New fossil earwigs from the lowermost Eocene amber of Paris basin (France) (Insecta, Dermaptera, family *incertae sedis*)

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KEY WORDS
Insecta,
Dermaptera,
Forficulidae,
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Chelisoficula caussaneli n. gen., n. sp.,
lowermost Eocene,
France,
fossil,
amber,
phylogeny,
new genus,
new species.

ABSTRACT
Chelisoficula caussaneli n. gen., n. sp. and two other representatives of Dermaptera *incertae familiae* are described from the lowermost Eocene amber of the Paris basin. *C. caussaneli* n. gen., n. sp. has a unique structure of the cerci with tuft of spiny hairs. Its position relative to both the Forficulidae and Chelichosidae is not solved, because of a conflicting distribution in *Chelisoficula* n. gen. of the characters currently used to discriminate these families. More extensive studies of the phylogenetic relationships between these families and new characters shall be necessary for future progresses in dermapteran phylogenetic analysis.

MOTS CLÉS
Insecta,
Dermaptera,
Forficulidae,
Chelichosidae,
Chelisoficula caussaneli n. gen., n. sp.,
Éocène basal,
France,
fossile,
ambre,
phylogénie,
nouveau genre,
nouvelle espèce.

RÉSUMÉ
Nouveaux dermaptères fossiles de l'ambre éocène inférieur du Bassin de Paris (France) (Insecta, Dermaptera, famille incertae sedis*).*
Chelisoficula caussaneli n. gen., n. sp. et deux autres Dermaptera *incertae familiae* sont décrits de l'ambre éocène basal du Bassin de Paris. La structure des cerques de *C. caussaneli* n. gen., n. sp. est totalement originale, à cause de la présence de touffes de poils épineux. Ce taxon ne peut être attribué aux Forficulidae plutôt qu'aux Chelichosidae, à cause d'une distribution conflictuelle chez *Chelisoficula* n. gen. des caractères actuellement utilisés pour discriminer ces familles. Des études plus approfondies des relations phylogénétiques entre ces familles et de nouveaux caractères seront nécessaires à tout futur progrès dans l'analyse de la phylogénie des Dermaptera.

INTRODUCTION

Earwigs are very scarce in the insect fossil record. Nel *et al.* (1994) listed only 73 taxa of Dermaptera described, figured or simply mentioned in literature. These species span from the Lower Jurassic to the Pleistocene. Among them only nine species are described from Baltic amber, one from Burmese amber, one from Dominican amber and one from Saxonian amber.

Zhang (1994) described the new archidermapteran family Longicerciatidae (*Longicerciata mesozoica* Zhang, 1994 and *L. rumpens* Zhang, 1994), and the new genus and species *Archaeosoma serratum* of Pygidicranidae Verhoeff, 1902, Echinosomatinae Burr, 1910, all from the Late Jurassic of Shandong Province (China). This last species belongs to the modern dermapteran lineage, demonstrating its great antiquity. Coram *et al.* (1995) cited a dermapteran forewing from the Lower Cretaceous (Purbeck Formation, UK). After their figure, this hemelytra is probably not that of a Dermaptera, but of a Hemiptera because it has four to five longitudinal veins and a probable clavus. More astonishing, Bechly (1998) restudied the alleged Odonata larva named *Cordulagomphus santanensis* Carle & Wighton, 1990 (Lower Cretaceous, Crato Formation, Brazil) and reattributed it to the Dermaptera. Pike (1994) mentioned an undescribed nor figured Dermaptera from the Upper Cretaceous amber of Grassy Lake (Alberta, Canada). Andersen & Andersen (1996) figured, and later Rust (1999) cited and revised *Forficula paleocaenica* Willmann, 1990, from the Paleocene/Eocene (Fur Formation, Denmark). Because of the lack of visible detailed structures on the legs, genitalia, neck, etc., on these fossils, their attribution to the Forficulidae and to the genus *Forficula* Linné, 1758 is still doubtful. Lewis (1992, 1994) listed seven specimens of the family Forficulidae but figured only one in 1992 (i.e. the last abdominal segment with the cerci) from the Eocene (*c.* 49 million years) of the Klondike Mountain Formation (Washington, USA). The attribution of such a fragmentary fossil to a precise family remains dubious. Pribyl *et al.* (1996) mentioned four undescribed fossil Dermaptera from the Eocene Green River Formation (Colorado, USA). Weitschat & Wichard (1998) listed the Dermaptera families Forficulidae, Labiduridae Verhoeff, 1902 ("*Labidura*? sp.") and Pygicranidae Verhoeff, 1902 ("*Pygicrana*? sp.") from Baltic amber and figured two undescribed specimens (adult and larva). Zhang (1989) described an "*Anechura* sp. cf. *A. japonica*", redescribed *Allodahlia shanwangensis* Zhou, 1986, and described a new genus with two new species *Apanechura asceta* and *A. ooides*. Later, Zhang *et al.* (1994) described the new genus and species *Hadanechura sisypha*. All these species are attributed to the Forficulidae and all come from the Miocene of Shanwang (Shandong Province, China).

Even with the addition of these 10 species, the fossil record of the Dermaptera remains incomplete, standing at 83 species, for about 2000 modern species (Sakai 1996). Furthermore, numerous fossils are poorly preserved; many of them are not described. Therefore, the origin and history of the modern families are still poorly known. Thus, the discovery of well preserved specimens in the lower Eocene amber (Paris basin) is of great systematic and phylogenetic interest.

SYSTEMATICS

Order DERMAPTERA de Geer, 1773

Family *incertae sedis*

REMARKS

The following new genus should be attributed to family Chelisochidae Burr, 1907 or Forficulidae Stephens, 1829.

Genus *Chelisoficula* n. gen.

TYPE SPECIES. — *Chelisoficula caussaneli* n. gen., n. sp.

ETYMOLOGY. — The generic name is an artificial combination of *Chelisoches* and *Forficula*, giving the name *Chelisoficula*. This is allowing, if necessary, the possibility to erect in the future a new family with this name.

DIAGNOSIS. — This genus has a unique combination of characters: second tarsal segments strongly extending below the third, from which they are deeply separated;

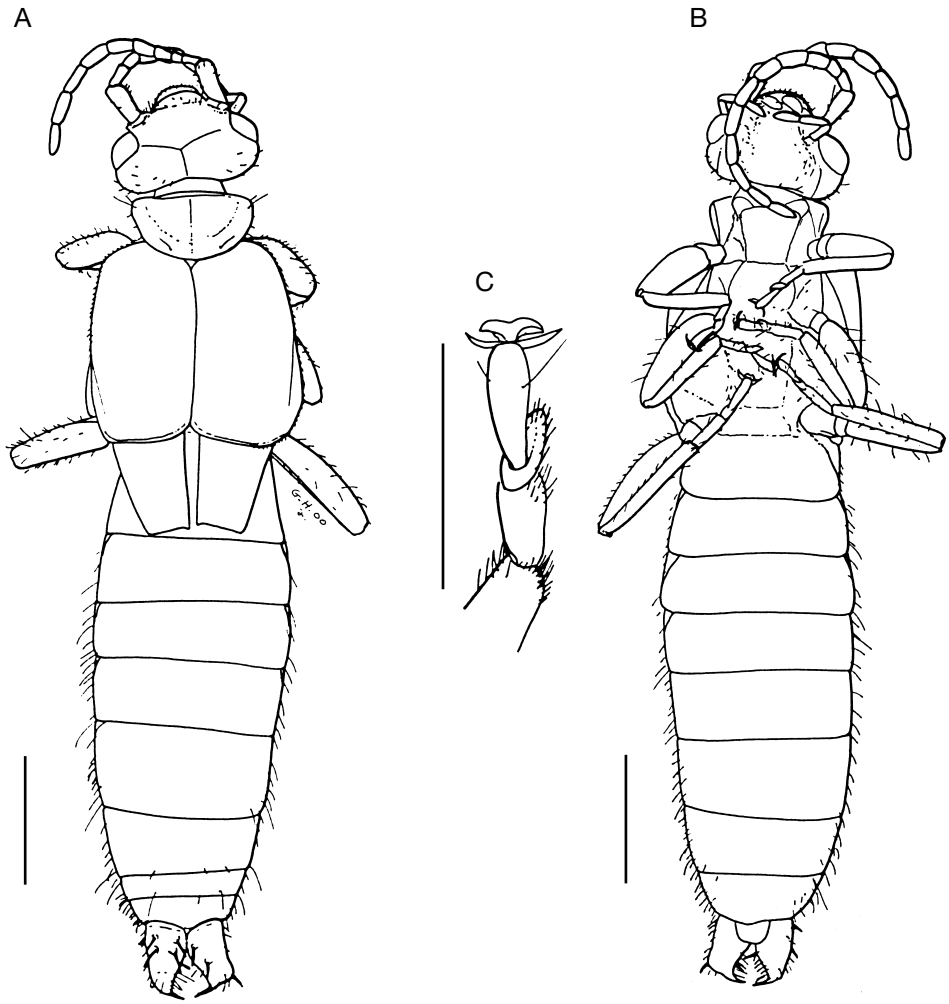

FIG. 1. — *Chelisoficula caussaneli* n. gen., n. sp., female holotype specimen PA 29; **A**, general habitus, in dorsal view; **B**, general habitus, in ventral view; **C**, foreleg tarsi, in dorsal view. Scale bars: A, B, 1 mm; C, 0.5 mm.

tarsal claws strong and separated by a large arolium; apex of cercus strongly curved and making an angle of 90° with the inner margin of the cercus; structure of the female cerci very particular, with numerous spines composed of long and strong setae, in the centre of tubercles (autapomorphy, unique character among the Dermaptera).

Chelisoficula caussaneli n. sp.
(Figs 1-5)

TYPE MATERIAL. — Female holotype specimen PA 29, male paratype specimen PA 205, both specimens mounted in Canada balsam, in collection De Ploëg and Indivision Langlois-Meurine, deposited in Muséum national d'Histoire naturelle, Paris. Specimens collected in Le Quesnoy all bear the letters PA for Paris (meaning Paris basin), the following number is the ordinal number in the collection.

ETYMOLOGY. — Named after the late Professor Claude Caussanel, former director of the Laboratoire d'Entomologie du Muséum national d'Histoire naturelle de Paris and a well known specialist of Dermaptera.

TYPE LOCALITY. — Le Quesnoy, Chevrière, region of Creil, Oise department, France.

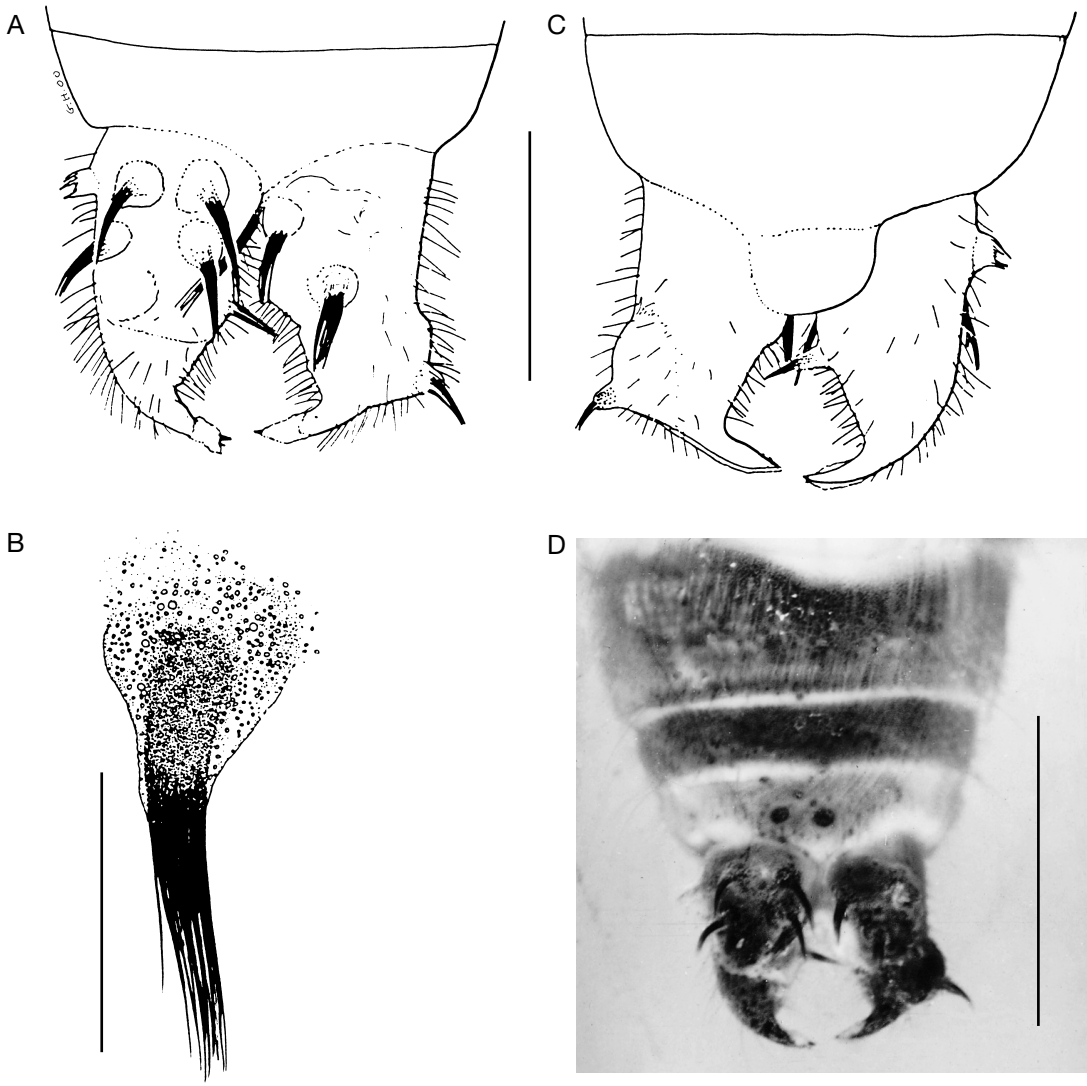

FIG. 2. — *Chelisoficula caussaneli* n. gen., n. sp., female holotype specimen PA 29; **A**, cerci, in dorsal view; **B**, detail of a spine of the cerci; **C**, cerci, in ventral view; **D**, cerci. Scale bars: A, C, 0.5 mm; B, 0.1 mm; D, 1 mm.

GEOLOGICAL AGE. — Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal. We have demonstrated that the amber is autochthonous and very different from the Baltic amber in age, chemical composition and origin (Feugueur 1963; De Ploëg *et al.* 1998; Nel *et al.* 1999).

STATE OF PRESERVATION. — Both holotype and paratype are complete very well preserved specimens in clear pieces of amber. Numerous small air bubbles surround the cerci of the holotype.

DESCRIPTION

Female holotype specimen PA 29 (Figs 1-3)

Body about 8.0 mm long, including the cerci, 0.72 mm long; body dark yellow; head prognathous, 1.2 mm wide, 0.86 mm long; eyes 0.3 mm wide, slightly smaller than the distance between them and the back of the head; antenna divided into 12 smooth segments, all of equal

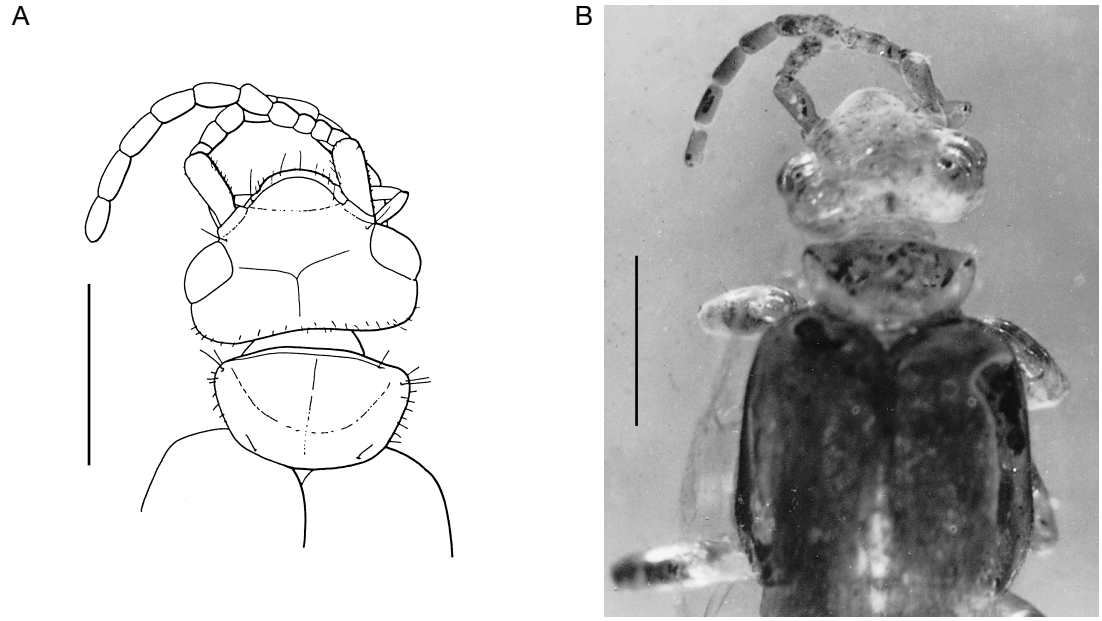

FIG. 3. — *Chelisoficula caussaneli* n. gen., n. sp., female holotype specimen PA 29, head and thorax, in dorsal view. Scale bars: 1 mm.

length from the third to the apex; antennal scape three times longer than wide; second antennal segment small, shorter than the third; occiput slightly concave with the angles well rounded; frontal and occipital sutures not visible; labial and maxillary palps visible and similar to those of a modern Dermaptera (see Albouy & Caussanel 1990); mandibles not visible; pronotum transverse, 1 mm wide and 0.6 mm long, slightly broader than long, with anterior part slightly convex and posterior part semi-circular; one strong setae at each anterior angle of the pronotum, other setae on the outer margin; tegmina strongly bulging, with its anterior margin rounded leaving place to a small equilateral scutellum, posterior margin slightly concave; hindwings clearly visible, covering the second and third abdominal segments; thoracic sternites similar to those of modern Dermaptera: Forficulidae, i.e. prothoracic sternite smaller than the others, with a posterior constriction and a lateral carina anteriorly, mesothoracic sternite nearly quadrangular; metathoracic sternite as long as the pro- and mesothoracic sternites together, not posteriorly concave (Waller *et al.* 1999); forelegs slightly smaller than median and hindlegs; femora bearing no dorsal or ventral carina; second tarsal segments not bilobed and strongly extending below the thirds, from which they are deeply separated (Fig. 1C); all tarsal claws stout and separated by a large arolium; abdomen progressively narrowed; eight abdominal segments; last visible segment 0.3 mm long and 1.0 mm wide, wider than long; tegument of abdomen punctuated, with no dorso-lateral tubercle; numerous visible setae on the posterior edges of the segments; pygidium not visible, probably absent; two thirds of total length of inner margin of cerci straight; apex of cerci strongly curved, making an angle of 90° with the inner margin; cerci covered by a tegument-like material from which emerge about 10 tubercles, on their whole surface, except the apical parts (Fig. 2A, C, D); in the centre of each tubercle, presence of a thick and long spine made of agglutinated setae, apically separated (Fig. 2B). We have no argument if it was movable or fixed. At low magnification, these spines appear like "normal" spines, i.e. very strong and stout. When

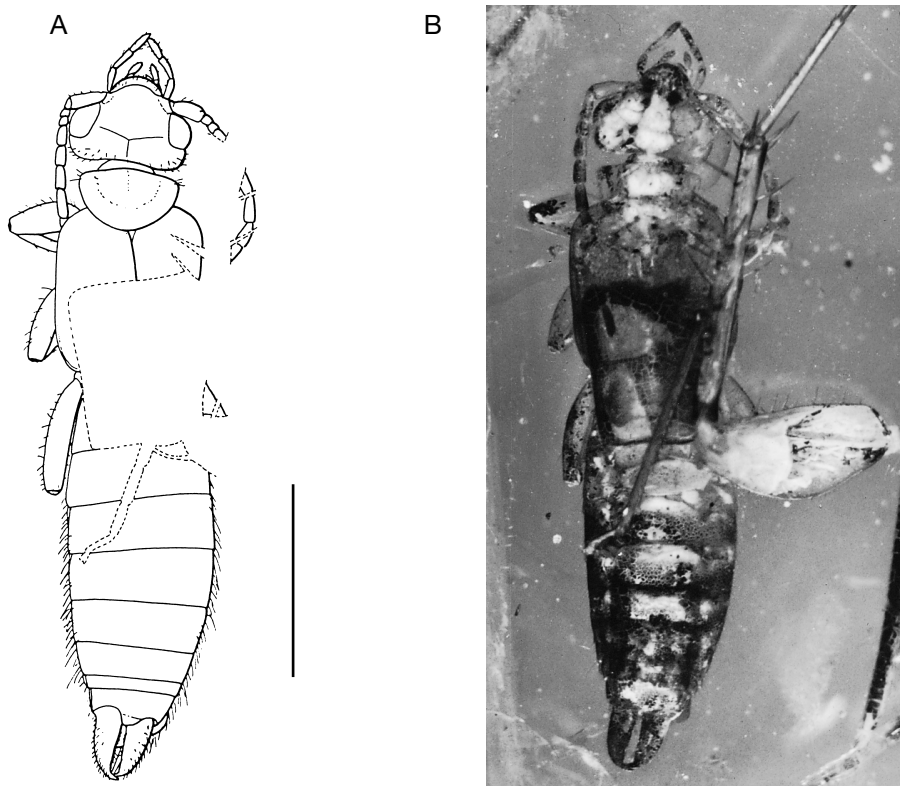

FIG. 4. — *Chelisoficula caussaneli* n. gen., n. sp., male paratype specimen PA 205, general habitus, in dorsal view. Scale bar: 2 mm.

seen at higher magnification, these spines appear as a set of thinner hair, agglomerated and approximate. The cerci bear also numerous long single setae. The last abdominal sternite bears two dark spots, which may correspond to remnants of spines like those of the cerci.

Male paratype specimen PA 205 (Figs 4; 5)

Body about 8.0 mm long, including the cerci, 0.8 mm long. The characters not visible on the female holotype and differences with it are as follows: the two apical teeth of the mandibles are clearly visible and sharp; neck of forficuloid type, i.e. posterior lateral sclerite enlarged, postero-lateral sclerite completely reduced, posterior ventral sclerite enlarged and joining prosternum (Steinmann 1986); nine visible abdominal segments; cerci identical to those of the female, but crossing and with numerous small denticles on their inner margin (Fig. 5C, D); cerci covered by no special tegument-like material; cerci bearing no tuft of long setae or strong spines, except for two small apical spines, that could be homologous to the female spines; male genitalia partly exposed; only one genital lobe visible, from which the virga is clearly extruded; the two parameres seem to be visible at the base of the lobe.

DISCUSSION

All the visible differences between the two specimens are sexual characters. The main difference is the presence of strong spines on the female cerci. This unique character justifies by itself the creation of a new genus and species.

The phylogenetic relationships between the different families of Dermaptera remain very controversial. We discuss the possible phylogenetic relationships of *Chelisoficula* n. gen. after the different existing classifications.

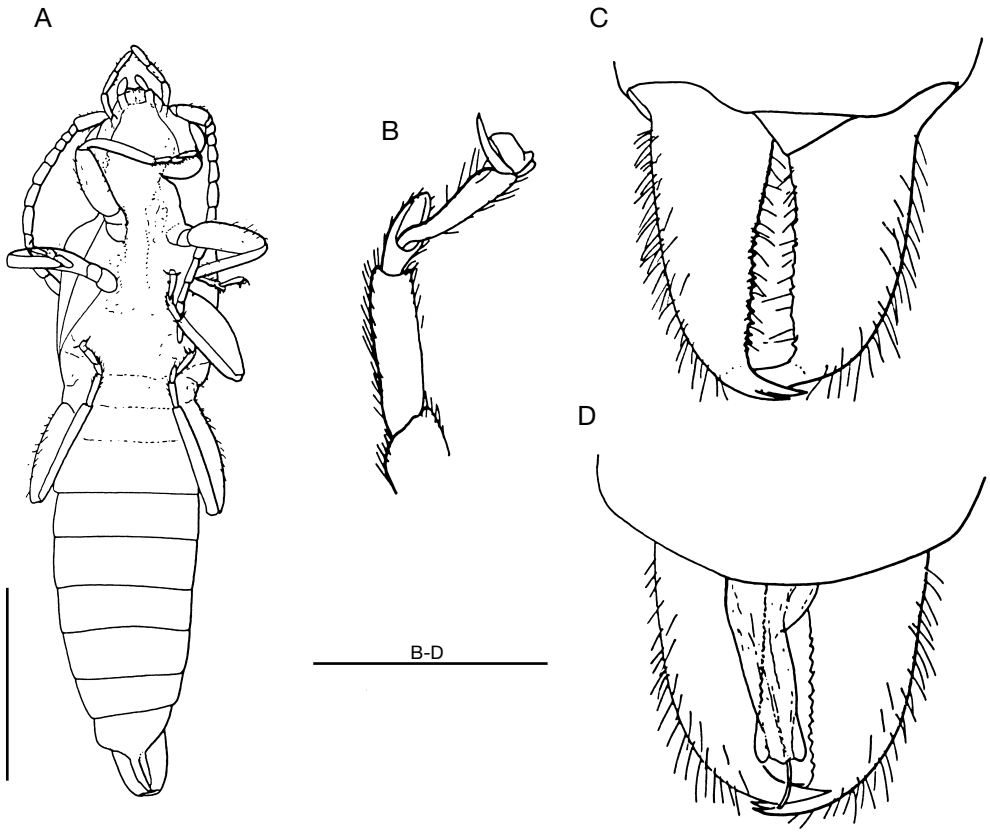

FIG. 5. — *Chelisoficula caussaneli* n. gen., n. sp., male paratype specimen PA 205; **A** general habitus, in ventral view; **B**, foreleg tarsi, in dorsal view; **C**, cerci, in dorsal view; **D**, cerci, in ventral view. Scale bar: A, 2 mm; B-D, 0.5 mm

Steinmann (1986), on a strict systematic point of view, proposed to divide the Dermaptera into two suborders, i.e. Catadermaptera and Eudermaptera, on the basis of the male genitalia: bilobate for the first suborder and with only one lobe for the second. Thus at least one of these suborders (Catadermaptera) can be suspected to be paraphyletic. *Chelisoficula* n. gen. probably has only one lobe, which is currently considered as the derived state. It would belong to the Eudermaptera (= Labiidae + Chelisochidae + Forficulidae). Within this group, considering the key of the families proposed by Steinmann (1990), *Chelisoficula* n. gen. would belong to the Forficulidae because of its reduced number of antennal segments, as well as in the Chelisochidae because of its unilobed tarsal segment.

After Popham (1965, 1985) and Albouy & Caussanel (1990), *Chelisoficula caussaneli* n. gen., n. sp. can be excluded from the Pygidicranidae because of its neck of forficuloid type. It would belong to the group of families Forficuloidea (= [(Apachyidae + Labiduridae) + (Chelisochidae + Forficulidae)] *sensu* Popham 1985 and *sensu* Albouy & Caussanel 1990). After Albouy & Caussanel (1990), it would belong more precisely to (Chelisochidae + Forficulidae), because of its second tarsal segments strongly prolonged below the third. In the Labiduridae *Allosthetus* Verhoeff, 1903, the second segments are prolonged below the third, but in *Allosthetus*, the third segments are much longer than the seconds, unlike in *Chelisoficula* n. gen. and (Chelisochidae + Forficulidae). Also, the second segments of

Allosthetus are not as long as in Chelisochidae Burr, 1907 and *Chelisoficula* n. gen.

Also, *Chelisoficula* n. gen. would be related to the Forficulidae because it has less than 13 antennal segments. The reduced number of antennal segments (between 10 and 16) is supposed to be an apomorphy of the Forficulidae, after Popham (1985). Nevertheless, the Chelisochidae *Chelisochella superba* (Dorhn, 1865) may have 17 antennal segments (pers. obs.). Steinmann (1983, 1993) indicated that the number of antennal segments greatly varies in Chelisochidae, i.e. 11 for *Hamaxas singhi* Kapoor, 1966, 14 for *H. bidentatus* Ramamurthi, 1965, 15 for *Schizoproreus delicatulus* (Burr, 1911), 16 for *Adiathetus glaucopterus* (Bormans, 1888), and 36 segments for *Genitalata mahajani* Kapoor, 1974. Steimann (1983) added that the number of segments varies between 15 to 20 in *Chelisoches* Scudder, 1876. Thus, the value of this character remains dubious.

The second tarsal segment deeply separated from the third is a character supposed to be only present in the Forficulidae. Hovewer it occurs in the chelisochid *Proreus simulans* (Stål, 1860) (pers. obs.). Thus the value of this character is also dubious.

The second tarsal segment bilobate is only present in Forficulidae (+ the Pygicranidae *Tagalina*) (Steinmann 1986). Thus it is probably a synapomorphy of the modern Forficulidae, even if its presence in *Tagalina* suggests that it can be subject to convergency. Consequently, if attributed to the Forficulidae, *Chelisoficula caussaneli* n. gen., n. sp. could be in a basal position within this group. Furthermore the second tarsal segment being very long is a character only present in the Chelisochidae, and is probably apomorphic.

Chelisoficula caussaneli n. gen., n. sp. has very well developed arolia, which could be a plesiomorphic state, as it is present in several genera of the Pygidicranidae Verhoeff, 1902 (*Echinosoma* Audinet-Serville, 1839, *Bormansia* Verhoeff, 1902, *Diplatys* Audinet-Serville, 1831, *Haplodiplatys* Hincks, 1955, *Lobodiplatys* Kirby, 1891; see Giles 1963; Waller *et al.* 1999), which is supposed to be the most basal family after Popham (1985). Within the Forficuloidea *sensu* Popham (1985), the arolia are absent in (Chelisochidae + Forficulidae), but present in Apachyidae Verhoeff, 1902 (at least in *Apachyus* Audinet-Serville, 1831) (Waller *et al.* 1999). The arolia are also absent in some Labiidae Burr, 1909 (at least in *Spongovostox cornutus* Brindle, 1973), but present in others (at least in the Geracinae *Nesolabia longicollis* Hincks, 1957). It is absent in some Labiduridae (*Forcipula* (*Decolyi*) *decolyi* Bormans, 1900) but present in *Allosthetus lombokianum* Verhoeff, 1904. Thus, the character "presence versus absence of arolia" is clearly homoplastic within the whole order.

If we admit the phylogenetic hypotheses of Popham and of Albouy & Caussanel, the three solutions: 1) *Chelisoficula* n. gen. as sister group of (Chelisochidae + Forficulidae); 2) *Chelisoficula* n. gen. as sister group of Chelisochidae; and 3) *Chelisoficula* n. gen. as sister group of Forficulidae, all imply two convergences. But these hypotheses are based on weakly polarized and/or homoplastic characters.

Sakai (1987, 1988) and Haas (1995) also considered the Forficulidae and Chelisochidae as sister groups. These authors differentiated these families on the basis of the second tarsal segment. More precisely, Haas (1995) considered that the "forficuloid-type lobed" or "chelisochoid-type lobed" are both derived from a primitive, "normal" type. *Chelisoficula* n. gen. would belong to the Chelisochidae after this hypothesis. This does not solve the problem related to the presence of arolia in *Chelisoficula* n. gen.

We consider that there is an unresolved trichotomy between the three taxa *Chelisoficula* n. gen., the Forficulidae and Chelisochidae. The discovery of *Chelisoficula* n. gen. suggests that the characters that are currently used in the classification and phylogenetic analyses of the Dermaptera are probably more homoplasic than previously thought.

Dermaptera family indet. 1
(Fig. 6A)

MATERIAL EXAMINED. — Specimen PA 2780, 1/3, in the same piece of amber with an adult Ephemeroptera and a Lepidoptera; in collection De Ploëg and Indivision Langlois-Meurine, deposited in Muséum national d'Histoire naturelle, Paris.

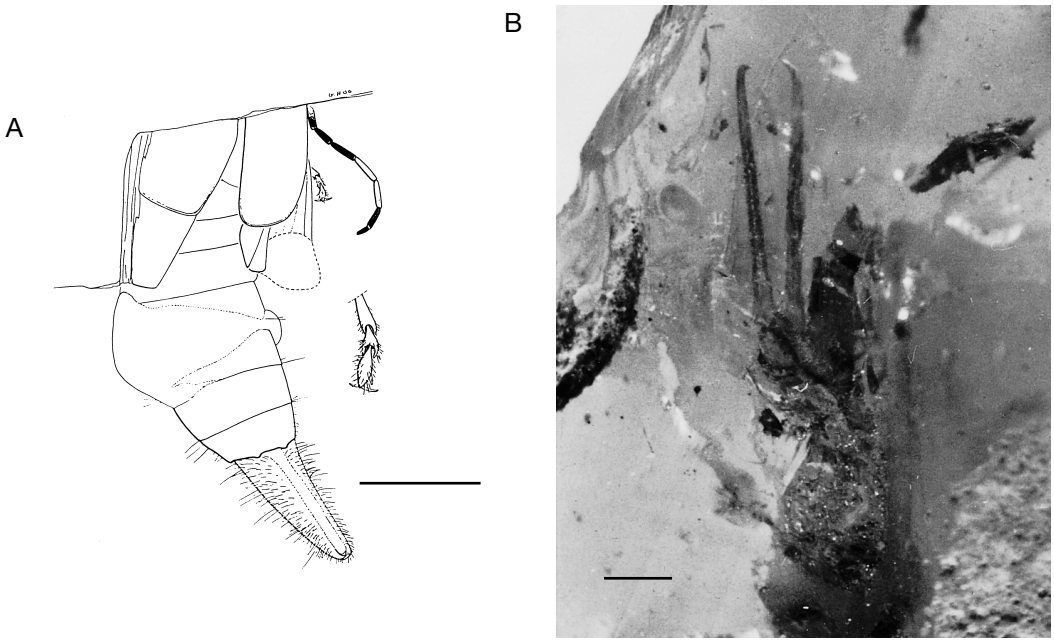

FIG. 6. — **A**, specimen PA 2780, 1/3 (Dermaptera family indet. 1), general habitus; **B**, specimen PA 2987 (Dermaptera family indet. 2). Scale bars: A, 2 mm; B, 1 mm.

TYPE LOCALITY. — Le Quesnoy, Chevrière, region of Creil, Oise department, France.

GEOLOGICAL AGE. — Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal.

STATE OF PRESERVATION. — This specimen is incomplete, the head and main part of thorax are missing. Three tarsal segments of a leg and five apical segments of an antenna are visible.

DESCRIPTION

Length of the abdomen 4.8 mm, width 2.3 mm; seven abdominal segment visible, thus it is probably a female; two very short extensions, 0.6 mm long, on the last abdominal segment, overlapping cerci; cerci long and narrow, 2.5 mm long, about 0.5 mm wide, crossing apically, curved upwards at the apex; only distal parts of tegmina preserved, with a darker strip along inner margin and posterior margin straight; hindwings present; antenna bicoloured: the two apical segments are dark; the two following ones are clear coloured, others are dark; tarsal segments pubescent, especially the first and the second; second tarsal segment not bilobate, weakly prolonged below the third, both being clearly separated; third tarsal segment short, in a form of enlarged club; no arolium.

DISCUSSION

The preserved parts of this fossil are very similar to those of the extant Dermaptera. It is most probably a female, thus difficult to attribute to a precise family, even if it was more complete. It clearly corresponds to a genus and species different from *Chelisoficula caussaneli* n. gen., n. sp. (cerci very different, second tarsal segment less prolonged below the third). It is probably not a chelisochid-forficulid type. It could correspond to a labiid-type but with no accuracy.

Dermaptera family indet. 2
(Fig. 6B)

MATERIAL EXAMINED. — Specimen PA 2987, in the same piece of amber with organic remains; in collection De Ploëg and Indivision Langlois-Meurine, deposited in Muséum national d'Histoire naturelle, Paris.

TYPE LOCALITY. — Le Quesnoy, Chevrière, region of Creil, Oise department, France.

GEOLOGICAL AGE. — Lowermost Eocene, Sparnacian, level MP7 of the mammal fauna of Dormaal.

DESCRIPTION

Only the two cerci with the five last abdominal segments are preserved; cerci narrow and relatively long, 3.8 mm long for a total length of 2.0 mm for the five distal abdominal segments; cerci straight, with the apices crossing; small teeth on the inner sides of cerci and few sparse setae.

DISCUSSION

It is not possible to determine whether this fossil is a larva or an adult. Nevertheless, this type of long and narrow cerci occurs in modern dermapteran families Labiidae or Forficulidae. The main interest of this fossil is to show that there is a third species of Dermaptera in the amber of this outcrop.

CONCLUSION

The presence of three very different Dermaptera in the lowermost Eocene suggests that the order was already very diverse at this time. Interestingly, these discoveries suggest that the separation of Dermaptera into Catadermaptera and Eudermaptera (*sensu* Steinmann 1986) is much more ancient, and probably occurred in the Lower Cretaceous or before.

Acknowledgements

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