Gregarious behaviour in Cretaceous earwig nymphs (Insecta, Dermaptera) from southwestern France

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ABSTRACT

The first earwigs in Early Cretaceous (latest Albian) amber from southwestern France are described and figured. The amber piece in question, ARC-240, contains a complete earwig nymph as well as three partial nymphs preserved in a single piece of fossiliferous resin from Archingeay (Charente-Maritime, France). The morphology of the nymphs is discussed in relation to their possible taxonomic placement as well as their developmental stage. The preservation of so many nymphs in a single piece is curious and comments about the gregarious nature of modern earwigs in relation to the fossil are provided.

MOTS CLÉS
Crétacé,
Albien,
Insecta,
Neodermaptera,
Dermaptera,
perce-oreilles,
fossiles,
soins maternels,
ontogénie,
comportement,
nymphes.

RÉSUMÉ

Comportement grégaire chez des nymphes de perce-oreilles (Insecta, Dermaptera) du Crétacé du Sud-Ouest de la France.
Les premiers perce-oreilles de l'ambre crétacé inférieur (Albien terminal) du Sud-Ouest de la France sont décrits et figurés. Une nymphe complète et trois nymphes partielles ont été découvertes fossilisées dans un même morceau d'ambre provenant du gisement d'Archingeay (Charente-Maritime, France). La morphologie de ces nymphes est discutée par rapport à leur possible positionnement taxonomique ainsi que leur stade de développement. La préservation d'autant de nymphes dans un même morceau d'ambre est curieuse, et des commentaires sont fournis sur la nature grégaire des perce-oreilles modernes par rapport aux fossiles.

INTRODUCTION

Earwigs (order Dermaptera) are "social" animals. Female earwigs care for their clutches of eggs and earliest stage nymphs (Günther & Herter 1974; Lamb 1976; Matzke & Klass 2005; Costa 2006). Nymphs of most earwigs typically remain with the mother as first instars but by the time they molt to the second instar their aggressiveness is manifest and they will attack or be attacked (only in some higher Neodermaptera, of the Metadermaptera [*sensu* Engel 2003; Engel & Haas 2007], do mother-nymph associations extend beyond the first instar). Thus, the gregarious association of most earwigs, and certainly in the more primitive lineages, is relatively short-lived after the eggs hatch, although some aggregative behaviour is documented for adults (e.g., Sauphanor & Sureau 1993). Nonetheless, during those days the mother is attentive and may even sit atop her brood as part of the defense of her young. Despite the limited biological data available for many earwig lineages, parental behaviour is apparently common across the order (Lamb 1976; Matzke & Klass 2005; Costa 2006).

The fossil record of earwigs is relatively scant, with most material deriving from a few deposits, particularly from the Tertiary (Wappler *et al.* 2005). Earwigs have been documented from a variety of Mesozoic deposits (e.g., Engel & Chatzimanolis 2005; Wappler *et al.* 2005), but relatively few have been discovered in Cretaceous ambers (e.g., Engel & Grimaldi 2004). It is therefore significant to report herein the discovery of a group of nymphal earwigs in Early Cretaceous (latest Albian) amber from southwestern France. Amber piece ARC-240 contains a nearly entire nymph (missing only the apical antennal articles) and three partial nymphs tightly packed together (Fig. 1A). Wappler *et al.* (2005) tabulated the fossil records of Dermaptera to which can be added the taxon here. In their numbering system the French amber earwigs would be placed as 34b and with the citation of Perrichot *et al.* (2007: as "Dermaptera indet."). In addition, record number 30 of Wappler *et al.* (2005) can be updated by the new placement of *Cretolabia* Popham, 1990 in its own subfamily, Cretolabiinae, by Engel & Haas (2007); to record number 100 can be added the citation of Martinez (1982); the Early Cretaceous species *Caririlabia berghoffi* Haas, 2007, *Cratoborellia gorbi* Haas, 2007, and *Kotejalabis haeuseri* Haas, 2007 can be added as records 31b, 31c, and 32b, respectively; and the Early Cretaceous (Albian) *Geosoma prodromum* Zhang, 1997 can be added as record number 32b, although this species is quite dubiously assigned to Dermaptera. The system of Dermaptera followed is that outlined by Engel & Haas (2007).

The systematics of immature earwigs sadly lags behind that of comparative studies based on adults. Frequently nymphs can only be positively identified to species when captured in association with adults, as such no attempt is made herein to establish new taxonomic names for these specimens although they assuredly represent a new species. It is greatly hoped that adult material that can be associated with these nymphs may eventually be recovered from the same deposits.

MATERIAL AND METHODS

The specimens treated herein were studied using an Olympus SZX12 Stereomicroscope and measurements made with an ocular micrometer. Photomicrographs were prepared by the author using a Nikon D1x digital camera attached to an Infinity® K-2 lens. The age and origin of the amber is discussed by Néraudeau *et al.* (2002) and its diversity summarized by Perrichot *et al.* (2007).

SYSTEMATICS

Order DERMAPTERA de Geer, 1773
Suborder NEODERMAPTERA Engel, 2003

Neodermaptera sp. indet.
(Fig. 1)

Dermaptera indet. – Perrichot *et al.* 2007: 218.

MATERIAL EXAMINED. — ARC-240 (Fig. 1); Archingeay-Les Nouillers, Charente-Maritime, southwestern France; Early Cretaceous, uppermost Albian (Néraudeau *et al.* 2002); deposited in the Muséum national d'Histoire naturelle, Paris.

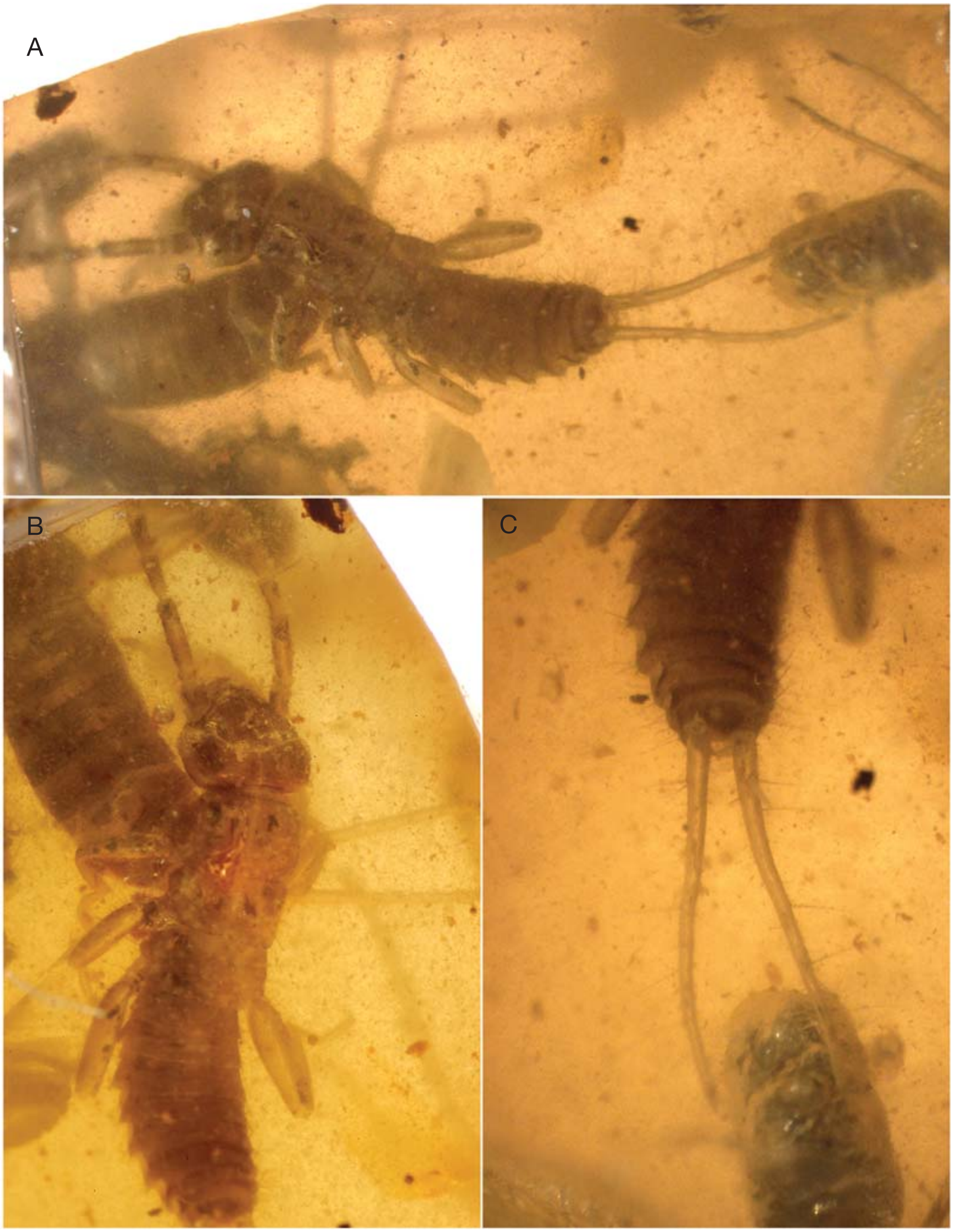

FIG. 1. — Neodermaptera nymphs (Labiduroidea?) in latest Albian amber from Archingeay-Les Nouillers, Charente-Maritime, southwestern France (ARC-240), length of primary nymph 2.41 mm, excluding cerci: **A**, view of most of amber piece showing primary nymph, as well as portions of two other nymphs (isolated cerci at extreme right), abdomen and leg fragments at extreme left) and shadow of third fragmentary nymph in background (upper right); **B**, detail of primary nymph excluding cerci; **C**, detail of abdominal apex and cerci of primary nymph (cercal length 1.25 mm). A, C, photo by V. Perrichot; B, photo by M. S. Engel.

DESCRIPTION

First instar (see Discussion): small earwigs, total length (excluding cerci) approximately 2.41 mm; integument faintly imbricate, without punctation, where evident brown, although very light brown on thorax, legs, and cerci; specimen is, however, largely cleared so this may not be indicative of coloration in life (see Fig. 1B). Head length 0.46 mm (as measured from posterior head margin to labral base), maximal width 0.56 mm; posterior border of head straight, posterior angles acutely rounded; Y-shaped coronal ecdysial cleavage line present, posterior longitudinal section short, much shorter than lateral sections. Compound eyes well developed, circular, separated from posterior margin of head by distance equal to compound eye length (compound eye length 0.13 mm); ocelli absent. Scape longer than wide (length 0.15 mm, width 0.1 mm) and longer than compound eye, pedicel wider than long (length 0.05 mm, width 0.075 mm), meriston (= first flagellar article) much longer than wide (length 0.3 mm, width 0.088 mm), second flagellar article longer than wide (length 0.18 mm, width 0.069 mm), third flagellar article identical to second flagellar article, longer than wide (length 0.18 mm, width 0.069 mm).

Pronotum broad, slightly wider than long, slightly narrower than head (length 0.37 mm, width 0.45 mm), corners acutely rounded; medial longitudinal furrow absent; opposing margins parallel, relatively straight. Mesonotum and metanotum more strongly transverse, each wider than long (mesonotal length 0.28 mm, width 0.47 mm; metanotal length 0.20 mm, anterior width 0.47 mm, posterior width 0.55 mm); posterior margin of mesonotum straight, posterior margin of metanotum weakly concave. Femora not compressed nor keeled dorsally or ventrally; metafemur 0.5 mm in length; tarsi trimerous; tarsal articles simple, second article not extended ventrally beneath succeeding articles nor broadened, all articles tubular and articulating at their apices; pretarsal ungues simple, slender; arolium absent.

Abdominal length 1.1 mm, maximal width 0.54 mm; lateral abdominal margins gently convex; terga transverse, wider than long, posterior margins relatively straight; ultimate tergum slightly longer than penultimate tergum, posterior margin weakly concave above cercal bases, medially weakly convex; pygidium apparently absent. Cerci long (length 1.25 mm), longer than abdomen, tubular and rounded (not trigonal in cross-section), relatively straight, simple, margins smooth, without dentition, crenulations, or serrations, gently tapering in width along length to acutely rounded apices, apices not curved inward (Fig. 1C), cercal bases widely separated.

Setae generally sparse, simple, short, and lightly fuscous except some moderately long, stiff setae on lateral margins of abdominal terga and scattered elongate, stiff setae on cerci (Fig. 1C).

DISCUSSION

Perhaps the greatest significance of ARC-240 is the number of nymphs present in such a tiny fragment of amber (the piece measures approximately 3.5 × 5 × 2 mm). The only means by which so many of these frequently aggressive animals would have been entombed together in a minute fragment is if there had been some association of the individuals in life. As noted, after hatching the first instar nymphs remain clustered together and with their mother. The tight association of these nymphs indicates that they were likely relatively newly hatched and were part of a brood from a single mother who was caring for them. Prior to oviposition all earwig females construct a nest, consisting of a short tunnel or chamber, or in more primitive families simply a shallow trough in the soil. It is possible that these nymphs were clustered together in such a trough and became entrapped when resin flowed over their nest. Unfortunately, the remainder of the brood and the adult female were either spared this fate or were not recovered when the amber was excavated.

Staging the nymphs is a challenge but these are likely first instars. The great length of the meriston (first flagellar article) relative to the lengths of the second and third flagellar articles is indicative of a first instar nymph (Günther & Herter 1974; Matzke & Klass 2005). In addition, the shape of the basal flagellar articles is representative of the first instar. In first instars the basal flagellar articles are relatively more elongate in form and have not yet assumed the compact, transverse form seen in the latter instars and the adult (Günther & Herter 1974; Brindle 1987). This is also in accordance with the occurrence of the nymphs clustered together which would be exceedingly unlikely for more aggressive and even cannibalistic later stages.

These nymphs can be readily recognized as belonging to the suborder Neodermaptera on the basis of their trimerous tarsi and absence of ocelli. More primitive lineages of earwigs have pentamerous tarsi and possess ocelli, among other notable plesiomorphies (see Engel 2003; Grimaldi & Engel 2005). The structure of the tarsi, with unmodified, simple, rounded tarsal articles excludes placement among the Forficulidae Latreille, 1810 and Chelisochidae Verhoeff, 1902. Among more primitive Neodermaptera, however, it is challenging to place ARC-240 taxonomically. Unfortunatly, the ventral surface is entirely obscured by particules and the amber cannot be prepared closer to the complete specimen owing to the position of other inclusions in the piece. Thus, the structure of the ventral cervical sclerites (which separates protodermapterans from epidermapterans) cannot be discerned. Nonetheless some comment on the possible affinities of these nymphs can be made. For example, the profemora are not keeled suggestive of a placement more derived than pygidicranids.

The non-annulated (also often called incorrectly "unsegmented") cerci exclude placement in the basal families Diplatyidae Verhoeff, 1902 and Karschiellidae Verhoeff, 1902. In these families the nymphal cerci are long, multi-annulated, and filiform and the basal cercal article alone develops into the forceps of the adult. Thus, ARC-240 is more derived than the Karschiellidae and Diplatyidae. The cerci are, as is almost universal for Neodermaptera (except for the families just noted), non-annulated but are not forceps-like. Many neodermapteran nymphs have elongate, thin, and unornamented (i.e. no dentition or basal expansions) cercal forceps, the cerci being more filament-like. Nonetheless, the cerci often still have inner margins in alignment and each a slight apical point that minutely curves inward to meet the corresponding apex of the other cercus giving them a weak, clasper-like design. During the ontogeny of the nymphal instars the cerci gradually become more and more completely developed into true cercal forceps (e.g., Matzke & Klass 2005). This is not the case in the nymphs recorded here where the cerci are tubular and lack any hint of a forceps-like design, instead resembling the cerci of Hemimeridae Sharp, 1895 or Arixeniidae Jordan, 1909. The fossils do not, however, belong to either of these epizoic, parasitic families. Hemimerids and arixeniids are viviparous and there is apparently no maternal care, with the immatures immediately dispersing from the mother. The hemimerids are largely paedomorphic as adults and, therefore, resemble their immatures which are broad, flattened (particularly the head) earwigs with short broad abdomens and thin, elongate, non-annulated cerci (Vosseler 1907; Günther & Herter 1974). The legs are relatively short and stout for clinging to their rat hosts, and the basal tarsomeres have pads not found in the fossil or most other earwigs (Haas & Gorb 2004; Beutel & Gorb 2006). The antennae are similarly short, with few articles. The arixeniids are similarly peculiarly modified earwigs whose immatures generally resemble the adults. Moreover, crown-group arixeniids which are confined to bats are likely of Tertiary origin since their hosts did not appear until that time. Regardless, for all of the above reasons ARC-240 is not representative of either of these highly derived families.

While the absence of arolia may be of interest, in nymphs it is of less value than its presence/absence in adults. Nymphal instars typically lack arolia even when the adult possesses such structures (e.g., *Tagalina papua* (Bormans *in* Burr, 1903); Matzke & Klass 2005). Thus, the absence of arolia in these early nymphs is not necessarily indicative of any particular placement. Moreover, the absence of arolia is widespread throughout the order and may be too labile to be of considerable taxonomic value.

Further placement of ARC-240 becomes more problematic. ARC-240 does not appear to represent a primitive form of Spongiphoridae Verhoeff, 1902 as the pygidium is not visible and the inner margins of the cerci are not crenulated or armed with some form of weak dentition. Placement in Anisolabididae Verhoeff, 1902 also seems unlikely owing to the more slender cerci, more distinctly separated at their bases and in the first instar the cerci are typically quite short. The fossil appears to represent a primitive form of Labiduridae owing to the small or indistinct pygidium and long cerci in the first instar. Labidurids are already documented from approximately the same time period (Engel & Grimaldi 2004). Despite these details, conclusive assignment of ARC-240 cannot be made until such time as material of later instars or, ideally, an adult is discovered.

The phylogenetic distribution of taxa studied for parental behaviour – from pygidicranoids to forficuloids – indicates that maternal care is likely a groundplan feature of Neodermaptera. Unfortunately, the extinct, basal suborders of Archidermaptera and Eodermaptera (the latter sister to Neodermaptera) are unknown in terms of their behaviour and it cannot be assumed that such gregarious associations are therefore characteristic of Dermaptera as a whole (i.e. including the extinct suborders). Nonetheless, the presence of neodermapterans as long ago as the earliest Cretaceous (e.g., Wappler *et al.* 2005) indicates that such maternal behaviours are likely of similar age, and both the suborder and the correlated behaviour may have originated in the latest Jurassic.

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