



General Palaeontology, Systematics, and Evolution (Invertebrate Palaeontology)

The first sclerodermine and pristocerine flat wasps in Lowermost Eocene amber of France (Hymenoptera: Bethylidae)



Les premières guêpes plates sclérodermiques et pristocérines dans l'ambre de l'Éocène inférieur français (Hyménoptères : Béthylidae)

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ARTICLE INFO

Article history:

Received 5 February 2019

Accepted after revision 24 April 2019

Available online 27 July 2019

Handled by Annalisa Ferretti

Keywords:

Insecta

Hymenoptera

Bethylidae

Scleroderminae

Pristocerinae

Gen. et sp. n.

Oise amber

France

ABSTRACT

Two new bethyliid wasps, one Scleroderminae *Paleoscleroderma lamarrei* gen. et sp. n. and one Pristocerinae *Pristocera alaini* sp. n., are described from the Lowermost Eocene amber of Oise (France). Together with the Bethylinae and the three Epyrinae already described from the same amber, they show that this family was already very diverse during the Lower Paleogene.

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RÉSUMÉ

Mots clés :

Insecta

Hymenoptera

Bethylidae

Scleroderminae

Pristocerinae

Gen. et sp. n.

Ambre de l'Oise

France

Deux nouvelles guêpes bethylides, une Scleroderminae *Paleoscleroderma lamarrei* gen. et sp. n. et une Pristocerinae *Pristocera alaini* sp. n., sont décrites dans l'ambre Éocène basal de l'Oise (France). Avec la Bethylinae et les trois Epyrinae déjà décrites du même ambré, elles montrent une famille déjà très diversifiée au Paléogène inférieur.

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1. Introduction

Bethylidae are rather frequent in the amber, but the majority of fossil taxa belong to the Bethylinae and Epyrinae, even if all the subfamilies have fossil representatives (Azevedo et al., 2018). The lowermost Eocene Oise amber has given one Bethylinae (*Eupsenella eocenica* De Ploëg and Nel, 2004), three Epyrinae, viz. *Elektroepyris magnificus* Perrichot and Nel, 2008, and *Chlorepypyris gallicus* (Perrichot and Nel, 2008), and *Epyris moulyi* Falières and Nel, 2018. Here we describe the first representatives of the Scleroderminae and Pristocerinae from this amber, confirming the diversity of this group in the Paleogene. The fossil record of the Scleroderminae consists of only four species, one from the Eocene Baltic amber (*Plastanoxus atrescens* Sorg, 1988), two from the Late Cretaceous amber from Taymir, Siberia (*Celonophamia taimyria* Evans, 1973), Canada (*Celonophamia granama* McKellar and Engel, 2014), and one from the ‘mid’-Cretaceous of Myanmar [*Sclerodermus quadridentatus* (Cockerell, 1917)]. The fossil record of the Pristocerinae consists of only four species, from the Miocene Dominican amber [*Apenesia miki* (Terayama, 2004)], the Oligocene of France (*Protisobrachium oligocenicum* Théobald, 1937), the middle Eocene Baltic amber [*Pristocera skwarrae* (Brues, 1933)], and the ‘mid’-Cretaceous amber of Myanmar [*Eleganesia electriphila* (Cockerell, 1917)] (McKellar and Engel, 2014), and one from the ‘mid’-Cretaceous of Myanmar [*Sclerodermus quadridentatus* (Cockerell, 1917)] (Brues, 1933;

Cockerell, 1917; Sorg, 1988; Terayama, 2004; Théobald, 1937).

2. Material and methods

The fossils were embedded in small clear pieces of amber. They have been prepared using a diamond disk, examined using a Nikon binocular microscope SMZ 1500. Photographs have been taken with an AmScope camera MU900, and the images treated with Adobe Photoshop Element 12.

The nomenclature and classification follow Azevedo et al. (2018). Main measurements and indices used are as follow: length of forewing (LFW); length of head (LH); width of head (WH); width of frons (WF); height of eye (HE); ocello-ocular line (OOL); width of ocellar triangle (WOT); diameter of anterior ocellus (DAO); vertex-ocular line (VOL). The nomenclature of integument sculpture follows Harris (1979).

3. Systematic paleontology

Class: Insecta Linnaeus, 1758

Order: Hymenoptera Linnaeus, 1758

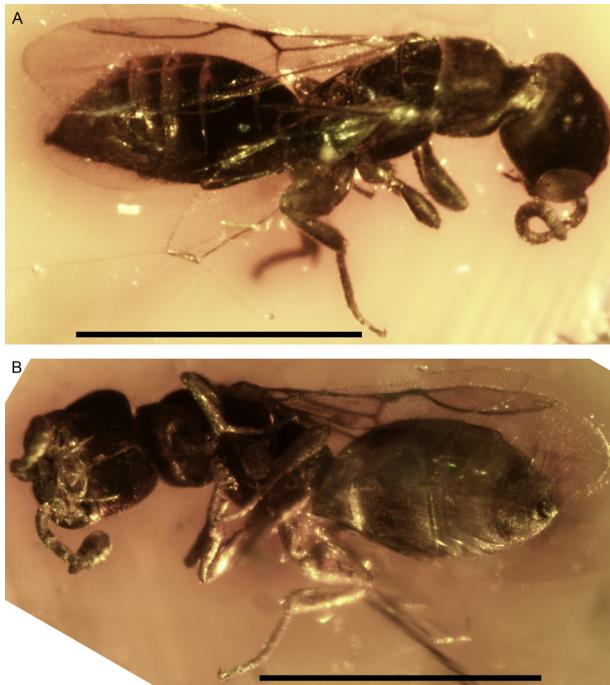


Fig. 1. *Paleoscleroderma lamarrei* gen. et sp. n., holotype MNHN.F.A70917. General habitus. **A.** Dorso-lateral view. **B.** Ventral view. Scale bars = 1 mm.

Fig. 1. *Paleoscleroderma lamarrei* gen. et sp. n., holotype MNHN.F.F.A70917. Habitus général. **A.** Vue dorso-latérale. **B.** Vue ventrale. Barres d'échelle = 1 mm.

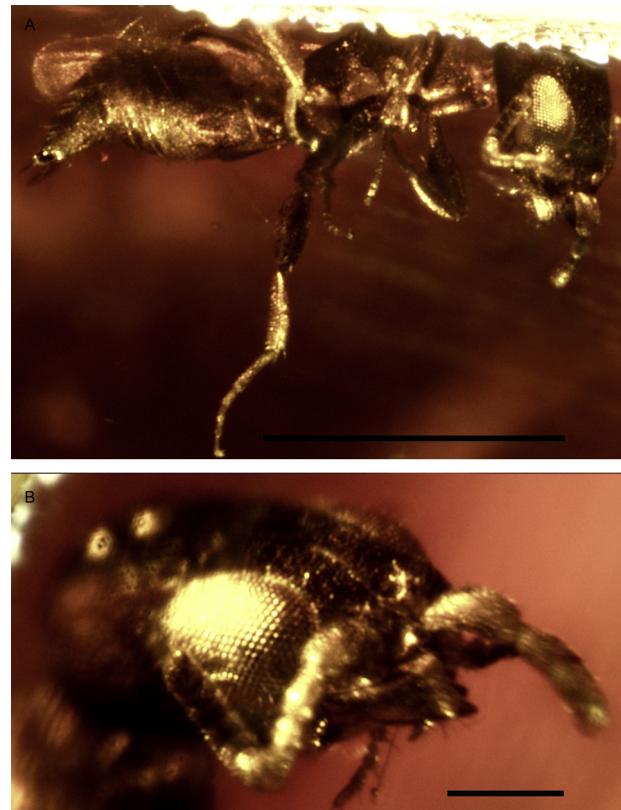


Fig. 2. *Paleoscleroderma lamarrei* gen. et sp. n., holotype MNHN.F.A70917. **A.** Lateral view habitus. **B.** Head lateral view. Scale bars = 1 mm (A), 0.1 mm (B).

Fig. 2. *Paleoscleroderma lamarrei* gen. et sp. n., holotype MNHN.F.F.A70917. **A.** Habitus en vue latérale. **B.** Vue latérale de la tête. Barres d'échelle = 1 mm (A), 0,1 mm (B).

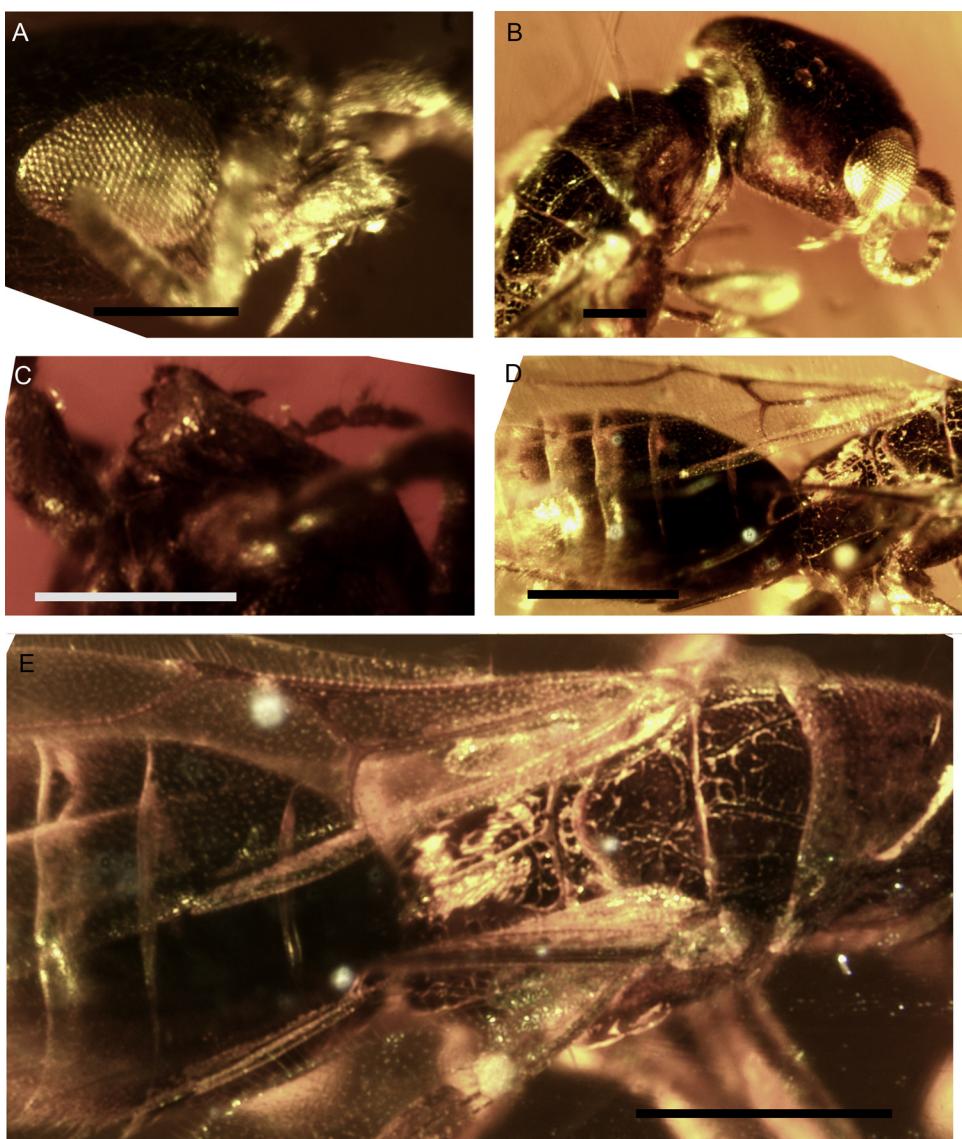


Fig. 3. *Paleoscleroderma lamarrei* gen. et sp. n., holotype MNHN.F.A70917. **A.** Eye. **B.** Head posterolateral view. **C.** Mandible. **D.** Wing and metasoma. **E.** Posterior part of mesosoma.

Fig. 3. *Paleoscleroderma lamarrei* gen. et sp. n., holotype MNHN.F.F.A70917. **A.** Yeux. **B.** Vue postéro-latérale de la tête. **C.** Mandibule. **D.** Aile et métasome. **E.** Partie postérieure du mésosome.

Family: Bethylidae Haliday, 1840

Subfamily Scleroderminae Kieffer, 1914

Genus ***Paleoscleroderma*** gen. n.

Type species. *Paleoscleroderma lamarrei* sp. n.

Etymology. Named after the genus *Scleroderma* and 'paleo' for ancient.

Diagnosis. Male characters only. Antenna with 11 flagellomeres; body not depressed; eye distinctly shorter than head in lateral view; mandible with five teeth; occipital carina absent; well-developed notauli; metapectal-propodeal complex strongly sculptured with carinae; mesoscuto-mesoscutellar suture partially closed but with two lateral foveae; transepisternal fovea absent; poststigmal abscissa of radial 1 very short; metasomal segment II 1.5 as long as segment III.

Paleoscleroderma lamarrei sp. n.

(Figs. 1–3)

Etymology. Named after Mr. Lamarre Gauthier, husband of the first author.

Locus typicus and **stratum typicum**. Le Quesnoy, Chevrière, region of Creil, Oise department, France; lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal.

Holotype. MNHN.F.A70917 (PA 8508), male, stored in the collections of the "Muséum national d'histoire naturelle", Paris, France.

Main measurements. Body ca. 2.5 mm long; WH 0.44 mm; LH 0.35 mm; HE 0.062 mm; WF 1.137 × HE; OOL 0.148 × WOT.

Description. Male; body 2.01 mm long, not depressed, not strongly foveolate; LFW 1.37 mm; head black; metasoma black and castaneous, legs castaneous, antenna castaneous; wings hyaline; head and thorax 'setose'.

Head. Mandible with five apical teeth, lowermost tooth of mandible triangular, not directed inward; four visible maxillary palpomeres (probably five), two or three labial palpomeres hardly visible; clypeus hardly visible; antenna with 11 flagellomeres; scape: 0.126 mm long \times 0.044 mm wide, pedicel: 0.066 \times 0.038 mm, F1: 0.027 \times 0.033 mm, F2: 0.038 \times 0.033 mm, F3: 0.038 \times 0.033 mm, F4: 0.033 \times 0.033 mm, F5: 0.055 \times 0.033 mm, F6 and F7 not visible, F8: 0.027 \times 0.033 mm, F9: 0.027 \times 0.033 mm, F10: 0.022 \times 0.033 mm, F11: 0.033 \times 0.0033 mm; eyes pubescent; frons coriaceous with median depression; occipital carina absent; WH 0.44 mm; LH 0.35 mm; HE 0.062 mm; WF 1.137; OOL 0.148; ocellar triangle equilateral.

Mesosoma: thoracic dorsum weakly coriaceous covered with setae; pronotal disc with anterior transverse carina weak, dorsal pronotal area elongate, longer than anteromesoscutum; dorsal pronotal area without elevation wider anteriorly; metanotum neither developed medially nor overlapping mesoscutellum posteriorly; mesoscuto-mesoscutellar suture not complete, opened in its median part, but with two lateral foveae linked to suture by line; well-developed notaui; parapsidal signum almost complete; mesopleuron without any transepisternal line on mesopleuron; strongly sculptured metapectal-propodeal complex with carinae, but not depressed medially, without posterior spines, as broad as long, with distinct lateral carinae, and posterior carina very weak medially.

Wings covered with short setae and bordered with small setae; forewing with anterior border angularly incurved anterior to pterostigma; costal vein absent; vein 2r+rs&Rs vein long and as strong as other veins; cells R and 1Cu closed; first medial cell absent; no basal stub of Rs+M; poststigmal abscissa of R1 very short, distal ghost veins present (Azevedo et al., 2018; Terayama, 2006: 14).

Metasoma: short petiole; six tergites, convex, partly covering sternites; posterolateral margin of tergite II not strongly concave, without pair of spots, pits or depressions; tergites III and IV with concave part in middle; genitalia and subgenital structures hardly or not visible.

Tergites length \times height: T1: 0.173 \times 0.237 mm, T2: 0.181 \times 0.395 mm, T3: 0.126 \times 0.418 mm, T4: 0.102 \times 0.363 mm, T5: 0.086 \times 0.316 mm, T6: 0.11 \times 0.181 mm.

Remarks. This fossil differs from *Eupsenella eocenica* in its more reduced venation (De Ploeg and Nel, 2004). It differs from *Epyris moulyi* in the shape of the head, the ornamentation of the metapectal-propodeal complex, etc. It differs from *Chloreypis gallicus* in the shape of the pronotum, and from *Elektroepyris magnificus* in the shape of the eyes and head, and the very reduced poststigmal abscissa of radial 1 (Perrichot and Nel, 2008). Thus it corresponds to a new species.

After the key to subfamilies of Azevedo et al. (2018), this fossil would fall in the Scleroderminae because of the following characters: winged forms (macropterous); forewing with Rs+M vein absent; metanotum neither

developed medially nor overlapping mesoscutellum posteriorly; metapectal-propodeal complex not depressed medially, without posterior spines; body not strongly foveolate; metasomal segment II much less than twice as long as subsequent ones; mesopleuron without transepisternal line; forewing with anterior border angularly incurved anterior to pterostigma; costal vein absent; occipital carina absent, occiput rounded.

More precisely, the metasomal segment II of *Paleoscleroderma* gen. n. is 1.5 as long as segment III, while it is twice or more as long as III in the Mesitiinae (Argaman, 2003). There is a transepisternal line on the mesopleuron of the Mesitiinae and Epyrinae, unlike in *Paleoscleroderma* (Argaman, 2003; Azevedo et al., 2018).

After the key to sclerodermine genera of Azevedo et al. (2018), *Paleoscleroderma* would fall near *Glenosema* Kieffer, 1905 for the following combination of characters: antenna with 11 flagellomeres; body not depressed; eye distinctly shorter than head in lateral view; mandible with five teeth. *Paleoscleroderma* strongly differs from *Glenosema* in the well-developed notaui and the strongly sculptured metapectal-propodeal complex with carinae.

The ornamentation of the metapectal-propodeal complex of *Paleoscleroderma* more strongly resembles those of *Chloreypis* Evans, 1964 (which has no notaui and mandible with three teeth), *Discleroderma* Kieffer, 1904 (which has notaui even if less pronounced than in *Paleoscleroderma*, and mandible with four apical teeth), and *Nothepyris* Evans, 1973 (with pronounced notaui, but mandible with two teeth). In *Paleoscleroderma*, the mesoscuto-mesoscutellar suture is partially closed, unlike in these genera.

Fossil Scleroderminae are quite rare, with only the Late Cretaceous genus *Celonophamia* Evans, 1973, with two species *C. taimyria* Evans, 1973 and *C. granama* McKellar and Engel, 2014, the extant genus *Sclerodermus* Latreille, 1809 with the species *S. quadridentatus* (Cockerell, 1917) (original spelling *Scleroderma* (?) *quadridentatus*) from the Cretaceous Burmese amber, and the extant genus *Plastanoxus* Kieffer, 1904 with the species *P. atrescens* Sorg, 1988 from Baltic amber.

P. atrescens differs from *Paleoscleroderma* in a more reduced wing venation and presence of only four mandibular teeth (Sorg, 1988). *S. quadridentatus* differs from *Paleoscleroderma* in the very long pronotum (Cockerell, 1917). *C. taimyria* Evans, 1973 and *C. granama* have a very short pronotum, unlike *Paleoscleroderma* (Evans, 1973; McKellar and Engel, 2014).

Subfamily: Pristocerinae Mocsáry, 1881
Genus **Pristocera** Klug, 1808

Pristocera alaini sp. n.
(Figs. 4–5)

Etymology. Named after Mr. Alain Falières, father of first author.

Locus typicus and stratum typicum. Le Quesnoy, Chevrière, region of Creil, Oise department, France; lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormal.

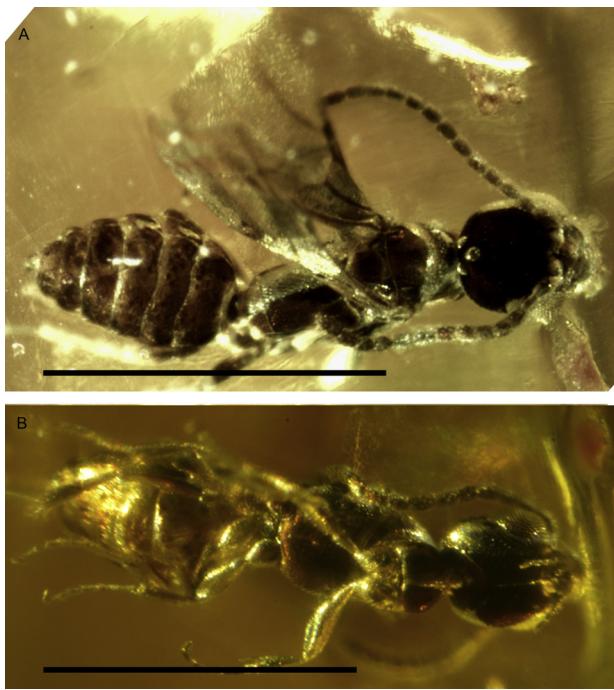


Fig. 4. *Pristocera alaini* sp. n., holotype MNHN.F.A70916. General habitus. **A.** Dorsal view. **B.** Ventral view. Scale bars = 1 mm.

Fig. 4. *Pristocera alaini* sp. n., holotype MNHN.F.F.A70916. Habitus général. **A.** Vue dorsale. **B.** Vue ventrale. Barres d'échelle = 1 mm.

Holotype. MNHN.F.A70916 (PA 3389), male, stored in the collections of the “Muséum national d'histoire naturelle”, Paris, France.

Diagnosis. Antenna long, reaching the level of mid part of metapectal-propodeal complex; a strong vein cu-a; antennomeres basally narrowed; frons setose; wings hyaline.

Description.

Male; body 1.72 mm long, not depressed, not strongly foveolate; LFW 0.714 mm (preserved part); head black; gaster castaneous lightly iridescent, legs castaneous, antenna castaneous; wings hyaline.

Head smooth, not roughly sculptured; mandible with three apical teeth; five visible maxillary palpomeres, two or three hardly visible labial palpomeres; no spine on gena; medial clypeal lobe trapezoidal with apical margin slightly incurved; antenna rather long, reaching mid part of metapectal-propodeal complex; 11 flagellomeres, cylindrical but basally narrowed; scape: 0.031 mm long × 0.026 mm wide, pedicel: 0.073 × 0.021 mm, F1: 0.052 × 0.021 mm, F2: 0.052 × 0.021 mm, F3: 0.052 × 0.026 mm, F4: 0.052 × 0.026 mm, F5: 0.052 × 0.031 mm, F6: 0.052 × 0.031 mm, F7: 0.052 × 0.031 mm, F8: 0.052 × 0.026 mm, F9: 0.052 × 0.026 mm, F10: 0.052 × 0.026 mm, F11: 0.068 × 0.0021 mm; frons with numerous setae disposed in several parallel longitudinal lines; ventral part of occipital carina present, but dorsal part hidden; eyes glabrous; WH 0.32 mm; LH 0.32 mm; WF 0.15; OOL 0.14; ocellar triangle equilateral.

Mesosoma: dorsum smooth, not roughly sculptured; pronotum with anterior margin of disc carinate; pronotal declivity accentuated; propleuron junction region elevated triangularly and extending to prosternum; notaui present with internal region weakly foveolate; parapsidal signum strongly reduced; mesoscuto-mesoscutellar suture opened in its median part, with two lateral foveae, each linked to the suture by a thin line; metanotum with medium region narrower than lateral regions, developed medially and overlapping mesoscutellum posteriorly; metanotal groove with six foveae; metapectal-propodeal complex smooth without carinae and posterior spines.

Forewing covered with punctuation and bordered with small setae; anterior border not angularly incurved anterior to pterostigma; costal vein present; vein 2r+rs&Rs vein long and as strong as other veins but with apex destroyed; strong vein cu-a; cells R and 1Cu closed; discoidal cell absent; no basal stub of Rs+M; poststigmal abscissa of R1 short, ghost FRR and SMC veins present.

Metasoma: short petiole; six tergites, convex, partly covering sternites; posterolateral margin of tergite II not strongly concave, without a pair of spots, pits or depressions; tergites III and IV without concave part in middle; hypopygium medially divided into two parts or strongly concave with two very deep lobes (extreme base of hypopygium not visible).

Tergites length: T1 0.115 mm, T2 0.94 mm, T3 0.94 mm, T4 0.073 mm, T5 0.073 mm, T6 0.136 mm.

Remarks. Following the key to subfamilies of [Azevedo et al. \(2018\)](#), *Pristocera alaini* sp. n. falls in the *Pristocerinae* because of the following characters: fully winged; forewing with Rs+M vein absent; metanotum developed medially and overlapping mesoscutellum posteriorly. After the key to pristocerine genera, it would fall in the genera *Pristocera* Klug, 1808 because of the hypopygium medially divided into two parts (main synapomorphy of the genus after [Zamprogno and Azevedo, 2014](#)), or strongly concave with two deep lobes as in *Propristocera* Keffer, 1905. The impossibility to dissect the hypopygium renders difficult to choose between the two situations (see [Zamprogno and Azevedo, 2014](#); figs. 33, 35–36, 40).

Pristocera alaini would fall in *Pristocera* rather than *Propristocera* because of the clypeus rectangular with apical margin slightly incurved instead of having a median clypeal lobe projected and angulate (after the diagnoses of the two genera in [Azevedo et al., 2018](#)). The extant species of *Pristocera* have short antennae, reaching at most the distal part of mesonotum, while in *Pristocera alaini* they can reach the mid part of the metapectal-propodeal complex. *Pristocera alaini* has the following diagnostic characters of *Pristocera*: pronotum with anterior margin of disc carinate; pronotal declivity accentuated; propleuron junction region elevated triangularly and extending to prosternum; notaui present with internal region weakly foveolate; metanotum with medium region narrower than lateral regions; metanotal groove with six foveae. Thus, we attribute this new fossil to the genus *Pristocera*, but because of the impossibility to examine the internal structure of the hypopygium, this attribution remains somewhat hypothetical.

Pristocera is a genus that comprises 133 valid species distributed in the Afrotropical, Palaearctic, and Oriental

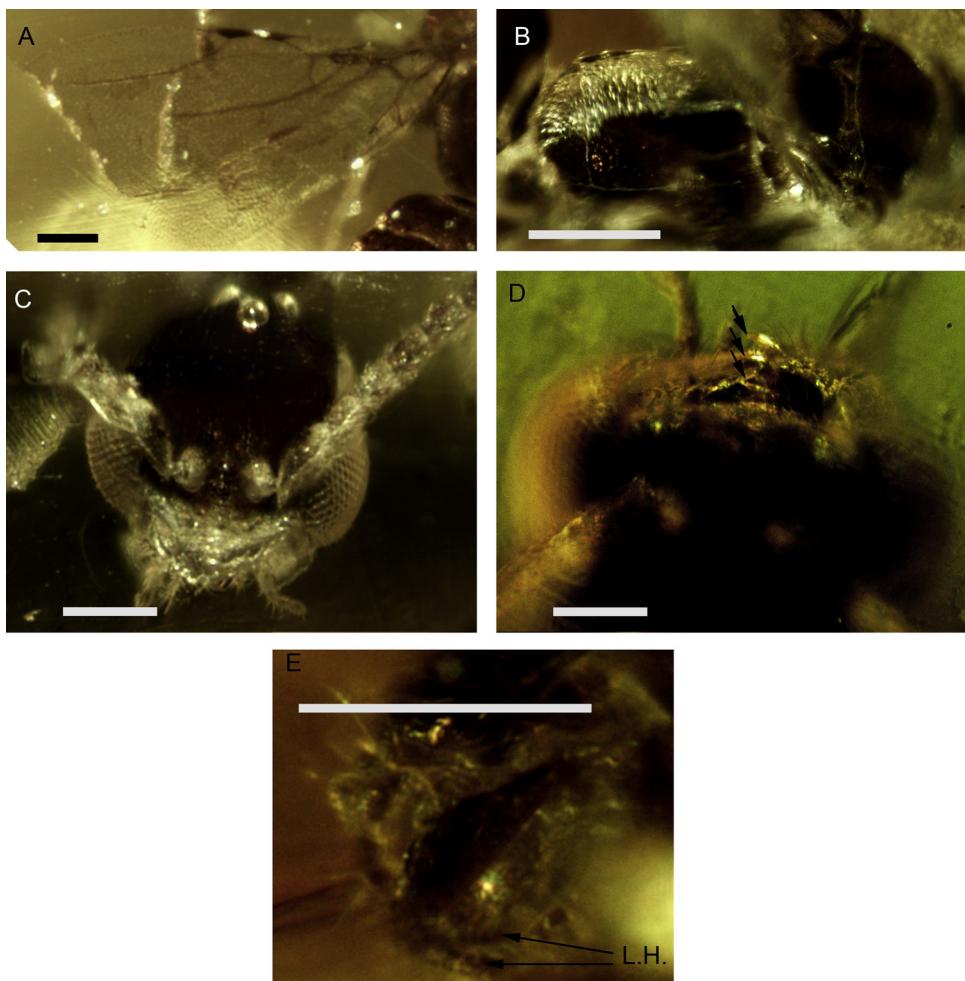


Fig. 5. *Pristocera alaini* sp. n., holotype MNHN.F.A70916. **A.** Wings. **B.** Posterior part of mesosoma. **C.** Clypeus. **D.** Mouthparts. Arrows teeth of mandible. **E.** Metasomal terminalia. L.H. Lobes of hypopygium. Scale bars = 0.1 mm.

Fig. 5. *Pristocera alaini* sp. n., holotype MNHN.F.F.A70916. **A.** Ailes. **B.** Partie postérieure du mésosome. **C.** Clypeus. **D.** Pièces buccales. Dents fléchées de la mandibule. **E.** Terminaux métasomaux. L.H. Lobes d'hypopygium. Barres d'échelle = 0,1 mm.

regions, including *Pristocera skwarrae* (Brues, 1933) from the Eocene Baltic amber. Because of the lack of information on the genital structures, it is not possible to compare *Pristocera alaini* to these taxa. *Pristocera alaini* shares with *Pristocera skwarrae* [originally in the fossil genus *Parapristocera* Brues, 1933, synonymized with *Pristocera* by Alencar (2017), Alencar et al. (2018), and Azevedo et al. (2018)], the following characters: head and thorax smooth; antennae of similar lengths, with antennomeres cylindrical, but *Pristocera alaini* has a strong vein cu-a ('nervulus' sensu Brues, 1933), the antennomeres basally narrowed, a frons setose, and hyaline wings, unlike *P. skwarrae*.

Remark. *Protisobrachium oligocenicum* Théobald, 1937 (Middle Oligocene, Céreste, France) is a Hymenoptera *incertae sedis* based on a poorly preserved compression fossil (Théobald, 1937).

4. Conclusion

Two new bethylide wasps, one Scleroderminae *Paleoscleroderma lamarrei* gen. et sp. n. and one Pristocerinae

Pristocera alaini sp. n. are described from the lowermost Eocene amber of Oise (France). Together with the Betylinae and the three Epyrininae already described from the Oise amber, these new bethylid wasps show that this family was already very diverse during the Lower Paleogene. Further specimens identified as Betylididae, but different from those already known, remain to be described.

Acknowledgements

We thank Alexander Rasnitsyn and an anonymous referee for their useful comments on the first version of this paper. We thank the Lafarge-Granulat company for help with the fossil sampling and the Langlois-Meurinne family for the authorization of working on their property.

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