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***Apachyus madseni* (Dermaptera: Apachyidae) sp. nov. from the Ypresian Fur Formation of Denmark: the first fossil record of the enigmatic earwig family Apachyidae**

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Abstract

We describe *Apachyus madseni* sp. nov. based on an almost complete fossil from the Fur Formation in northwestern Denmark. The fossil is the second Dermaptera species described from the early Ypresian Fur Formation and the first fossil representative of the enigmatic family Apachyidae. Today, Apachyidae are restricted to Central Africa, and the Orient from southern India to the Philippines and northern Australia. The new fossil thus represents not only a new addition to the fossil mo-clay fauna, but also a considerable expansion of the historical biogeographical ranges of Apachyidae.

Keywords: Neodermaptera, Post-Paleocene-Eocene Thermal Maximum, subtropical-paratropical, range expansion

Introduction

Recent decades have seen an increased focus on the rich record of fossil insects found in the earliest Ypresian Fur Formation in northwest Denmark (e.g., Madsen & Nel, 1997; Rust, 1999; Engel & Kinzelbach, 2008; Petrulevičius *et al.*, 2008; Rust *et al.*, 2008; Zessin, 2011, 2017, 2019; de Jong, 2016; Heikkilä *et al.*, 2018; Klopfstein, 2022; Simonsen, 2022, 2024; Archibald *et al.*, 2023; Dietrich & Perkovsky, 2023; Legalov *et al.*, 2024; Makarkin & Perkovsky, 2024; Prokin *et al.*, 2024; Shaw *et al.*, 2024). This activity has expectedly resulted

in considerably increased knowledge in Eocene Odonata, Orthoptera, Auchenorrhyncha, Neuroptera, Coleoptera, Ichneumonidae and Lepidoptera.

One insect order that has to some extent avoided this surge in taxonomic knowledge from the Fur Formation is the Dermaptera, commonly known as earwigs. Willmann (1990) described *Forficula paleocaenica* Willmann (Forficulidae)—which is still the oldest known representative of the family—based on 13 specimens representing both sexes. Rust (1999) mentioned more than 90 fossils, which he—as far as the preservation state allows identification—assigned to *F. paleocaenica*. Also from the Western Palearctic Nel *et al.* (1994) described *Forficula paleoligura* Nel, Albouy, Caussanel & Jamet from the Oligocene of southeast France, described without formally naming two species of *Forficula* and one Forficuloidea (gen. et sp. indet), and listed a further five species of *Forficula*, one potential *Pygidicrania* (Pygidicranidae), one potential *Labidura* (Labiduridae), and one family indet. from late Eocene Baltic amber (see also Weitschat & Wichard, 1998). Nel *et al.* (2003) described *Chelisoficula caussaneli* Nel, Waller, Albouy, Meiner, de Ploëg from the early Eocene Paris basin amber, and describe without naming a further two potential species in Paris amber. Wappler *et al.* (2005) erected one additional species of *Forficula*, *F. kotejai* Wappler, Engel & Haas, and described without formally naming two Neodermaptera, all from the German middle Eocene Eckfeld maar deposits, which is *ca.* 11 My younger

than the Fur Formation (Wappler *et al.*, 2005). Outside the Western Palearctic Cockrell (1925) described and illustrated a single specimen from an incomplete pair of fossil cerci (forceps) from Argentina. Nel *et al.* (1994) listed ten species of the genus *Labiduromma* Scudder (Labiduridae) from the Eocene/Oligocene American Florissant Formation. More recently Chatzimanolis & Engel (2010) transferred the genus *Laasbium* Scudder from Coleoptera to Dermaptera (family incerta sedis), and name six new genera for most of the *Labiduromma* species listed by Nel *et al.* (1994)—see Chatzimanolis & Engel (2010) for details. The diversity of Dermaptera from the Jurassic and Cretaceous is even higher as a number of species and genera from several families are known from various continents including Asia (e.g., Engel & Grimaldi, 2004, 2014; Zhao *et al.*, 2010a, b; Engel, 2011; Zhao *et al.*, 2011; Nel *et al.*, 2012; Yang *et al.*, 2015; Ren *et al.*, 2017, 2018; Xiong *et al.*, 2021; Peng *et al.*, 2024), Europe (Perrichot *et al.*, 2011; Engel & Perrichot, 2014), and South America (Engel & Chatzimanolis, 2005).

Here we describe a new species of Dermaptera from the Fur Formation. We assign the fossil to the genus *Apachyus* Serville in the family Apachyidae. The new taxon represents the first fossil record of the family, which today comprise two species-poor genera distributed in the Indian Subcontinent, SE Asia, Australia and central Africa (e.g., Brindle, 1965).

Geological setting

The new taxon was collected from a calcareous concretion in the lower part of the Silstrup Member of the Fur Formation. The Fur Formation is *ca.* 60m thick, marine diatomaceous unit (Pedersen & Surlyk, 1983) that crops out in several coastal cliffs in the Western Limfjord area of northern Denmark, especially on the two islands of Mors and Fur. Lithologically, the Fur Formation is dominated by shells (or frustules) from siliceous algae, principally diatoms and silicoflagellates, but does also contain clay and volcanic ash particles, which settled on the sea floor 55 million years ago during the initial rifting of the northernmost Atlantic Sea between Norway, Greenland and Scotland (Larsen *et al.*, 2003). The sea bottom was characterised by a significant decay of organic remains—mainly from dead algae—and a poor water exchange. This implied that the oxygen content usually was very low near the sea floor, resulting in abundant and extremely well-preserved fossils. The climate was initially paratropical during the Paleocene-Eocene Thermal Maximum (PETM) strata of the Stolleklin Clay deposited immediately below the Fur Formation

but became mainly subtropical or slightly colder during the deposition of the Fur Formation (e.g., Stokke *et al.*, 2020). Despite the marine palaeoenvironment, transported terrestrial organisms are common together with marine organisms including e.g., algae, fishes, invertebrates, and reptiles (including birds). Fossil insects make up the most common terrestrial component, but also plants and nearly complete bird skeletons occur in smaller numbers (see reviews by Pedersen *et al.*, 2012; Madsen & Rasmussen, 2021).

Material and methods

We examined a single, mostly complete fossil, part and counterpart, from a calcareous concretion of the Fur Formation in northwest Denmark using an Olympus SZ60 stereo microscope. Photographs were taken using a Canon EOS 5DII camera and a Canon EF 100 Macro lens. To enhance contrast a droplet of deionized water was placed on the fossil prior to examination and photography. Terminology follows Rentz & Kevan (1991) and Haas & Kukalová-Peck (2001).

Systematic palaeontology

Order Dermaptera de Geer, 1773

Suborder Neodermaptera Engel, 2003

Family Apachyidae Verhoeff, 1902

Genus *Apachyus* Serville, 1831

Apachyus madseni Simonsen & Rasmussen, sp. nov.

(Fig. 1)

<http://zoobank.org/urn:lsid:zoobank.org:act:C9F091A7-540C-4AD1-96E2-078CAEF5C7C7>

Material. Holotype MM-5025, part and counterpart: head, thorax and abdomen preserved. Found in a calcareous concretion situated between ash layers +25 and +30, collected by Henrik Madsen, 2016, Ejerslev mo-clay pit (56°55'35"N, 8°54'38"E), deposited in the Fossil- and Mo-clay Museum, Museum Mors.

Etymology. An eponym in honour of the collector of the fossil, Henrik Madsen, who has been collecting fossils (particularly insects) in the Fur Formation of Denmark for more than three decades.

Diagnosis. *Apachyus madseni* sp. nov. can be distinguished from all other *Apachyus* species by the broad and short squamopygidium with a smooth, weakly convex distal margin.

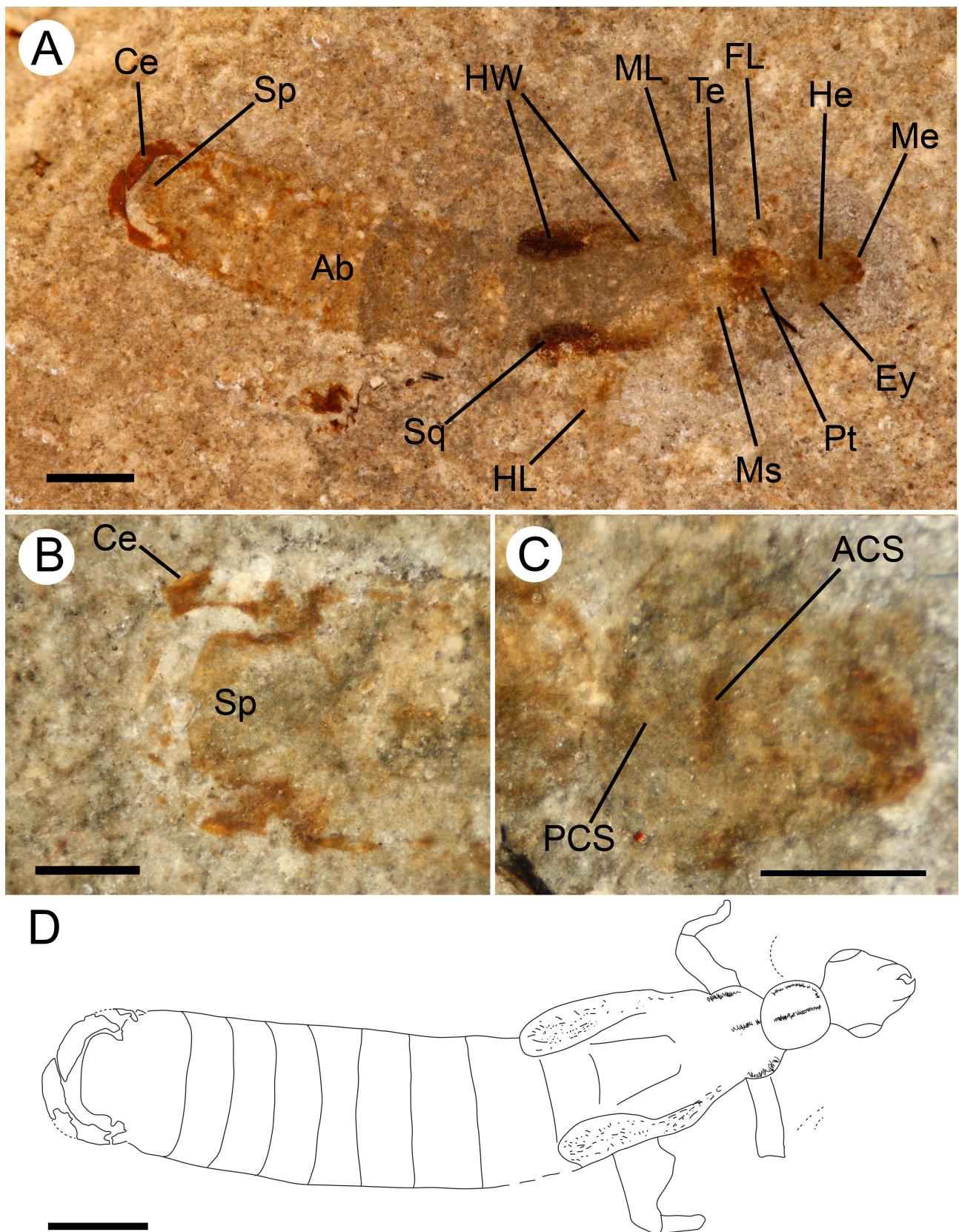


FIGURE 1. *Apachyus madseni* sp. nov. holotype (MM-5025). **A**, Photograph of the main part. **B**, Detail of the counterpart illustrating the squamopygidium (Sp). **C**, Detail of the main part illustrating the head with the anterior cervical sclerite (ACS) and posterior cervical sclerite (PCS). **D**, Drawing from the main part, with added interpretations from the counterpart. Abbreviations not already mentioned: Ab, abdomen; Ce, cercus; Ey, eye; FL, foreleg; He, head; HL, hind leg; HW, hind wing; Me, mandible; ML, midleg; Ms, mesothorax; Pt, prothorax; Sq, squama; Te, tegmina. Scale bars: 2 mm (**A**, **D**), = 1 mm (**B**, **C**).

Type locality and horizon. Ejerslev mo-clay pit, Denmark. Fur Formation, Silstrup Member.

Description. Total length (excluding cerci): 18.8 mm. Head subtriangular, prognathous with clearly preserved mandibles; antennae not preserved; eyes discernible; anterior cervical sclerite well preserved and small; posterior cervical sclerite poorly preserved but appearing larger than the anterior cervical sclerite. Pronotum well preserved, sub-circular with longitudinal groove, femur and tibia of forelegs poorly preserved. Mesothorax preserved with femur and tibia of both midlegs poorly preserved, tegmen poorly preserved but discernible, subrectangular. Metathorax with femur of right hindleg poorly preserved. Hind wings preserved with squama (Engel, 2011) clearly visible. Abdomen well preserved with most segments discernible; segment 10 well preserved and broad, with broad, subrectangular and smooth terminal squamopygidium obscuring the pygidium; cerci well preserved, simple, arcuate/broad sickle-shape, widely separated at base, strongly curved around the tip of the abdomen.

Remarks. The apparently enlarged posterior cervical sclerite places the fossil in the infraorder Epidermaptera (e.g., Engel, 2003). The squamopygidium is a diagnostic character for the family Apachyidae (Brindle, 1965; Haas, 1995; Cassis, 2010) and its presence places the fossil univocally in that family. Similarly, the arcuate cerci that curves strongly around the squamopygidium are similar to most of the species in the two constituent genera of the family: *Apachyus* and *Dendroiketes* Burr. Brindle's (1965) contribution is the latest taxonomic treatment of the family Apachyidae—although two species have since been described in *Apachyus* (Srivastava, 1976; Steinmann, 1977)—and his only diagnostic character to separate the two genera is the shape of the pronotum. Furthermore, there is no phylogenetic analysis of the family available, and we therefore do not know whether the two genera are monophyletic or if *Dendroiketes* (the youngest name) should be synonymized under *Apachyus*. However, the round and subcircular pronotum in *A. madseni* sp. nov. does not correspond to the pronotum in *Dendroiketes*, which according to Brindle (1965) is strongly transverse. In *Apachyus*, it is quadrate or longer than broad (Brindle, 1965; Srivastava, 1976, 2013; Steinmann, 1977), or subcircular as in *A. baloghi* (Steinmann, 1977: fig. 1d), which corresponds better to the pronotum in *A. madseni* sp. nov.. We therefore tentatively place the new species in *Apachyus* pending a formal phylogenetically based revision of Apachyidae.

Discussion

Apachyus madseni sp. nov. is the second species of

Dermaptera described from the Fur Formation, and the first fossil representative of Apachyidae described globally. Today the family is comprised by 15 current species in two genera (13 in *Apachyus* and two in *Dendroiketes*) (Brindle, 1965; Srivastava, 1976, 2013; Steinmann, 1977) as well as *A. madseni* sp. nov.. The current species are distributed in Central Africa (three species), and from India to the Philippines and Australia (the remaining species) (references above). The discovery of *A. madseni* sp. nov. in the Fur Formation thus represents a considerable range expansion of Apachyidae, demonstrating that the current distribution of the family is not necessarily indicative of its past distribution or biogeographical origin. In 1922, Henriksen interpreted the lowermost Eocene insect fauna of the Fur Formation as tropical (Henriksen, 1922). Even if more recent studies favour a palaeoenvironment varying from paratropical to subtropical or slightly colder (see above), it is not surprising if extant descendants of *Apachyus madseni* sp. nov. are limited to tropical or subtropical areas.

Apachyidae is a rather enigmatic family that in the past has been treated as anything from a suborder (Paradermaptera) to a subfamily (Apachyinae) of the Labiduridae (Brindle, 1965). Phylogenetically, Apachyidae have been difficult to place, but the latest phylogenomic analyses by Wipfler *et al.* (2020) rather surprisingly place Apachyidae as sister to all other current Dermaptera families. Whether this result is correct or not, the age of *A. madseni* (ca. 55 Ma) is most certainly not indicative of the age of the family as the Neodermaptera, which comprise all modern Dermaptera (e.g., Grimaldi & Engel, 2005), diversified in the Early Cretaceous (Grimaldi & Engel, 2005; Ren *et al.*, 2017, 2018; Peng *et al.*, 2024). The situation may therefore be rather similar to the moth *Eopyralis morsae* Simonsen (Heikkilä *et al.*, 2018). *Eopyralis pyralis* is similarly described from the Fur Formation and represents the oldest known representative of the Lepidoptera family Pyralidae (Heikkilä *et al.*, 2018), a family estimated to have originated in the mid-Cretaceous (Wahlberg *et al.*, 2013).

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