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TWO NEW *APHAENOGASTER* SPECIES (HYMENOPTERA, FORMICIDAE) FROM BALTIC AMBER

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Two New *Aphaenogaster* Species (Hymenoptera, Formicidae) from Baltic Amber. Radchenko, A. G., Gröhn, C. & Ribbecke, H.-W. — *Aphaenogaster groehni* Radchenko, sp. n. and *A. ribbeckei* Radchenko, sp. n., are described from the Late Eocene Baltic amber, each based on the holotype worker. *Aphaenogaster groehni* Radchenko, sp. n. differs from previously described species from the Late Eocene European ambers by a distinctly narrowed posteriorly head without pronounced occipital corners and a longer antennal scape, and *A. ribbeckei* Radchenko, sp. n. differs by a more slender mesosoma. The taxonomic position of the new species is discussed.

Key words: ants, Formicidae, Myrmicinae, new species, *Aphaenogaster groehni*, *Aphaenogaster ribbeckei*, Late Eocene, palaeontology, taxonomy.

Introduction

Aphaenogaster Mayr, 1853 is one of the most species-rich genera of the subfamily Myrmicinae Lepeletier, 1835, comprising more than 200 described modern species (Bolton, 2024). The geographical range of this genus is quite peculiar. More than half of the known species are distributed in the western Palaearctic Region, of which over 100 occur in the Mediterranean; four species are known from Madagascar; around ten species are found in Australia, six in New Guinea, around 40 in Central Asia, south of the eastern Palaearctic, and in the Oriental Region, and only about 25 occur in Nearctic and Neotropical Regions, from southern Canada to northern Columbia. At the same time, *Aphaenogaster* is absent in the Afrotropical region (Radchenko &

Perkovsky, 2016; Schifani et al., 2022). Its species inhabit relatively warm temperate deciduous forests, tropical forests, as well as various landscapes of the Mediterranean types, but are absent from steppes and deserts.

More than 20 fossil species were assigned to *Aphaenogaster* till recently, but Radchenko & Perkovsky (2016) transferred many of them to the morphotaxon *Paraphaenogaster* Dlussky, 1981. As a result, we now assign to the genus *Aphaenogaster* 11 extinct species described from the USA, Mexico, the Dominican Republic, Europe, China, Japan and the Russian Far East, dating from the middle Eocene (47–43 Ma) to the middle Miocene (26–15 Ma) (Radchenko & Perkovsky, 2016; Jessen, 2020). Four of them were described from the Late Eocene European ambers (Priabonian age, 37.8–33.9 Ma), particularly: *A. sommerfeldti* Mayr, 1868, *A. mersa* Wheeler, 1915, *A. oligocenica* Wheeler, 1915 and *A. antiqua* Dlussky, 2002. Recently we found two *Aphaenogaster* species from two pieces of Baltic amber, which are described below: *A. groehni* Radchenko, sp. n. and *A. ribbeckei* Radchenko, sp. n.

Material and Methods

We examined two workers from two pieces of amber. The holotypes of *Aphaenogaster groehni* Radchenko, sp. n. and *A. ribbeckei* Radchenko, sp. n. are deposited at the Leibniz Institute for the Analysis of Biodiversity Change, Hamburg (LIB).

The original photographs were taken with a Leica Z16 APO microscope equipped with a Leica DFC 450 camera and processed by LAS Core software, and with a SONY ILCE-6000 and stacked with the use of Helicon Focus 8.2.0 software (Kozub et al., 2023).

The specimens were measured using a Leica MZ6 stereomicroscope with an ocular-micrometer at a maximum magnification x100. Not all features of the specimens examined were properly visible and measurable, so we measured only well visible details (calculated to an accuracy of 0.01 mm), particularly:

HL — maximum length of the head in dorsal view, measured in a straight line from the anteriormost point of clypeus to the mid-point of occipital margin;

HW — maximum width of the head in dorsal view behind (above) the eyes;

FW — minimum distance between the frontal carinae;

FLW — maximum distance between outer margins of the frontal lobes;

SL — maximum length of the scape measured in a straight line from its apex to the articulation with the condylar bulb;

OL — maximum diameter (length) of the eye;

OW — minimum diameter (width) of the eye;

GL — length of the gena, measured from the anterior margin of the eyes to the articulation with the mandible;

ML — diagonal length of the mesosoma (seen in profile) from the anterior end of the neck shield to the posterior margin of the propodeal lobes;

MH — height of the mesosoma, measured from the upper level of promesonotum perpendicularly to the level of lower margin of mesopleuron;

PNW — maximum width of the pronotum from above;

PL — maximum length of the petiole, measured from the posterodorsal margin of the petiole to the articulation with the propodeum;

PH — maximum height of the petiole in profile, measured from the uppermost point of the petiolar node perpendicularly to the lowest point of the petiole;

PW — maximum width of the petiole from above;

PPL — maximum length of the postpetiole in dorsal view between its visible anterior and posterior margins;

PPH — maximum height of the postpetiole in profile from the uppermost to the lowermost point, measured perpendicularly to the tergo-sternal suture;

PPW — maximum width of the postpetiole in dorsal view;

HTL — maximum length of the metatibia;

HFL — maximum length of the metafemur;

ESL — maximum length of the propodeal spine in profile, measured along the spine from its tip to the deepest point of the propodeal constriction at the base of the spine;

ESD — distance between the tips of propodeal spine in dorsal view;

The length and width of the each funicular segment is also measured.

The approximate total length is calculated as the sum of HL+ML+PL+length of the gaster.

For simplicity, we give ratios of various measurements (e.g. HL/HW) rather than naming and abbreviating various indices (e. g., CI — cephalic index).

Taxonomy

Subfamily Myrmicinae Lepeletier, 1835
Genus *Aphaenogaster* Mayr, 1853
Aphaenogaster groehni Radchenko**, sp. n.** (fig. 1)

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Material examined. **Holotype worker**, complete specimen, No. GPIH 5079 (coll. CCGG No. 6831), Baltic amber, Late Eocene, Poland (LIB).

Etymology. The species is dedicated to Mr. Carsten Gröhn (Germany), who provided the piece of amber with the holotype specimen of this species for investigation.

Worker (fig. 1). Body length 3.7 mm. Head moderately elongated, HL/HW 1.17, with distinctly convex sides, suboval, gradually narrowed posteriorly, without marked occipital corners, occipital margin delineated by distinct ridge, but without "neck". Anterior clypeal margin feebly convex and not-notched medially. Frontal carinae short, feebly curved, diverging posteriorly, frons narrow, 0.27 times of head width, frontal lobes slightly extended, 1.15 times as wide as frons. Scape quite long, 1.28 times as long as head, exceeding occipital margin by ca. 1/3 of its length, very feebly curved at base and gradually widened to apex; funiculus with vaguely defined 4-segmented club; 2nd to 6th funicular segments distinctly elongated, 1.8 times as long as wide. Eyes quite small, their maximum diameter 0.17 times the head length and 1.43 times their minimum diameter, situated distinctly in front of sides of head, equal to length of gena. Dentition of mandibles obscured.

Mesosoma long and slender, about three times as long as pronotal width, mesosomal height is not properly measurable, but mesosoma seems about three times as long as height. Mesonotal dorsum does not raise over pronotal dorsum, so that promesonotal dorsum forming regular, not very convex arch, promesonotal suture well marked dorsally, humeri rounded. Mesonotum posteriorly and propodeal dorsum very weakly convex, metanotal groove distinct, propodeal lobes rounded. Propodeum with short pointed spines, directed backward and upward at an angle ca. 45° and strongly divergent. Petiole quite long, ante-

Fig. 1. Photos of *Aphaenogaster groehni* Radchenko, sp. n., holotype, worker, body in dorso-lateral view. Scale bar 1 mm.

rior surface of node very feebly convex, subvertical, posterior one more convex, gradually sloping posteriorly, anterior and posterior surfaces converge with distinct ridge. Postpetiole subglobular, 1.3 times as wide as petiole. Legs long and slender.

Head and mesosoma with not very coarse reticulated sculpture, surface between rugae finely and quite densely, but not coarsely, punctated and appears shiny. Petiole and postpetiole punctated, but appear quite shiny. Appendages and gaster smooth and shiny.

Temples with 8–9 quite long and coarse, slightly curved suberect setae, occipital margin with 2 setae, whole head dorsum with about 15 similar setae, gena with 3–4 shorter setae. Promesonotal dorsum with about 15 long suberect setae, propodeum with 2 setae, petiole with 6 setae, postpetiole with about 10 setae, gaster with several tens of similar setae. Decumbent pilosity on body absent. Scape with much shorter, thin subdecumbent or suberect setae, femora and tibiae non-setose, tarsi with short coarse bristles on inner surface.

Gynes and males unknown.

Measurements (in mm) and ratios: HL 0.78, HW 0.66, SL 1.00, FW 0.18, FLW 0.21, OL 0.13, OW 0.09, GL 0.13, ML 1.31, PnW 0.44, PL 0.34, PW 0.16, PPL 0.25, PPW 0.21, HTL 0.75, HFL 1.07, ESL 0.10, ESD 0.19;

HL/HW 1.17, SL/HL 1.28, SL/HW 1.51, FW/HW 0.27, FLW/FW 1.15, OL/HL 0.17, OL/OW 1.43, OL/GL 1.00, PL/PW 2.17, PL/HL 0.44, PW/HW 0.24, PPW/PW 1.33, PPW/HW 0.31, ESL/HL 0.14, ESL/HW 0.16, ESD/ESL 1.88, ML/PnW 2.97, HTL/ML 0.57, HFL/ML 0.82.

Comparative diagnosis. This species differs well from all previously described *Aphaenogaster* species from the Late Eocene European ambers primarily by the shape of the head, which is gradually narrowed posteriorly and without marked occipital corners, a significantly longer scape, which is about 1.3 times as long as head and exceeds occipital margin by about 1/3 of its length, and longer funicular segments. In addition, *A. groehni* differs from *A. sommerfeldti* by the shape of the mesonotal dorsum, which does not raise over pronotal dorsum, from *A. oligocenica* — in the longer and pointed propodeal spines.

Aphaenogaster ribbeckei Radchenko**, sp. n.** (figs 2, 3)

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Material examined. **Holotype worker**, complete specimen, No. GPIH 5204, Baltic amber, Late Eocene, Poland (LIB).

Etymology. The species is dedicated to Mr. Hans-Werner Ribbecke (Germany), who provided the piece of amber with the holotype specimen of this species for investigation.

Worker (figs 2, 3). Body length 5.2 mm. Head elongated, HL/HW 1.24, subrectangular, with feebly convex sides, with well marked and narrowly rounded occipital corners, occipital margin slightly convex and delineated by distinct ridge. Anterior clypeal margin feebly convex, with medial notch. Frontal carinae short, feebly curved, subparallel, frons narrow, 0.30 times of head width, frontal lobes slightly extended, 1.12 times as wide as frons. Scape of moderate length, subequal to head length, exceeding occipital margin by ca. 1/4 of its length, very feebly curved at base and gradually widened to apex; funiculus with quite well defined 4-segmented club; 2nd to 6th funicular segments moderately elongated, ca. 1.5 times as long as wide. Eyes of moderate size, their maximum diameter 0.20 times the head length and 1.55 times their minimum diameter, situated somewhat in front of sides of head, 0.86 times as long as gena. Dentition of mandibles obscured.

Mesosoma very long and slender, about 3.7 times as long as height and more than three times as long as pronotal width. Mesonotal dorsum distinctly raised over pronotal

Fig. 2. Photos of *Aphaenogaster ribbeckei* Radchenko, sp. n., holotype, worker, body in lateral view. Scale bar 1 mm.

level, so that promesonotal dorsum does not form regular arch, promesonotal suture well marked dorsally, pronotum widely rounded anteriorly, but humeri with short and pointed triangular denticles, directed backward. Promesonotal dorsum strongly convex, mesonotum posteriorly and propodeal dorsum somewhat flattened, metanotal groove distinct and quite deep, propodeal lobes projecting apically, but not pointed. Propodeum with relatively long pointed spines, directed backward and upward at an angle ca. 45° and moderately di-

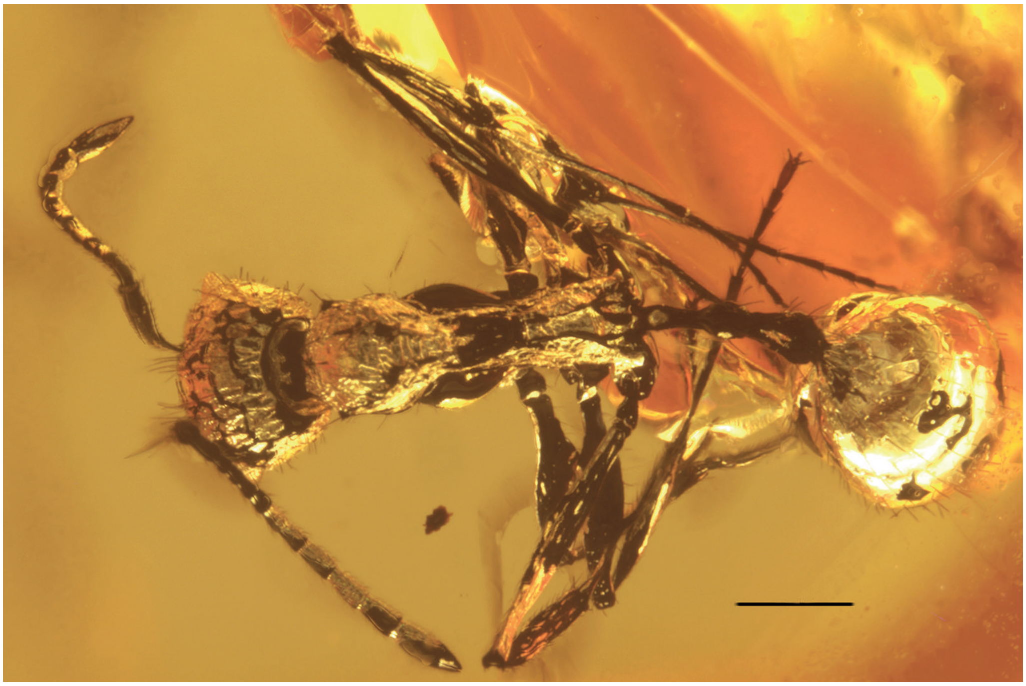

Fig. 3. Photos of *Aphaenogaster ribbeckei* Radchenko, sp. n., holotype, worker, body in dorsal view. Scale bar 0.5 mm.

vergent. Petiole very long and thin, 1.65 times as long as height, about 0.5 times as long as head, and more than 3 times as long as width; anterior surface of petiolar node very feebly concave, subvertical, posterior one very feebly convex, abruptly sloping posteriorly, anterior and posterior surfaces converge at an acute angle, so that node seems cuneiform (seen in profile). Postpetiole about 1.3 times as long as height and about 1.4 times as wide as petiole, its node somewhat flattened. Legs long and slender, meso- and metafemora strongly swollen.

Head dorsum with coarse reticulation, lateral sides of head with dense longitudinal rugosity. Lateral sides of mesosoma with coarse longitudinal rugosity, mesosomal dorsum with coarse reticulation. Surface between rugae densely punctated, but appears somewhat shiny. Petiole and postpetiole appear punctated, but shiny. Appendages and gaster smooth and shiny.

Whole head with numerous, quite long and rather coarse erect setae. Promesonotal dorsum with at least 20 similar setae, propodeal dorsum with two pairs of shorter setae, petiolar node with two pairs of long setae, postpetiole with about 10 similar setae. First gastral tergite and sternite with numerous setae, remainder sternites with much less abundant setae, remainder tergites non-setose. Decumbent pilosity on body absent. Scape with short subdecumbent pilosity, inner surface of femora with a few quite long suberect setae, tibiae and tarsi with abundant short subdecumbent pilosity.

Gynes and males unknown.

Measurements (in mm) and ratios: HL 1.01, HW 0.82, SL 1.08, FW 0.25, FLW 0.28, OL 0.20, OW 0.13, GL 0.23, ML 1.53, MH 0.42, PnW 0.49, PL 0.49, PH 0.30, PW 0.16, PPL 0.30, PPH 0.23, PPW 0.21, HTL 0.79, HFL 1.27, ESL 0.17, ESD 0.25.

HL/HW 1.24, SL/HL 1.06, SL/HW 1.32, FW/HW 0.30, FLW/FW 1.12, OL/HL 0.20, OL/OW 1.55, OL/GL 0.86, PL/PH 1.65, PL/PW 3.17, PL/HL 0.49, PW/HW 0.19, PPL/PPH 1.28, PPW/PW 1.38, PPW/HW 0.26, ESL/HL 0.17, ESL/HW 0.21, ESD/ESL 1.46, ML/MH 3.69, ML/PnW 3.11, HTL/ML 0.60, HFL/ML 0.83.

Comparative diagnosis. For the differences from *A. groehni* see above. *A. ribbeckei* differs well from other previously described *Aphaenogaster* species from the Late Eocene European ambers primarily by the much more slender mesosoma and waist, in particular, ML/MH 3.7 vs. < 3.0, PL/PW 3.2 vs. < 2.2. By the shape of promesonotum *A. ribbeckei* resembles *A. sommerfeldti*, but differs by this feature from other amber species. In addition, it differs from *A. oligocenica* by the longer and pointed propodeal spines, and from *A. antiqua* — by the longer scape and funicular segments.

Discussion

The genus *Aphaenogaster* belongs to the tribe Stenammini Ashmead, 1905 (sensu Ward et al., 2015). The characteristic features of the tribe are the distribution of the vast majority of its representatives in the temperate zone of the northern hemisphere, and the evolution of many genera toward adaptation to granivory: five of the seven genera of the tribe are specialised harvesters inhabiting arid and semiarid landscapes (Bernard, 1967, 1974; Arnoldi, 1976; Collingwood, 1978; Dlussky, 1981; Tohmé G. & Tohmé H., 1981; Bolton, 1982; Collingwood & Agosti, 1996; Demarco & Cognato, 2015; Salata & Borowiec, 2015; Johnson et al., 2022). Among them, *Goniomma* Emery, 1895 and *Oxyopomyrmex* André, 1881 are the Palaearctic endemics, *Novomessor* Emery, 1915 and *Veromessor* Forel, 1917 are the Nearctic endemics, and in the predominantly Palaearctic genus *Messor* Forel, 1890, only a small number of species are distributed in the arid regions of the Afrotropics, Arabian peninsula, Pakistan and India. At the same time, representatives of *Stenamma* Westwood, 1839 inhabit mesophytous temperate and partly tropical forests, and *Aphaenogaster* species live both in temperate deciduous forests and in open semiarid landscapes.

The origin of the Stenammini crown-group is assumed to be around 51 Ma (Early Eocene), and the *Aphaenogaster* clade is inferred to have originated in the Palaearctic 42.2 Ma (Middle Eocene) (Ward et al., 2015; Branstetter et al., 2022). The latter dating is quite consistent with paleontological data, although the time of origin of *Aphaenogaster* should be early rather than middle Eocene. The fact is that the oldest known fossil *Aphaenogaster dlusskyana* Radchenko et Perkovsky, 2016 has been found in Middle Eocene Sakhalin amber. It was already a "typical" *Aphaenogaster* with a slender body, a moderately elongated suboval head, a rather long scape, and palp formula 5, 3 (for details see Radchenko & Perkovsky, 2016). Thus, it can be assumed that *Aphaenogaster* arose before the middle Eocene.

Modern *Aphaenogaster* species are fairly diverse morphologically, which has led to the establishing of several subgenera in this genus, but all these names are considered now junior synonyms of *Aphaenogaster* (see Bolton, 2024). Branstetter et al. (2022) showed that *Aphaenogaster* in modern interpretation is a polyphyletic genus and is clearly divided into two clades: one includes Holarctic species form the former subgenera *Attomyrma* Emery, 1915 and *Aphaenogaster* s. str. + genus *Messor* Forel, 1890, and "*Deromyrma*" clade, containing species from the former subgenera *Deromyrma* Forel, 1913**,** *Nystalomyrma* Wheeler, 1916 and *Planimyrma* Viehmeyer, 1914, distributed in Central America, Madagascar, New Guinea and Australia.

More likely, the "true" *Aphaenogaster* evolved in the Eocene warm forests and led an epigean lifestyle. Further morphological radiation began much later and was associated with adaptation to the drier and open habitats in Miocene (Branstetter et al., 2022; Schifani et al., 2022). The main evolutionary-morphological trend can be the elongation of the head, body, legs and antenna, so that the head could become elongated-oval, strongly narrowed backward and without occipital corners. In this case Eocene-Oligocene fossil species do not appear to be specialised. These are species from the Late Eocene European ambers, as well as *A. donisthorpei* Carpenter, 1930 and *A. mayri* Carpenter, 1930 (Florissant, United States, terminal Eocene), *A. archaica* (Meunier, 1915) (Rott, Germany, Late Oligocene) and *A. enspelensis* Jessen, 2020 (Enspel Formation, Germany, Late Oligocene). At the same time, Miocene species from the Dominican and Mexican ambers were already quite specialised. For example, *A. amphieocenica* De Andrade, 1995 has a very elongated and narrowed posteriorly head with a "neck" (as in species of the former subgenus *Deromyrma*), and *A. praerelicta* De Andrade, 1995 has very long propodeal spines and a pair of short spines on the humeral angles (for more details see De Andrade, 1995).

However, all previously known *Aphaenogaster* species from the Late Eocene European ambers (Mayr, 1868; Wheeler, 1915; Dlussky & Perkovsky, 2002) are unspecialised: they have not very elongated head, mesosoma and appendages, a head with rounded, but clearly defined occipital corners, while all of these species well distinguished from each other and can be assigned to different species groups. On the other hand, the new species have some specialised features. Thus, mesosoma in *A. ribbeckei* is more slender (ML/MH 3.7 vs. < 3.0 in other species) and head in *A. groehni* is narrowed posteriorly and without marked occipital corners, and scape is distinctly longer than in all other amber species.

All these indicate that in the Late Eocene *Aphaenogaster* had undergone considerable diversification, ranking third in the number of species among the amber Myrmicinae genera, second only to *Temnothorax* Mayr, 1861 and *Myrmica* Latreille, 1804 with 18 and 9 species, respectively (Radchenko, 2023; Radchenko, unpubl.).

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