# New species of the extinct ant genus *Enneamerus* Mayr (Hymenoptera, Formicidae) and designation of the neotype of *E. reticulatus*

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**ABSTRACT.** A new species of the peculiar extinct myrmicine ant genus *Enneamerus* Mayr is described from Baltic amber (Late Eocene, Priabonian, ca. 34-38 Ma), and a neotype of *E. reticulatus* Mayr is designated. *Enneamerus costatus* sp. nov. differs from the previously known *E. reticulatus* by its much coarser, costulate sculpture on the frons and by the absence of long erect hairs on the antennal scape. Some additional diagnostic features for *Enneamerus* are provided and the taxonomic position of the genus is discussed.

**Keywords:** Myrmicinae, fossil, new species, *Enneamerus costatus*, *E. reticulatus*, neotype, Late Eocene, Baltic amber, Rovno amber

# **INTRODUCTION**

The quite unusual and highly specialized monotypic extinct ant genus *Enneamerus* was erected by Mayr (1868) to classify the species *E. reticulatus* Mayr, which at the time was described based on 3 workers from the collections of Berendt and Menge (Baltic amber). In his monograph, "The Ants of the Baltic Amber", Wheeler (1915) studied 10 additional workers of this species (but not Mayr's syntypes) and drew the specimen No. K-820, but added no further taxonomic comments or depictions of this species.

Primarily, the genus is characterized by its 9-segmented antennae with 3-segmented club, by the presence of antennal scrobes, and by its poorly developed, subvertical frontal lobes that expose the antennal sockets in full-face view. Besides this, the mandibles have well developed, quite wide masticatory margins armed with six teeth, the propodeum bears two moderately long spines, the middle and hind tibiae lack spurs, and the mesosoma is coarsely reticulated. During our ongoing revision of ants from the Late Eocene European ambers we have found several additional specimens of *E. reticulatus* in Baltic and Rovno ambers, as well as a specimen from Baltic amber that did not exactly match the description of the type species. Hence, we describe below the new species *E. costatus* sp. nov., provide some additional diagnostic features for *Enneamerus*, and discuss its taxonomic position. Additionally, we designate a neotype of *E. reticulatus*.

# MATERIAL AND METHODS

In total, I (AR) personally examined four specimens of *Enneamerus* from four pieces of amber. One was the single specimen (holotype worker) of *E. costatus* sp. nov., which is deposited in the Geological-Paleontological Institute and Museum, Hamburg University, Germany (GPMHU, from the collection of C. Gröhn). The other three were specimens of *E. reticulatus* – two workers from Baltic amber, which are deposited in the Muzeum Ziemi of Polish Academy of Sciences, Warsaw (MZ PAN), and one worker from the Rovno amber, which is deposited in the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev (SIZK).

Additionally, before his death, my coauthor Dlussky investigated four specimens of *E. reticulatus* in three pieces of Baltic amber from the old private collection of Prof. R. Klebs from Konigsberg, which are now preserved in the Geowissenschaftlicher Zentrum der Georg-August-Universitat Göttingen, Germany (GZG.BST). Because the original Mayr's syntypes seem to be lost, we propose to designate as the neotype the specimen GZG.BST 04660 (original Klebs' No. is K 1698), which previously has been investigated by Wheeler (1915) and determined by him as *E. reticulatus*.

The figures are based on original drawings of the specimens and photographs made using an Olympus Camedia C-3030 digital camera fitted to an Olympus SZX9 microscope.

Not all features of the examined specimens were properly visible and measurable, hence we measured only visible details (accurate to 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 midpoint of occipital margin;
- HW maximum width of the head in dorsal view behind (above) the eyes;
- SL maximum straight-line length of the scape from its apex to the articulation with condylar bulb;
- OL maximum diameter of the eye;
- 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;
- PNW maximum width of the pronotum from above;

- PL maximum length of the petiole, measured from the posterodorsal margin of petiole to the articulation with propodeum;
- PW maximum width of the petiole from above;
- PH maximum height of the petiole in profile, measured from the uppermost point of the petiolar node perpendicularly to the virtual line between the tip of subpetiolar process and posteroventral points of petiole;
- PPL maximum length of the postpetiole between its visible anterior and posterior margins;
- PPW maximum width of the postpetiole in dorsal view;
- PPH maximal height of the postpetiole in profile;
- HTL maximum length of the hind tibia;
- 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 the propodeal spine in dorsal view.

Approximate total length is calculated as the sum of HL+ML+PL+PPL+length of the gaster.

For simplicity, we give ratios of various measurements (e.g. HL/HW) rather than name and abbreviate various indices (e.g. CI) as we have done elsewhere.

# RESULTS

## Genus Enneamerus Mayr

*Enneamerus* Mayr, 1868: 98, worker, Baltic amber. Type species: *Enneamerus reticulatus* Mayr, 1868: 100, by monotypy.

**Species composition**: *E. reticulatus* Mayr and *E. costatus* sp. nov.



**Fig. 1.** Photographs of worker of *Enneamerus reticulatus* Mayr, specimen MZ PAN 15434. A) Body in dorso-lateral view. B) Head in dorso-lateral view. Scale bars -1 mm.



Fig. 2. Line drawings of worker of *Enneamerus reticulatus* Mayr, specimen MZ PAN 15434. A) Body in dorsolateral view. B) Head in dorso-lateral view. Scale bars -1 mm.



**Fig. 3.** Worker of *Enneamerus reticulatus* Mayr, specimen SIZK K-8937, body in lateral view. A) Photograph. B) Line drawing. Scale bars – 1 mm.

#### Diagnosis:

- antennae 9-segmented with 3-segmented club;
- antennal scrobes on the head dorsum well developed, extending above eyes;
- frontal lobes poorly developed, subvertical, antennal sockets fully exposed;
- central part of clypeus longitudinally concave and delineated by two lateral carinae; its anterior margin shallowly concave, without any teeth or dents and with set of longer and shorter setae;
- mandibles rather wide, masticatory margin with six teeth;
- middle and hind tibiae without spur;
- propodeum with moderately long spines, directed backward and upward, distinctly divergent, acute at apex.

## Enneamerus reticulatus Mayr, 1868 (Figs 1-3)

*Enneamerus reticulatus* Mayr, 1868: 100, worker, Baltic amber; Wheeler 1915: 71.

*Material examined*: neotype, worker, Baltic amber, No. GZG.BST.04660 (original Klebs' No. K 1698); 3 workers, Baltic amber, No. GZG. BST.04666 (original Klebs' No. K 1682; 1 specimen) and GZG.BST.04662 (original Klebs' No. K 4248, two specimens); 2 workers in two pieces of Baltic amber, No. MZ PAN 1221 and MZ PAN 15434; 1 worker, Rovno amber, No. SIZK K-8937.

## Diagnosis.

- head dorsum with fine longitudinal rugae, number of rugae between frontal carinae level with the eyes 4-5; surface between rugae densely but not too coarsely reticulated;
- mesosoma coarsely reticulated, petiole and postpetiole less coarsely but densely reticulated;
- antennal scape strongly bent at the base, without any trace of lobe or carina;
- body with quite abundant, long, slightly curved erect to suberect hairs; antennal scape with long abundant curved erect to suberect hairs that distinctly longer than maximum

width of scape; legs with abundant decumbent pilosity and sparser and longer subdecumbent hairs.

### **Morphometrics**

-- MZ PAN 15434:

**Measurements (in mm)**: HL 0.71, HW 0.59, SL 0.53, OL 0.16, ML 0.73, PPL 0.16, PPH 0.16, PPW 0.21, HTL 0.43, ESL 0.13, total length ca. 2.5.

Ratios: HL/HW 1.20, SL/HL0.75, SL/HW 0.90, OL/HL 0.23, PPL/HL 0.23, ESL/HL 0.18, ESL/ HW 0.23; -- SIZK K-8937:

**Measurements (in mm)**: HL 0.64, HW 0.52, SL 0.47, OL 0.14, ML 0.70, PL 0.23, PH 0.22, PPL 0.16, PPH 0.18, ESL 0.14, HTL 0.39, total length ca. 2.6.

**Ratios**: HL/HW 1.23, SL/HL 0.73, SL/HW 0.90, OL/HL 0.22, PL/HL 0.37, PL/PH 1.06, PPL/HL 0.24, PPL/PPH 0.86, ESL/HL 0.20, ESL/HW 0.27.

#### *Enneamerus costatus* sp. nov. (Figs 4-6)

*Material examined*. Holotype worker, Baltic amber, GPMHU, No. F-6763 from the collection of C. Gröhn.

*Etymology*. The name is derived from the Latin word "*costa*" – rib, edge, and refers to the costate sculpture on the frons.

**Worker**. Head widely oval, with convex sides and occipital margin and widely rounded occipital corners. Eyes of moderate size, subcircular, situated behind midlength of sides of head. Antennae 9-segmented, with distinct, large 3-segmented club that is somewhat longer than total length of 2<sup>nd</sup> to 5<sup>th</sup> funicular segments together; each of the latter segments somewhat longer than wide; scape strongly curved at base, without any trace of lobe or carina, relatively long, almost reach-



**Fig. 4.** Holotype worker of *Enneamerus costatus* sp. nov., specimen GPMHU, No. F-6763, body in dorsal view and larva. A) Photograph. B) Line drawing. Scale bars -1 mm.



Fig. 5. Photograph of holotype worker of *Enneamerus costatus* sp. nov., specimen GPMHU, No. F-6763, body in lateral view and larva. Scale bar -1 mm.

ing occipital margin. Antennal scrobes well developed, deep, extend above eyes. Clypeus with two coarse longitudinal medial carinae, surface between them distinctly longitudinally concave (depressed); anterior clypeal margin very shallowly concave, without teeth or denticles. Mandibles quite wide, masticatory margin with long apical tooth and 5 small teeth of the same size.

Mesosoma short and stout, narrowed posteriorly, promesonotal suture absent, metanotal groove distinct, wide and deep. Anterior margin of pronotum slightly convex, humeri very narrowly rounded. Dorsal surface of propodeum ca. twice shorter than posterior one. Propodeal spines not long (but not dentiform), widened at base, acute at tips, directed more upward than backward and divergent laterally. Petiole with distinct but relatively short peduncle, subequal to its height, its anterior surface strongly concave; petiolar node high, quite thin, with narrowly rounded dorsum and rather steep anterior and posterior surfaces; seen in profile, node subconical, narrowing to apex, with slightly convex crest. Postpetiole short and wide, rounded dorsally.

Frons with coarse longitudinal, slightly sinuous six costae between frontal carinae at level of eyes; surface between costae with fine reticulation. Occipital area, temples and sides of head with coarse reticulation. Mesosomal dorsum with coarse reticulation, mesopleura and sides of propodeum with coarse, short longitudinal rugae. Petiolar node and postpetiolar dorsum smooth and shiny. Gaster smooth and shiny. Mandibles longitudinally rugulose.

Body with sparse, not long, somewhat curved erect to suberect hairs. Scape with sparse, rather short suberect hairs, which are subequal or shorter than width of scape; funiculus with short subdecumbent hairs, legs with sparse short decumbent pilosity.



**Fig. 6.** Line drawings of holotype worker of *Enneamerus costatus* sp. nov., specimen GPMHU, No. F-6763. A) Body in lateral view and larva. B) Head in dorso-lateral view. Scale bars – 1 mm.

# **Morphometrics**

Measurements (in mm): HL 0.86, HW 0.68, SL 62, OL 0.21, ML 0.78, PNW 0.33, PL 0.30, PW 0.18, PH 0.29, PPL 0.13, PPW 0.22, PPH 0.17, ESL 0.18, ESD 0.27, HTL 0.51, total length ca. 3. Ratios: HL/HW 1.27, SL/HL 0.72, SL/HW 0.92,

PL/HL 0.35, PL/PH 1.03, PPL/HL 0.15, PPL/ PPH 0.76, ESL/HL 0.21, ESL/HW 0.26, ESD/ ESL 1.50.

## Comparative diagnosis.

*E. costatus* sp. nov. clearly differs from *E. re-ticulatus* by the much coarser, costate sculpture

on the frons, the much less abundant and shorter standing hairs on the antennal scape, and the generally less abundant pilosity on the body.

# DISCUSSION

As was already stressed by Wheeler (1915) and supported by modern data (Guénard *et al.* 2015), the ants from Baltic and other Late Eocene European ambers might be placed into two main zoogeographic complexes: temporary Palaearctic/ Holarctic, and tropical, mainly Indomalayan and Australasian.

Only five other myrmicine genera are known to have workers with 9-segmented antennae and a distinct 3-segmented club. These are *Rostromyrmex* Rosciszewski, *Meranoplus* F. Smith and *Perissomyrmex* M. Smith, while in the genera *Pheidole* Westwood and *Atopomyrmex* André such structure of antennae occurs in only some species. This feature of *Enneamerus* suggests that it may be grouped with these five genera, but it is different from them as follows.

The structure of the clypeus, frontal lobes and presence of the antennal scrobes well differentiate Enneamerus from Pheidole and the small Afrotropical genus Atopomyrmex (see also Bolton 1994, Fisher & Bolton 2016). The peculiar monotypic Malaysian genus Rostromyrmex similarly has antennal scrobes, but it differs from Enneamerus by its well developed, horizontal frontal lobes that partly cover the antennal sockets (at least the torulus is concealed), by the extremely narrowed, strip-like median portion of clypeus, and by the distinctly prominent anterior clypeal margin that forms s narrow tooth-like rostrum; additionally, the eyes in Rostromyrmex are very small and situated distinctly in front of the midlength of the sides of the head (Rosciszewski 1994).

The genus *Meranoplus* is similar to *Enneamerus* in its head and antennal structure, both having well developed antennal scrobes on the head dorsum that extend above the eyes, and rather large eyes situated distinctly behind the midlength of the sides of head. However, *Meranoplus* well differs from *Enneamerus* by the very peculiar shape of its promesonotum that

forms a shield that overhangs the pleurae laterally, and usually overhands the propodeum posteriorly. Moreover, according to Bolton (2003, p. 68) the genus *Meranoplus* "...is a strongly isolated and very divergent taxon whose members are morphologically very uniform. The number of unique morphological specialisations renders its relationships difficult to discern".

Among all genera mentioned above, *Enneamerus* is most similar by its general appearance to the peculiar Old and New World tropical genus *Perissomyrmex*, but well differs from it by the presence of the antennal scrobes, the lack of any teeth or dents on the anterior clypeal margin, and the structure of mandibles, which have a fairly wide masticatory margin with six teeth in *Enneamerus* and a narrower masticatory margin with only three teeth and with an additional tooth on the inner margin in *Perissomyrmex* (Smith M. 1947, Baroni Urbani & de Andrade 1993, Radchenko 2003, Xu & Zhang 2012).

*Enneamerus* is also very similar to the Old World tropical genus *Pristomyrmex* Mayr (one extinct species of this genus was recently described from the Late Eocene Danish amber by Dlussky & Radchenko 2011). However, *Pristomyrmex* differs in having 11-segmented antennae (see also Wang 2003).

Based on the similarities to the other genera, Bolton (1994, 1995, 2003) considered that Enneamerus had a high probability of belonging to the tribe Myrmecinini (sensu Bolton 2003). According to the system recently proposed by Ward et al. (2014) this corresponds to the clades comprising Myrmecina Curtis and Pristomyrmex + Perissomyrmex within the tribe Crematogastrini. However, the structure of the clypeus of Enneamerus does not fully correspond with that of the genera Myrmecina, Pristomyrmex and Perissomyrmex: its central part is longitudinally concave (depressed) and delineated by two lateral carinae, while the anterior clypeal margin is shallowly concave, without any teeth or dents though with a set of longer and shorter setae. By these features, it is more similar to some Solenopsidini and Stenammini, so that in our opinion, the taxonomic position of Enneamerus is less obvious than supposed by Bolton (2003). We suggest that Enneamerus represents an extinct specialized lineage within the subfamily Myrmicinae and cannot be considered as a direct ancestor of any known either extinct or extant myrmicine genera.

Finally, the holotype worker of *E. costatus* has been trapped in resin together with an ant larva (see Figs 4-6), and such findings are very rare in ambers. We suppose that the worker was carrying the larva while changing the nest site. Perhaps this species was able to form polycalic colonies and had quite high level of sociality. On the other hand, we cannot exclude the alternative, perhaps less likely, possibility that it was a larva of another ant species taken as prey.

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