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First record of Berothidae (Neuroptera) from the early Eocene of Denmark

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Abstract
Danoberotha verkleijorum gen. et sp. nov. is described from the early Eocene Fur Formation, Denmark. This is the first record of Berothidae from this formation. The key distinguishing feature of the new genus is the pectinate CuP of the forewing. It differs from other genera possessing the pectinate forewing CuP by other characters (*e.g.*, the configuration of CuA; the number of crossveins between RA and RP proximad the fusion of Sc and RA). It is assumed that the climate of the Fur Formation when layers +25 to +30 were deposited was upper microthermal.

Key words Neuroptera, Berothidae, new genus, Fur Formation, climate.

Introduction

The small Neuroptera family Berothidae comprises slightly more than 125 extant species including the subfamily Rhachiberothinae (Oswald & Machado 2018). Fossils are numerous and are considered to occur from the Triassic to the Miocene (Whalley 1980; Martins-Neto & Vulcano 1990; Ren & Guo 1996; Grimaldi 2000; Makarkin *et al.* 2011; Jepson *et al*. 2012; Azar & Nel 2013; Khramov 2015, 2020, 2023; Pérez-de le Fuente *et al*. 2021; Boderau *et al.* 2024; Khramov *et al*. 2024). However, some taxa are erroneously assigned to this family, including all from the Triassic (VNM, pers. obs.). Berothids with cursorial legs are especially diverse and numerous in mid-Cretaceous Kachin amber of Myanmar,

with 28 species described to date (Engel & Grimaldi 2008; Yuan *et al*. 2016; Makarkin 2018; Huang *et al*. 2019; Shi *et al*. 2019; Q. Yang *et al*. 2019; Y. Yang *et al*. 2020; Khramov 2021; Wang *et al*. 2022; Zhang *et al*. 2022; Chen *et al*. 2024; H. Li e*t al.* 2023; R. Li *et al.* 2024).

Only four species of Berothidae with cursorial legs have been described from the Cenozoic: the early Eocene *Microberotha macculloughi* Archibald & Makarkin, 2004 from Hat Creek amber, British Columbia, Canada; the early Eocene *Xenoberotha angustialata* Makarkin, 2017 from the Green River Formation, Colorado, U.S.A.; the late Eocene *Elektroberotha groehni* Makarkin & Ohl, 2015 from Baltic amber; and the late Miocene *Isoscelipteron bertrandi* Boderau *et al*., 2024 from Sainte-Reine (Cantal, France) (Archibald & Makarkin 2004; Makarkin & Ohl 2015; Makarkin 2017; Boderau *et al*. 2024). An undescribed species similar to the mid-Cretaceous *Haploberotha* Engel & Grimaldi, 2008 is known from Baltic amber (VNM, pers. obs.).

Berothidae with raptorial legs belong to the Mesithoninae, Paraberothinae, and Rhachiberothinae. Paraberothinae are often considered a subfamily of Rhachiberothidae (*e.g*., Aspöck *et al*. 2020; Nakamine *et al*. 2020). Only three fossil species of Rhachiberothinae are known, all from the Eocene: *Whalfera venatrix* (Whalley, 1983) from English amber, *W. wiszniewskii* Makarkin & Kupryjanowicz, 2010 from Baltic amber, and *Oisea celinea* (Nel *et al*. 2005) from Oise amber (Makarkin & Kupryjanowicz 2010).

Mesithoninae and Paraberothinae are exclusively Mesozoic. Their wing venation differs from that of the new genus, and they will not be considered further in this study.

The earliest Eocene Fur Formation of the Limfjord area of Northern Jutland (Denmark) is one of the oldest known insect-bearing Lagerstätten from the European Paleogene (Pedersen & Surlyk 1983). Fossil insects are abundant, with more than 20,000 specimens already reported 25 years ago (Rust 1999). Overviews of this Lagerstätte can be found in several publications (*e.g.*, Larsson 1975; Archibald & Makarkin 2006; Pedersen *et al*. 2012; Rasmussen *et al*. 2016; Jenkins Shaw *et al*. 2024). To date, more than 200 species of 15 insect orders have been described from the Fur Formation (Willmann 1990; Rust 1998; Willumsen 2004; Bechly & Rasmussen 2019), and important discoveries are reported every year, *e.g*., the oldest Cicadellinae leafhoppers (Dietrich & Perkovsky 2023), Spondylidinae longhorn beetles (Legalov *et al.* 2024), butterflies (de Jong 2016), and Pyralidae snout moths (Heikkilä *et al.* 2018); the youngest representative of the limaiine green lacewing genus *Mesypochrysa* Martynov, 1927 (Chrysopidae), previously known from the Middle Jurassic to the Early Cretaceous (Makarkin & Perkovsky 2023). At the same time, extant genera are also reported from the Fur Formation (Waichert *et al*. 2021; Prokin *et al*. 2024 and references therein).

Here, we describe the first species of Berothidae from the early Eocene Fur Formation.

Material and methods

The specimen examined was collected by Jan & Elly Verkleij in a large calcareous concretion on the beach near Rødsten, Fur Island, 56°50’37”N 9°11’E (Figure 1), locality 15 (Fur Østklint) of Pedersen *et al*. 2012 (see their Fig. 1). The estimated age for ash-layers +25 to +30 is about 55.4 Ma (Stokke *et al.* 2020). The specimen was photographed with a Canon EOS 5D II camera attached to an Olympus SZ60 stereomicroscope. A droplet of deionized water was added to the fossil to enhance contrast and reveal more morphology. The type is deposited in Museum Salling, Fur Museum.

Venational terminology follows Breitkreuz *et al.* (2017). Crossveins are designated by the longitudinal veins to which they connect and are numbered in sequence from the wing base, *e.g*., 2icu, crossvein in second gradate series between CuA and CuP; 2m-cu, crossvein in second gradate series between RP and MA.

Abbreviations: CuA, anterior cubitus; CuP, posterior cubitus; MA, anterior media; MP, posterior media; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; Sc, subcosta.

Figure 1. The type locality of *Danoberotha verkleijorum* sp. nov.: A – the beach near Rødsten; B – the stone (calcareous concretion), in which the specimen is found (photographs: Jan Verklej).

Systematic paleontology

Order Neuroptera Linnaeus, 1758

Family Berothidae Handlirsch, 1906–1908 [1906]

Subfamily *incertae sedis*

Genus *Danoberotha* gen. nov.

https://zoobank.org/urn:lsid:zoobank.org:act:0EDB9378-86BD-48B2-85B9-4D130CF0825D

Type and only species. *Danoberotha verkleijorum* sp. nov.

Etymology. From Denmark, and *Berotha*, a genus-group name. Gender feminine.

Diagnosis. Distinguished from other genera by a combination of the following forewing character states: One crossvein between RA, RP proximad fusion of Sc, RA; RP with six branches; MP deeply forked; CuA pectinate, with three branches; CuP pectinate, with at least two branches.

***Danoberotha verkleijorum* sp. nov.**
https://zoobank.org/urn:lsid:zoobank.org:act:A5FB9202-3D1D-4046-8C13-2A2B3A763894
(Figure 2)

Type material. Holotype: FUM-N 10523 (Verkleij collection number c-06-17b), collected by Jan and Elly Verkleij on 6 June 2006, deposited in Fur Museum. An incomplete and poorly-preserved specimen.

Type locality and horizon. Limfjord Denmark: Fur: the beach near Rødsten. Early Eocene (Fur Formation: Silstrup Member: calcareous concretion, ash-layers +25? to +30).

Etymology. After the surname of Jan and Elly Verkleij (Rozenburg, Netherlands), who collected the specimen.

Diagnosis. As for the genus.

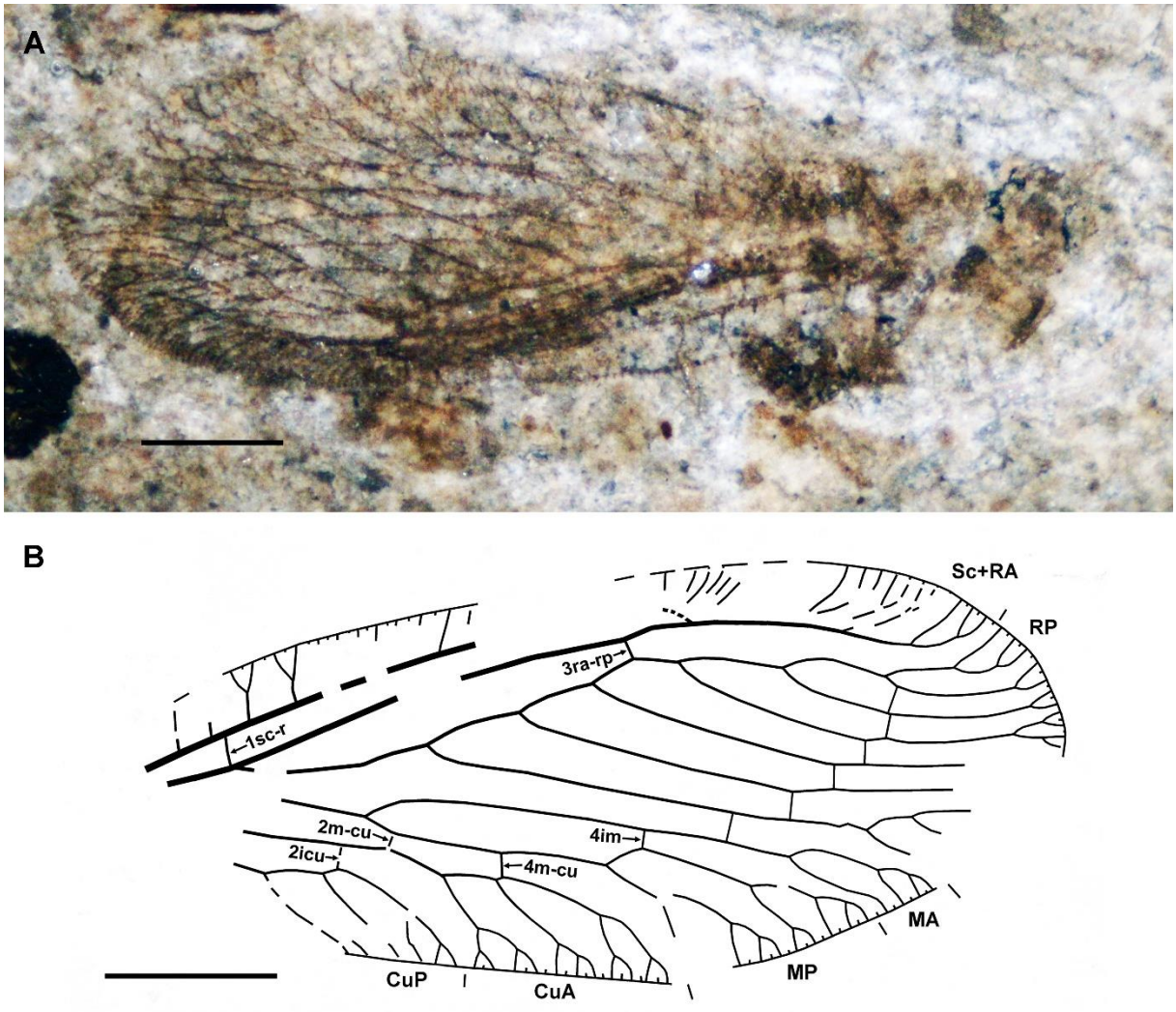

Figure 2. *Danoberotha verkleijorum* sp. nov., holotype FUM-N 10523: A – specimen as preserved; B – forewing venation. Scales: 1 mm.

Description. Body very poorly preserved, details indiscernible. Antennae, legs not preserved.

Forewing oval, *ca*. 6.5 mm long, 3.4 mm wide. Costal space moderately narrow, slightly dilated in proximal half. At least two subcostal veinlets forked in proximal half, two simple, configuration of

others unknown; rather closely spaced. Subcostal space with one basal subcostal crossvein visible, located approximately opposite origin of RP. Sc and RA probably fused distally (poorly discernible). Sc+RA long, terminating on wing margin before wing apex, with more than ten veinlets (mostly forked). RA space (between RA, RP) with one crossvein visible before fusion with Sc. RP with six branches. RP1 more deeply forked than other RP branches, which are shallowly forked one to three times. M forked far from wing base, well distad the origin of RP. MA dichotomously branched. MP deeply dichotomously branched. Two crossveins preserved between M, Cu: 2m-cu located distad M fork; 4m-cu belongs to outer gradate series of crossveins. Anterior trace of CuA shallowly forked, with three pectinate branches, which are forked one to three times. Anterior trace of CuP shallowly forked, with at least two pectinate branches originating proximad 2icu (branching not clearly discernible). Anal veins not preserved. Two gradate series of crossveins in radial to medio-cubital spaces: two crossveins discernible in second series, between MP, CuA and CuA, CuP; outer (fourth) series with eight crossveins from RP6 to CuA.

Hind wing fragmentarily preserved. RP with at least five branches parallel to posterior margin. MA, MP distally forked. CuA long, parallel to posterior margin. Other details unclear.

Discussion

The subfamily affinity of the specimen is impossible to determine due to its incomplete and poor preservation. It lacks legs, and we cannot detect if its foreleg is cursorial or raptorial. The key distinguishing feature is, therefore, the pectinate CuP in the forewing.

In extant Berothidae, the pectinate forewing CuP is only present in all species of *Lomamyia* Banks, 1904 (Berothinae), *Trichoberotha* Handschin, 1935 and some specimens of *Trichoma gracilipenne* Tillyard, 1916 (both Trichomatinae) (see *e.g*., Handschin 1935: Fig. 12; Carpenter 1940: Fig. 59; Aspöck & Aspöck 1985: Figs 35, 36; Faulkner 1992: Figs 27–40). The CuP of other extant berothids is usually deeply forked (*e.g*., Aspöck & Aspöck 1981: Fig. 6, 10, 21) or not forked before the terminal branching (*e.g*., Aspöck & Aspöck 1981: Fig. 30), and is only extremely rarely dichotomously forked (*e.g*., Aspöck & Aspöck 1985: Figs 1, 5). *Danoberotha* gen. nov. differs clearly from these extant genera by the non-falcate forewings (slightly to strongly falcate in these genera) and the presence of only one crossvein between RA and RP proximad the fusion of Sc and RA (at least two in these genera).

The pectinate forewing CuP is also characteristic of some berothid genera from mid-Cretaceous Myanmar amber (see *e.g*., Yuan *et al*. 2016: Figs 3, 6; Y. Yang *et al*. 2020: Figs 6A, 10A, 13, 15A, 18A, 20A, 22A; Khramov 2021: Figs 1C, D). But these genera are distinguished by other characters, *e.g*., *Cornoberotha* Y. Yang *et al*. 2020, *Dolichoberotha* Y. Yang *et al*., 2020 and *Ansoberotha* Y. Yang *et al*., 2020 all have three or more crossveins between RA and RP before the fusion of Sc and RA, and CuA often has more branches; CuA in *Maculaberotha* Yuan *et al*., 2016 and *Magniberotha* Yuan *et al*., 2016 is dichotomous, not pectinate.

CuP in other Cretaceous and Cenozoic berothids is deeply (Grimaldi 2000: Figs 18, 19; Makarkin & Ohl 2015: Fig. 3A) or shallowly forked (Archibald & Makarkin 2004: Fig. 5; Azar & Nel 2013: Fig. 7), or its configuration is unknown (Martins-Neto & Vulcano 1990: Fig. 1; Pérez-de le Fuente *et al*. 2021; Makarkin 2017: Fig. 1C; Boderau *et al*. 2024: Fig. 5). Of these berothids with unknown CuP configuration, the new genus is most similar to the early Eocene *Xenoberotha angustialata*, but it is easily distinguished from the latter by the much wider forewing and more distal fork of M.

CuP in all Rhachiberothinae (both extant and fossil) is deeply forked (Aspöck & Mansell 1994: Figs 6, 43; Aspöck & Aspöck 1997: Fig. 36; Makarkin & Kupryjanowicz 2010: Fig. 3; Aspöck *et al.* 2020: Fig. 7).

Although the specimen is poorly preserved, it may surely be assigned to a new genus and species of Berothidae. Previously, Neuroptera of the Fur Formation were represented by Hemerobiidae, Chrysopidae, Osmylidae, and Polystoechotidae. No species of the Osmylidae have been described to date. Hemerobiidae are most abundant, but only one species has been described (Henriksen 1922). Chrysopidae and Polystoechotidae have been studied in more detail, with five species of each family described to date (Andersen 2001; Archibald & Makarkin 2006; Makarkin & Perkovsky 2023, 2024).

The climatic parameters of the environment may be not deduced from the finding of *Danoberotha verkleijorum* gen. et sp. nov. However, the holotype of Darwin wasp *Crusopimpla weltii*

Viertler *et al*., 2022 (Hymenoptera: Ichneumonidae) was found in that calcareous concretion (J. Verkleij, pers. comm., 2024). In the original description (Viertler *et al*. 2022), the type locality was mistakenly indicated as 'Lynghøj on Mors Island'. The type and three species of *Crusopimpla* Kopylov *et al*., 2018 were described from the presumed early Eocene of Tadushi Formation (Primorskii Krai, Russia). The climate of the Tadushi Formation is assumed to have been upper microthermal that was characteristic of the montane Okanagan Highlands localities in western North American (Archibald *et al*. 2018). Darwin wasps of the genus *Crusopimpla* Kopylov *et al.*, 2018 (as well as other Pimplinae) are very common and diverse in the Tadushi and Fur formations (Kopylov *et al.* 2018; Klopfstein *et al*. 2022; Viertler *et al.* 2022); this family is generally very common in both formations. The forewing venation of *Asiachrysa* Makarkin, 2014 from the Tadushi Formation is most similar to that of *Cimbrochrysa* Schlüter, 1982 from the Fur Formation (Neuroptera: Chrysopidae) (Makarkin 2014). We may therefore assume that the climate of the Tadushi and Fur formations was similarly upper microthermal, at least when layers +25 to +30 were deposited, where both Darwin wasps and aphids are especially common (Rust 1999). The abundance of aphids indicates the warm-temperate conditions (Perkovsky & Wegierek 2018).

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