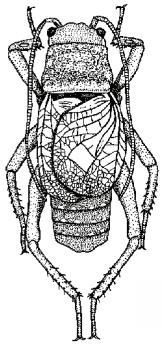

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FIRST RECORD OF A MALE OF THE GENUS *APHAENOGASTER* MAYR, 1853 (HYMENOPTERA, FORMICIDAE) FROM LATE EOCENE AMBERS

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Summary. A new species *Aphaenogaster wennebergi* Zharkov et Dubovikoff, **sp. n.** is described from late Eocene Danish amber. The holotype is the first known male of the genus *Aphaenogaster* Mayr from Late Eocene ambers and we consider it appropriate to describe it as a new species. Current classification problems of the ant genus *Aphaenogaster* and related taxa, both recent and fossil, are discussed. We also present a complete palaeoreconstruction of the new ant based on computer microtomography.

Key words: fossil ants, taxonomy, new species, Danish amber, micro-CT, μCT, 3D model.

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Резюме. Из позднеэоценового датского янтаря описан *Aphaenogaster wennebergi* Zharkov et Dubovikoff, **sp. n.** Голотип является первым известным самцом рода *Aphaenogaster* Mayr из янтаря позднего эоцена, и мы считаем целесообразным описать его как новый вид. Обсуждаются текущие вопросы классификации, связанные с муравьями рода *Aphaenogaster* и близкими таксонами, как современными, так и ископаемыми. Мы также представляем полную палеореконструкцию (3Д модель) нового муравья, основанную на компьютерной микротомографии.

INTRODUCTION

The Upper Eocene amber of Europe is the largest source of palaeontological information about insects in the world. At the moment, about 20,000 ant inclusions have been studied and more than 190 species have been described. Baltic amber is the most famous of them, and the largest in terms of the number of described species and known specimens. Its age remains a matter of debate, but recent studies confirm a Late Eocene age (Iakovleva *et al.*, 2022). The main locations are concentrated in Russia (Kaliningrad region) and Poland (near the city of Gdansk). Currently, it is generally accepted that Rovno amber, Ukraine and the Baltic amber formed independently of each other at the same geological time, but in different territories (Maidanovich & Makarenko, 1988; Perkovsky *et al.*, 2010; Karlovich & Prokopets, 2014; Radchenko & Dlussky, 2018; Perkovsky, 2018). Bitterfeld amber was initially considered redeposited Baltic amber, then dated first to the Miocene, then to the Oligocene. However, geochemical studies have shown that these ambers are most likely of the same age, but originate from climatically different ecosystems (Wolfe *et al.*, 2016). Similar studies with Danish amber have not yet been conducted, and the question of its independent origin remains open. There are limited faunistic data (Radchenko & Dlussky, 2018; Shavrin *et al.*, 2023; Simutnik & Perkovsky, 2023; Anisyutkin *et al.*, 2024; Belokobylskij *et al.*, 2024; Legalov *et al.*, 2024), and further research is needed. For the purposes of this study, we adopt a modern view of considering Danish amber as a separate deposit, following the approach outlined by previous researchers (quoted above).

Here, we report the first male ant from the genus *Aphaenogaster* Mayr, 1853 preserved in Late Eocene amber. Based on our morphological study, we describe a new species of ants and provide a palaeoreconstruction in the form of a three-dimensional model, created using computer microtomography (μCT).

MATERIAL AND METHODS

The studied fossil was found in small piece of amber that was collected by Lars Wenneberg on the coast of Denmark near Hvide Sande (55°58'12" N 8°08'01"E). The holotype of the described species [NHMD 873929] is stored in the Natural History Museum of Denmark, Copenhagen.

The studies were performed on the equipment of the Research Park of St. Petersburg State University (“Centre for X-ray Diffraction Studies”, project No. 103-23769; “Resource Centre for Microscopy and Microanalysis”, project No. 112-23465, “Computing Centre”, project No. 110-27449 and “Centre for Molecular and Cell Technologies”, project No. 109-34813).

Photographing and morphological analysis of the specimen were performed using a Leica M205C motorized stereomicroscope. Subsequent image processing was carried out using the Helicon Focus Pro 8, Kritta 5.0.2 and Inkscape 1.2 software.

Arrays of microtomographic sections were obtained using a NeoScan N80 High Resolution Microtomograph. Visualization, volume rendering and segmentation of tomographic sections were performed in 3DSlicer 5.1 and Drishti 3.0 software. The specimen (NHMD 873929) was scanned with the following parameters: voltage 50 kV, current 200 μA, without a filter, with a pixel size of 2.0 microns and a resolution of 4896×4896 pixels per slice with a continuous 360° rotation (rotation step 0.2°) and a shutter speed of 145 ms per frame (3681 X-ray projections).

The inclusion was segmented and subsequently isolated from the surrounding background using the software segmentation editor. Part of poorly preserved morphological structures were previously segmented in the segmentation editor by manually labeling of each slice.

The measurements indicated below were performed by volume rendering of specimen in 3DSlicer which made all morphological structures available for study (as opposed to studying samples directly in amber with the help of a microscope) and made it possible to measure the with precision of 0.01 mm. The results of segmentation (in 3DSlicer) in the file format PLY were imported into the free and open Blender 3.1 software for "straightening" (changing the position of limbs and other parts of the body), painting and animation of reconstruction of ant. The sample was "straightened" using the Auto-Rig PRO tool. All the individual parts of the reconstruction were transformed into polygonal grids using the Smart UV project tool and painted manually (the color of the model is not the natural color of the specimen or the assumed lifetime color). Reconstructed body parts that have not been preserved directly in amber are indicated in gray. We assumed what a complete ant would look like and reconstructed it.

The dimensional values of morphological structures are given in millimeters. The following abbreviations are used in the text: HL – head length, maximum length of the head, measured from the transverse line connect-ing the posterior-most points of the head to the anterior-most extremity of the clypeus; HW – head width, measured along the upper line of the eyes; FW – the maximum width measured between the frontal lobes; SL – the maximum straight-line length of the scape measured from antennal bulb to the apex; PdL – pedicellum length; Fl1 – the length of the first flagellomere; Fl2 – the length of the second flagellomere; OL – the maximum length of the right eye measured by maximum diameter; OD – the maximum distance between inner margins of eyes; MdL – the length of the right mandible, measured from the mandibular apex to the place of attachment to the head, measured in ventral view; WL – weber’s length, the diagonal length of the mesosoma in profile from the point

at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron; ML – mesosoma length, diagonal length of the mesosoma as measured from the anteriormost pronotal point to the posteriormost apex of the propodeal projection in dorsal view; PnW – the maximum width of the pronotum in dorsal view; MtL – mesoscutum length. Maximum length of the mesoscutum in dorsal view; MtW – mesoscutum width. Maximum width of the mesoscutum in dorsal view; MsL – mesoscutellum length. Maximum length of the mesoscutellum in dorsal view; MsW – mesoscutellum width. Maximum width of the mesoscutellum in dorsal view; PrdL – the maximum length of the propodeum in dorsal view; PrdW – the maximum width of the propodeum in dorsal view; PrdH – the height of the propodeum in profile, measured as the perpendicular distance from the ventral edge to the highest point of the propodeum; PtL – the length of the petiolar node in profile, measured as the distance from the place of attachment to the propodeum to the place of attachment to the gaster; PtW – the maximum width of the petiolar node in dorsal view; PtH – the height of the petiolar node in profile, measured as the perpendicular distance from the ventral edge to the highest point of the petiolar node; PpW – maximum width of postpetiole in dorsal view; MsFL – the maximum length of the right mesofemur, measured in anterior view; MsTL – the maximum length of the right mesotibia, measured in anterior view.

Indices: CI (cephalic index) = HL/HW; SI1 (scape length index) = SL/HL; SI2 (scape width index) = SL/HW; OI1 (eye length index) = OL/HL; OI2 (eye width index) = OL/HW; PI1 (petiole height index) = PtL/PtH; PI2 (petiole width index) = PtL/PtW; MI (mesosomal index) = WL/PnW; PRI (propodeal index) = PrdL/PrdH.

The nomenclature of wing venation in this work follows Perfilieva *et al.*, (2017).

DESCRIPTION OF NEW SPECIES

Family Formicidae Latreille, 1809

Subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1835

Genus *Aphaenogaster* Mayr, 1853

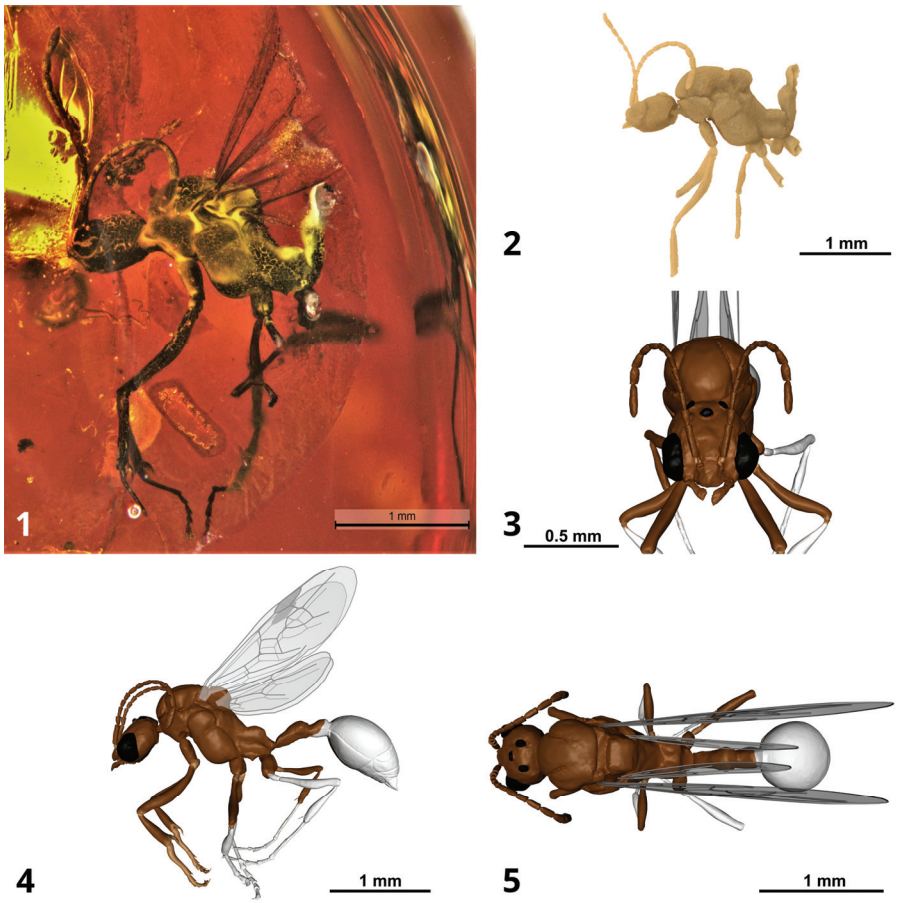
***Aphaenogaster wennebergi* Zharkov et Dubovikoff, sp. n.**

https://zoobank.org/NomenclaturalActs/AEA7AE5E-28F3-428A-A564-BA964554A77F

Figs 1–5

TYPE MATERIAL. Holotype: ♂, NHMD 873929. The described ant species is found in a small piece of late Eocene Danish amber, along with the syninclusions of another ant, NHMD 873928 (Dolichoderinae), and a beetle, NHMD 874111 (Coleoptera).

TYPE LOCALITY AND AGE. The piece of amber was collected by Lars Wenneberg on the coast of Denmark near Hvide Sande (55°58'12" N 8°08'01"E). The holotype of the described species [NHMD 873929] is stored in the Natural History Museum of Denmark, Copenhagen. Late Eocene (?).



Figs 1–5. *Aphaenogaster wennebergi* sp. n. (Formicidae, Myrmicinae) from late Eocene Danish amber. 1 – holotype (male), NHMD 873929, photomicrograph; 2 – μCT volume rendering of holotype (wings are not shown); 3 – palaeontological reconstruction (3D model), head, frontal view; 4 – palaeontological reconstruction (3D model), habitus, left lateral view; 5 – palaeontological reconstruction (3D model), habitus, dorsal view. Reconstructed body parts that have not been preserved directly in amber are indicated in gray.

NOTES. In the taxonomy of ants, there is a problem of attributing different castes of ants to the same species. Even recent ant males are difficult to compare with females, which can lead to an artificial increase in the number of described species. The study of a new male does not allow us to associate it with any described species. Another complication is that its abdomen and wings have been cut off, which reduces a number of important taxonomic features, such as wing venation and the structure of the genitals. Given that this specimen is the first known male of the genus *Aphaenogaster* from Late Eocene ambers, we consider it appropriate to describe it as a new species.

DIGNOSIS. Male. The new ant specimen is defined as a member of the *Aphaenogaster* (*s. l.*) by the following combination of features: distinctly flat and more or less elongate head; compound eyes large and prominent; triangular mandibles; antenna 13-segmented, scape short, not reaching posterior margin of head; funiculus filiform, incrassate; trunk slender; pronotum small, completely overhung by mesonotum; mesonotum massive; mesoscutum convex dorsally with notauli; mesoscutellum convex, overhanging metanotum; propodeum long, low and narrow, constricted just anterior to propodeal spiracle; propodeal spines reduced to form obtuse lobes. Legs long and slender; middle and hind tibiae each with a small simple spur.

DESCRIPTION. Male. *Head*: Mandibles small and smooth without distinct teeth. Anterior clypeal margin slightly convex, in middle not concave. Head flattened, slightly longer (0.62) than wider (0.52) and narrower than maximum pronotal width (0.61). Very large ovoidal compound eyes (~ ½ length of the head capsule) that significantly protrude out of the head capsule, slightly shifted forward. The posterior border of the eye straight, not rounded. Ocelli well developed, not large, and of medium size. Antenna 13–segmented. Antennal club 4-segmented. Scape short, not reaching posterior margin of head; funicular segments from 1.5 to 2 times longer than wide. Sparse erect and suberect setae mostly occur dorsally over the head.

Mesosoma: Pronotum small, completely overhung by mesonotum. Mesonotum massive. Mesoscutum convex dorsally with broad notauli. Mesoscutellum convex, slightly erect above mesoscutum. Propodeum long, low and narrow. Distal end of the propodeum with two, dorsally flattened, obtuse knobs. A weak groove is found between them. Corner of end of propodeum not sharp, not dentate. A ventral cuticular process protrudes from the metasternum. Sparse erect and suberect setae mostly occur dorsally over the mesosoma.

Legs: Legs relatively long and slender; middle and hind tibiae each with a small simple spur. Sparse erect and suberect setae mostly occur on coxae.

Metasoma: Long pedunculate petiole, globose.

Female unknown.

MEASUREMENTS (in mm). HL – 0.62; HW – 0.52; FW – 0.13; SL – 0.21; PdL – 0.10; Fl1 – 0.11; Fl2 – 0.08; OL – 0.30; OD – 0.36; MdL – 0.22; WL – 1.38; ML – 1.37; PnW – 0.61; MtL – 0.57; MtW – 0.57; MsL – 0.27; MsW – 0.28; PrdL – 0.58; PrdW – 0.38; PrdH – 0.35; PtL – 0.44; PtW – 0.23; PtH – 0.22; PpW – 0.27; MsFL – 0.92; MsTL – 0.71.

INDICES. CI – 1.19; SI1 – 0.34; SI2 – 0.4; OI1 – 0.48; OI2 – 0.58; PI1 – 2.00; PI2 – 1.91; MI – 2.26; PRI – 1.66.

ETYMOLOGY. After Lars Wenneberg and his son, Danish amber enthusiasts, who provided amber for this study.

DUSCUSSION

Ants from the genus *Aphaenogaster* have a complex taxonomic history, as thoroughly outlined in Schifani *et al.* (2022). To date, over 200 species have been described worldwide, with the exception of the Afrotropical region (Bolton, 2025).

However, it is increasingly evident that *Aphaenogaster* is a polyphyletic genus, necessitating its division into at least two distinct clades. The "*Aphaenogaster* clade" includes species from the former subgenera *Aphaenogaster s. str.* and *Attomyrma* Emery, 1915, while the "*Deromyrma* clade" includes tropical representatives, most species having a neck-like elongation of the head and an always open rm cell on the forewing. This classification has been confirmed by several independent studies (Branstetter *et al.*, 2022; Schifani *et al.*, 2022; Juve *et al.*, 2025). The restoration of *Deromyrma* Forel, 1913 as a genus is long overdue. It is imperative that this issue be resolved in a timely manner. The ongoing taxonomic uncertainty engenders unnecessary complexity in the classification of recent and fossil taxa, which has already led to confusion.

Until recently, more than 20 fossil species were classified as *Aphaenogaster*. However, Radchenko & Perkovsky (2016) have transferred a significant number of these species to the morphotaxon †*Paraphaenogaster* Dlussky, 1981. Only 11 extinct species are currently recognised under the genus *Aphaenogaster* (Radchenko *et al.*, 2024). In turn, the genus †*Paraphaenogaster* includes 20 valid species (Bolton, 2025). The primary issue is the absence of reliable distinguishing characteristics that would enable unambiguous classification of these two genera. Various authors have repeatedly discussed this issue and agreed that the only distinguishing feature between these genera is absence/presence of the RS-M vein (Radchenko & Perkovsky 2016; Jessen, 2020; Perfilieva, 2022). Although this feature is absolutely unstable within *Aphaenogaster* (*s. l.*) and among its close genera, *Stenamma* Westwood, 1839 and *Messor* Forel, 1890. Thus, further revision of its taxonomy is required until a complete understanding of its diversity is achieved both in recent and fossil taxa.

Six species of the genus *Aphaenogaster* have been described in the Upper Eocene ambers of Europe. All these ants were described from workers: †*Aphaenogaster sommerfeldti* Mayr, 1868; †*Aphaenogaster mersa* Wheeler, 1915; †*Aphaenogaster oligocenica* Wheeler, 1915; †*Aphaenogaster antiqua* Dlussky, 2002; †*Aphaenogaster groehni* Radchenko, 2024 and †*Aphaenogaster ribbeckei* Radchenko, 2024. Gustav Mayr, in his landmark work (Mayr, 1868), described the species †*Aphaenogaster berendti* based on a single male specimen found in Baltic amber. However, William M. Wheeler discovered an additional male in the Geological Institute of Königsberg's collection. As a result, he transferred this species to the genus *Stenamma* (Wheeler, 1915). In this paper, we describe the discovery of the first male specimen of the genus *Aphaenogaster* in Eocene amber from Europe. Based on its morphology, this male is clearly related to the "*Aphaenogaster* clade", which includes recent Holarctic members of the genus. The specimen is poorly preserved, with missing wings and a cropped gaster. Therefore, we applied 3D modeling to create complete palaeoreconstruction of it (Fig. 3–5).

Apparently, all the species of the genus *Aphaenogaster* found in European Eocene ambers, belong to the subgenus *Attomyrma* Emery, 1915 or the subgenus *Aphaenogaster s. str.*, i.e., to the clade containing recent Holarctic species. Since

others species are described from worker specimens, it is nearly impossible to correlate a new male specimen with any of these described species.

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SUPPLEMENTARY MATERIALS

The following supporting information can be downloaded at: https://doi.org/10.5281/zenodo.8432646

S1: Video Palaeoreconsrtuction *Aphaenogaster* sp. n. (Male).mkv, S2: 3D model Palaeoreconstruction *Aphaenogaster* sp. n. (Male).ply and S3: volume rendering of †*Aphaenogaster wennebergi* Zharkov & Dubovikoff, sp. nov., holotype, male.

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