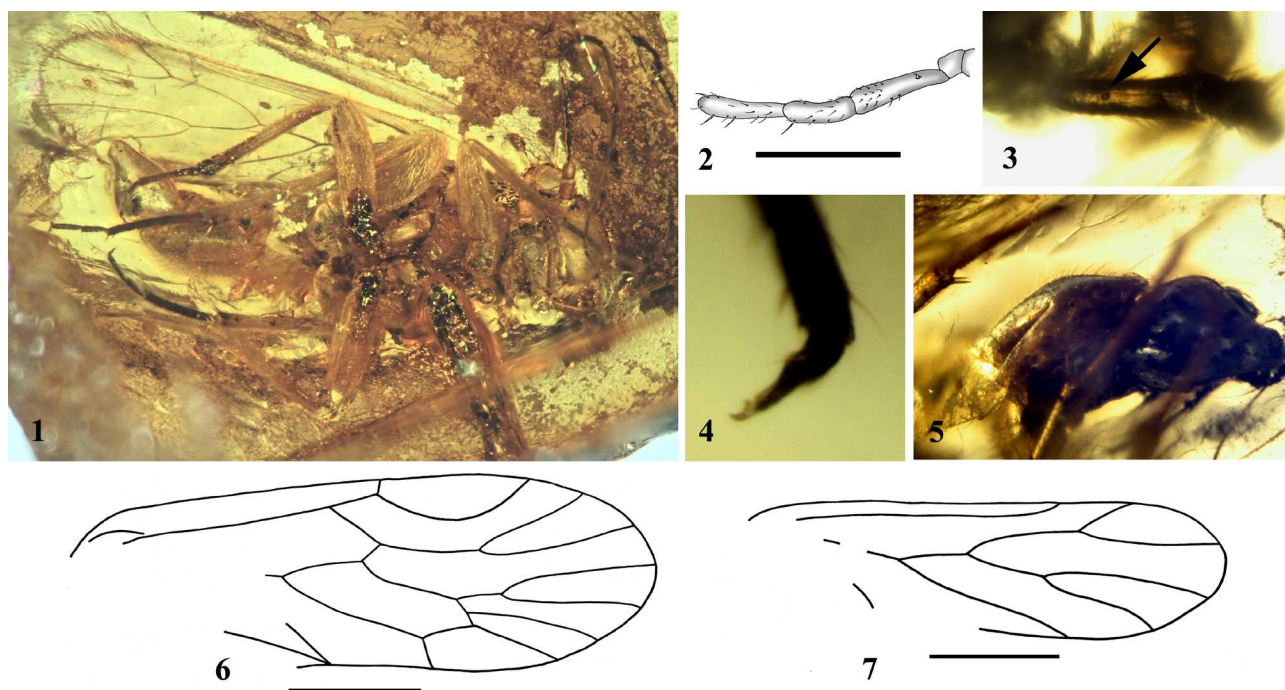


Figure C2. *Scocompus atelisis* n. gen. and sp., holotype female IGR.GAR-40, in Late Cretaceous Vendean amber. 1, habitus in ventral view; 2, drawing of maxillary palps, scale bar = 0.3 mm; 3, second maxillary palp, with conical sensillum indicated by arrow; 4, detail of tarsal claw; 5, detail of genitalia; 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 ἀξιοπεριεργός (axioperiergos) = particular; the gender of the genus, which was not stated in the original description, is feminine.

Diagnosis.—Very similar to *Proprioglaris 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; perostigma 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 anteriorly, 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 nodule 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 *Prionoglaris* 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 atelisis* 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 (in 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 trimmerous; 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-

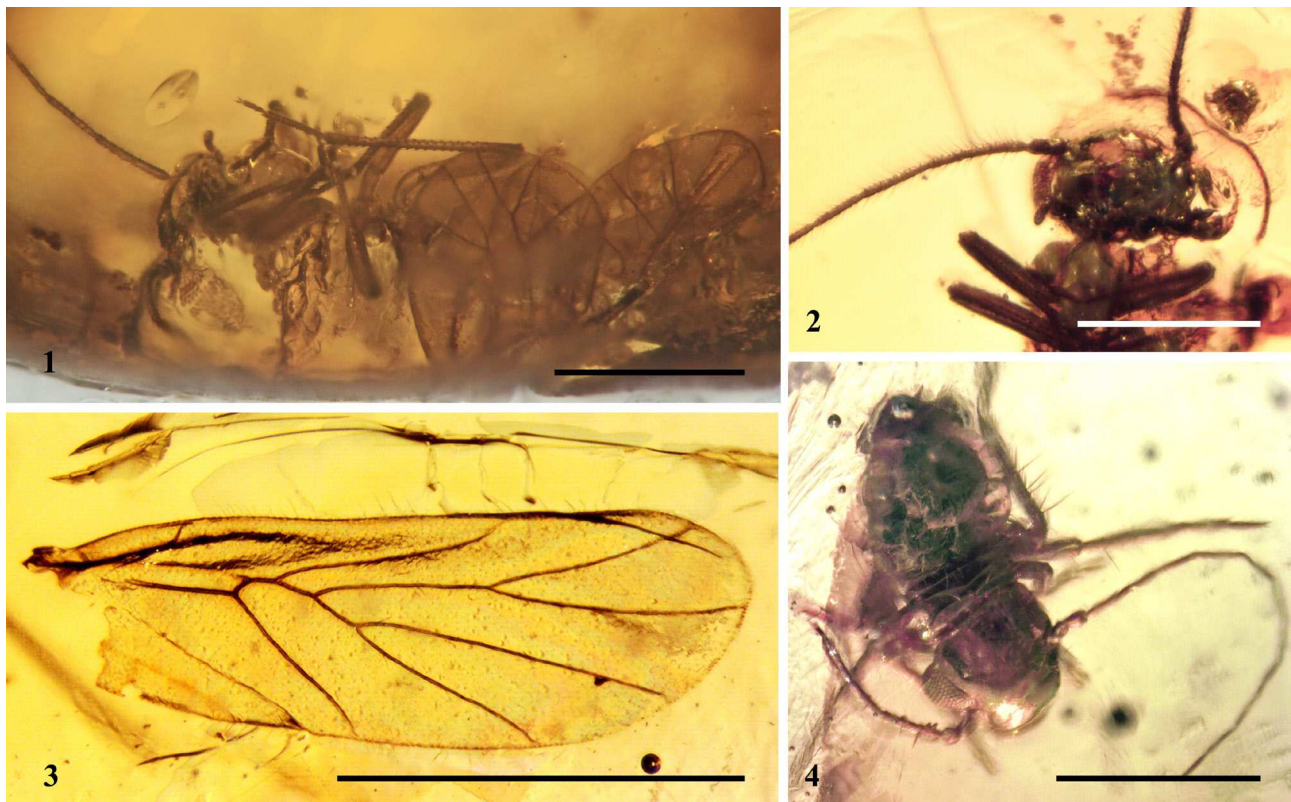


Figure C4. Partial, undetermined psocopterans in Late Cretaceous Vendean amber. 1–2, specimen IGR.GAR-81, habitus and detail of head in ventral view; 3, specimen IGR.GAR-105, hind wing of an undetermined Psocodea; 4, specimen IGR.GAR-3, an undetermined larva. All scale bars = 0.5 mm.

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; pulvillus 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 Mesopsocidae 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 *Propriionoglaris 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 *Propriionoglaris*, 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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