A new ant genus from the late Eocene European amber

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Eocenomyrma gen. nov. of extinct ants of the family Formicidae, subfamily Myrmicinae, is described from the late Eocene European amber (ca. 40 Ma), based on six specimens from six pieces of amber; three of them contain *E. rugosostriata* (Baltic and Saxonian ambers); the remainder contain three new species: *E. orthospina* (Baltic Amber), *E. electrina* (Scandinavian Amber), and *E. elegantula* (Baltic Amber). *Eocenomyrma* resembles two extant genera: *Myrmica* and *Temnothorax* (both of which also occur in late Eocene European amber), but differs from them by the following apomorphies: clypeus short and broad, with two lateral longitudinal carinae and distinctly marked anterolateral corners, its median portion faintly concave transversally, anterior margin broad and shallowly concave medially, with pairs of long setae situated on the anterolateral clypeal corners, and central part of the anterior clypeal margin without setae; middle and hind tibiae lacking the spurs. Palp formula in *Eocenomyrma* is 4, 3 *versus* 6, 4 in *Myrmica*. We include *Eocenomyrma* in the tribe Formicoxenini. *Nothomyrmica rugosostriata* is transferred to *Eocenomyrma*, and the neotype of the latter species is designated; *Nothomyrmica petiolata* is transferred to the genus *Temnothorax*. A key for the identification of all known *Eocenomyrma* species is compiled.

Key words: Formicidae, Myrmicinae, Eocenomyrma, Baltic Amber, Saxonian Amber, Danish Amber, Eocene.

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Introduction

The ants of the Baltic Amber (late Eocene, ca. 40 Ma) are the best studied among all known fossil ant faunas in the world. Many thousands of specimens preserved in amber have been studied until now, and 97 Formicidae species from 46 genera are known (Mayr 1868; André 1895; Emery 1905; Wheeler 1915; Dlussky 1967, 1997, 2002a, b). However, the ant fauna from other ambers of the same age either have not been studied to any extent (Saxonian and Scandinavian ambers) or studies have only recently started (Rovno Amber; Dlussky 2002a; Dlussky and Perkovsky 2002).

Among other species from the Baltic Amber, Mayr (1868) described *Macromischa petiolata*, *M. rugosostriata*, and *M. rudis*. Wheeler (1915) erected a new genus *Nothomyrmica* to include all Mayr's *Macromischa* species mentioned above, and the new species—*N. intermedia* Wheeler, 1915; he designated *M. rudis* as the type species of this genus. In that paper, Wheeler emphasised the similarity between genera *Nothomyrmica* and *Myrmica* Latreille, 1804, and considered as the main distinguishing character of *Nothomyrmica* from *Myrmica* the lack of spurs on the hind and middle tibiae in *Nothomyrmica*. However, the feature of reduced tibial spurs is considered much less diagnostic nowadays, since many extant *Myrmica* species have reduced tibial spurs (Bolton 1988; Radchenko and Elmes 2003). In our opinion, genus *Nothomyrmica* is heterogenic and artificially joins unrelated

species having one common feature—the absence of spurs on the hind and middle tibiae. Therefore, *N. intermedia* and *N. rudis* were very recently transferred to the genus *Myrmica*, and genus *Nothomyrmica* was formally synonymised with *Myrmica* (Radchenko et al. in press), because Wheeler (1915) designated *N. rudis* (Mayr, 1868) as its type species.

On the other hand, two of the *Nothomyrmica* species (*sensu* Wheeler 1915), *N. rugosostriata* and *N. petiolata*, definitely do not belong to *Myrmica*. *N. petiolata* is indistinguishable by all its characteristic features from *Temnothorax* Mayr, 1861 (*sensu* Bolton 2003), therefore we formally transfer it now to *Temnothorax* (comb. nov.). We could not place *N. rugosostriata* into a known extinct or extant ant genus. However, it clearly belongs to the same genus as three new species, that we had found in the course of our investigation of amber ants, which we considered represented a new genus—*Eocenomyrma*. Here we describe the new genus, the three new species, formally transfer *N. rugosostriata* to it, and finally provide a key for the identification of these four species.

Institutional abbreviations.—GPMHU, Geological-Palaeontological Institute and Museum, Hamburg University, Germany; MZ, Museum of Earth (Muzeum Ziemi) of the Polish Academy of Sciences, Warsaw, Poland; ZMHU, Zoological Museum of Humboldt University, Berlin, Germany; ZMUC, Zoological Museum of University of Copenhagen, Denmark. In total, we investigated six specimens in the six pieces of amber, three of which are assigned to *Eocenomyrma rugosostriata* and the others—three newly described species. This material is preserved in the MZ (Baltic Amber), ZMUC (Scandinavian Amber), ZMHU (Saxonian Amber), GPMHU (Baltic Amber), and in the personal collections of Manfred Kutscher, Sassnitz, Rugen, Germany (Saxonian Amber).

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 in conjunction with the computer program CorelDraw 8.

Morphometrics.—The specimens were measured (accurate to 0.01mm), and the measurements were used to calculate the various indices defined below. Since not all features were easily visible and measurable on the specimens examined, we measured as many as possible of them on each specimen.

Measurements.—AH, height of mesosoma, measured from upper level of mesonotum perpendicularly to the level of lower margin of mesopleuron; AL, diagonal length of the mesosoma seen in profile, from the neck shield to the posterior margin of propodeal lobes; ESD, distance between tips of propodeal spine from above; ESL, maximum length of propodeal spine in profile, measured along the spine from its tip to the deepest point of the propodeal constriction at the base of spines; FLW, maximum width between external borders of the frontal lobes; FW, minimum width of frons between frontal carinae; HL, length of head in full face view, measured in a straight line from the anterior point of median clypeal margin to mid-point of the posterior margin; HTL, length of tibia of hind leg; HW, maximum width of head in dorsal view behind the eyes; PH, maximum height of petiole in profile; PL, maximum length of petiole from above; PNW, maximum width of pronotum from above; PPH, maximum height of postpetiole

in profile; PPL, maximum length of postpetiole from above; PPW, maximum width of postpetiole from above; PW, maximum width of petiole from above; SL, maximum straight-line length of antennal scape seen in profile.

Indices.—AI = AL/AH; CI = HL/HW; ESDI = ESD/ESL; ESLI = ESL/HW; FI = FW/HW; FLI = FLW/FW; PI = PL/PH; PPI = PPL/PPH; SI₁ = SL/HL; SI₂ = SL/HW.

Systematic palaeontology

Family Formicidae Latreille, 1809 Subfamily Myrmicinae Lepeletier, 1835 Genus *Eocenomyrma* nov.

Type species: Eocenomyrma orthospina sp. nov.

Derivation of the name: After the Eocene, time when it existed, and Greek *myrmex*—ant.

Specimens examined	HL	HW	FW	FLW	SL	AL	AH	PNW	HT
Eocenomyrma orthospina, holotype	0.64	0.53	0.22	0.28	0.41	0.87	0.36		0.32
Eocenomyrma electrina, holotype	0.81	0.76	0.29	0.36	0.57	0.88	0.49		
Eocenomyrma elegantula, holotype	0.92					1.26	0.52		0.53
Eocenomyrma rugosostriata, neotype	1.02	0.84	0.43	0.48	0.60	1.20	0.50	0.45	0.50
Eocenomyrma rugosostriata, F-170						1.16	0.48		0.49
Eocenomyrma rugosostriata, MZ 20234	1.02	0.84	0.41	0.46		1.19		0.46	
	PL	PH	PW	PPL	PPH	PPW	ESL	ESD]
Eocenomyrma orthospina, holotype	0.32	0.17					0.24		1
Eocenomyrma electrina, holotype	0.27	0.21		0.25	0.25		0.27]
Eocenomyrma elegantula, holotype	0.52	0.28		0.31	0.25		0.22]
Eocenomyrma rugosostriata, neotype	0.46	0.29	0.18	0.28	0.28	0.36	0.27	0.25	1
Eocenomyrma rugosostriata, F-170	0.46	0.28		0.28	0.29]
Eccenomyrma rugosostriata M7 20234				0.28		0.36			1

Table 1. Measurement (in mm) of the Eocenomyrma species.

Table 2. Morphometric indices of the Eocenomyrma species.

Specimens examined	CI	FI	FLI	SI1	SI ₂	PI	PPI	ESLI	ESDI	AI
Eocenomyrma orthospina, holotype	1.21	0.42	1.25	0.63	0.76	1.92		0.44		2.38
Eocenomyrma electrina, holotype	1.07	0.39	1.24	0.71	0.76	1.27	1.00	0.35		1.80
Eocenomyrma elegantula, holotype						1.85	1.22			2.43
Eocenomyrma rugosostriata, neotype	1.22	0.52	1.10	0.59	0.72	1.57	1.00	0.32	0.94	2.39
Eocenomyrma rugosostriata, F-170						1.65	0.95			2.44
Eocenomyrma rugosostriata, MZ 20234	1.22	0.48	1.14							

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Diagnosis.-Clypeus short and broad, with two lateral longitudinal carinae and distinctly marked anterolateral corners, its median portion faintly concave transversally, anterior margin broad and shallowly concave; pairs of long setae situate on the anterolateral clypeal corners, central part of the anterior clypeal margin without setae (the latter features are not visible in all described species); clypeus posteriorly broadly inserted between frontal lobes; frontal lobes broad, anteriorly reaching or even surpassing anterior clypeal margin; maxillary palps with 4, labial palps with 3 segments (this feature is visible only in Eocenomyrma rugosostriata); antennae 12-segmented, with the remarkable 3-segmented apical club, which is clearly separated from the rest of funiculus; middle and hind tibiae are lacking spurs; body (except the gaster) distinctly sculptured (rugose and/or reticulate), not smooth; mesosoma with distinct metanotal groove; propodeum is with quite long spines; eyes well developed, big.

Eocenomyrma is superficially similar to some ant genera, both extinct and extant, particularly to the *Myrmica* and *Temnothorax* Mayr, 1861 (see also Bolton 2003), but clearly differs from them in the peculiar shape of the clypeus: in *Myrmica* and *Temnothorax* the median portion of clypeus is convex or somewhat flattened, but never concave transversally, without lateral longitudinal carinae and marked anterolateral corners; anterior clypeal margin is rounded or somewhat prominent, occasionally shallowly notched medially. In addition, the majority of the extinct and extant *Myrmica* and *Temnothorax* species have a well-developed spur on the middle and hind tibiae, absent from the new genus.

Eocenomyrma has palp formula 4, 3 *versus* 6, 4 in *Myrmica*, what precludes their close relationship.

Remarks.—Based on the tribal characters of the subfamily Myrmicinae proposed by Bolton (2003), we suggest to include *Eocenomyrma* in the tribe Formicoxenini. As mentioned above, *Eocenomyrma* most likely is related to *Temnothorax*, and its peculiar clypeal structure may be considered as the apomorphy; lack of tibial spurs also can be regarded as apomorphy, however apomorphies by reduction are much less significant evolutionary. On the other hand, *Eocenomyrma* has some plesiomorphic (regarding to *Temnothorax*) features, particularly *Myrmica*-like structure of head and frontal lobes, general shape and sculpture of the body, etc. We suggest that *Eocenomyrma* most probably did not arise from any extant Formicoxenini genera, but has common ancestor with them, including *Temnothorax*.

Eocenomyrma orthospina sp. nov.

Fig. 1; Tables 1, 2.

Derivation of the name: After Greek orthos—straight, and Latin spina —a spine, in relation to the shape of propodeal spines of this species. Holotype: MZ 13434, worker, complete specimen. Locality and horizon: Baltic Amber, late Eocene.

Diagnosis.—Total length ca. 3–3.5 mm. The new species is characterised by the following apomorphies: frontal carinae are short, quite strongly curved and merge with the rugae,





Fig. 1. Myrmicine ant *Eocenomyrma orthospina* sp. nov., the holotype worker, MZ 13434, from the Baltic Amber, late Eocene. A. Photograph in dorso-lateral view. **B**, **C**. Explanatory drawings, based on the original photographs; head, mesosoma and waist in dorso-lateral view (**B**), and mesosoma and petiole in lateral view (**C**).

which surround antennal sockets; frons quite wide, frontal lobes rather big and extended laterally; mesosoma of moderate length, not robust, not constricted behind so that propodeum not much narrower than promesonotum, metanotal groove distinct but shallow (seen in profile), promesonotal suture invisible (seen from above); propodeal spines quite long, not widened at the base, slender, more or less straight, pointed at the tips, directed backward and upward at an angle about 45°, and feebly divergent (seen from above); petiole much longer than high, with very long peduncle, petiolar node with rounded dorsum, without dorsal plate; frons with not coarse longitudinal, slightly sinuous rugae, lateral parts of head dorsum and occiput with reticulation; mesosoma with quite coarse reticulation (the sculpture of petiole is invisible).

By the complex of these features *Eocenomyrma orthospina* differs from the all known species of the genus *Eocenomyrma*, particularly from *E. elegantula*, which has a finely reticulated, not rugose body. It clearly differs from *E. rugosostriata* by the coarsely reticulated mesosoma, by the straight, not curved down propodeal spines, by the longer petiole, and by the strongly curved frontal carinae and distinctly narrower

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Fig. 2. Myrmicine ant *Eocenomyrma electrina* sp. nov., the holotype worker, ZMUC 328, from the Scandinavian Amber, late Eocene. **A**, **B**. Photograph in dorso-lateral view (**A**), and head and mesosoma in dorso-lateral view (**B**). **C**, **D**. Explanatory drawings, based on the original photographs; head, mesosoma, waist, and base of gaster in dorso-lateral view (**C**), and mesosoma, waist, and base of gaster in lateral view (**D**).

frons. *E. orthospina* most resembles *E. electrina*, but differs from the latter in the longer, not robust mesosoma, by the straight, not widened, pointed propodeal spines, and by the much longer petiole (PI 1.92 *versus* 1.27).

Eocenomyrma electrina sp. nov.

Fig. 2; Tables 1, 2.

Derivation of the name: After Latin electrum-amber.

Holotype: ZMUC 328, worker, complete specimen, leg. G.V. Henningsen, 16/5-1956.

Locality and horizon: Scandinavian Amber, late Eocene.

Diagnosis.—Total length ca. 3 mm. The new species is characterised by the following apomorphies: frontal carinae are short, quite strongly curved and merge with rugae, which surround antennal sockets, frons not very wide, but frontal lobes quite big and extended laterally; mesosoma short and robust, not constricted behind so that propodeum not much narrower than promesonotum, metanotal groove distinct, though not deep (seen in profile), promesonotum (seen from above) with weak but distinct promesonotal suture; propodeal spines of moderate length, wide and stout, rather blunt, slightly curved downwards, directed mainly backward and feebly divergent (seen from above); petiole only slightly lon-

ger than high, with distinct but not very long peduncle, petiolar node with rounded dorsum, without dorsal plate; lower (anterior) part of frons with not coarse longitudinal rugae, remainder part of head dorsum with longitudinal rugosity and reticulation; mesosoma with coarse reticulation, petiole and postpetiole with not coarse longitudinal rugae.

Eocenomyrma electrina differs from the all known *Eocenomyrma* species by its relatively short and robust mesosoma (AI 1.80 *versus* >2.30 in other species) and much shorter petiole (PI 1.27 *versus* >1.55 in other species). Additionally, it differs from *E. elegantula* by the body sculpture (see below); from *E. rugosostriata* it differs by the reticulated mesosoma, by the distinctly narrower frons (FI 0.39 *versus* 0.48–0.52), by the much more extended frontal lobes (FLI 1.24 *versus* 1.10–1.14), by the longer antennal scape (SI₁ 0.71 *versus* 0.59), by reticulated sculpture of the mesosoma, by the smaller body size; for the differences between *E. electrina* and *E. orthospina* see above.

Eocenomyrma elegantula sp. nov.

Fig. 3; Tables 1, 2.

Derivation of the name: After Latin *elegantis*—nice, pretty. *Holotype*: GPMHU 4404, worker, complete specimen.

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Fig. 3. Myrmicine ant *Eocenomyrma elegantula* sp. nov., the holotype worker, GPMHU 4404, from the Baltic Amber, late Eocene. **A**. Photograph in lateral view. **B**. Explanatory drawing, based on the original photograph; lateral view.

Locality and horizon: Baltic Amber, late Eocene.

Diagnosis.—Total length ca. 4 mm. This new species is characterised by the following apomorphies: frontal carinae and frontal lobes are obscure, but frontal lobes seem to be quite narrow, not extended laterally, frons quite wide; mesosoma long, not constricted behind so that propodeum not much narrower than promesonotum, metanotal groove distinct but wide and shallow (seen in profile), promesonotal suture marked (seen from above); propodeal spines of moderate length, quite wide, stout, blunt at the tips, slightly curved downwards, directed backward at an angle about 40°, slightly divergent (seen from above); petiole distinctly longer than high, with very long peduncle, petiolar node low, long, with slightly declined

posteriorly dorsal plate, but its anterolateral ant posterolateral corners not acute, narrowly rounded; head, mesosoma and waist with fine longitudinal rugosity and reticulation.

Eocenomyrma elegantula distinctly differs from the other species of the genus *Eocenomyrma* by the finely rugoso-re-ticulated head, mesosoma and waist, and by the long petiolar node with the distinct dorsal plate.

Eocenomyrma rugosostriata (Mayr, 1868) comb. nov. Fig. 4; Tables 1, 2.

- 1868 Macromischa rugosostriata sp. nov; Mayr 1868: 84, pl. 4: 83, workers, Baltic Amber.
- 1893 Macromischa rugosostriata Mayr, Dalla Torre 1893: 120.
- 1907 Macromischa rugosostriata Mayr, Handlirsch 1907: 876.
- 1915 Nothomyrmica rugosostriata (Mayr), Wheeler 1915: 61, fig. 25, workers, queen.

1995 Nothomyrmica rugosostriata (Mayr), Bolton 1995: 292.

Material examined.—Neotype (present designation), ZMHU F-191, worker; 1 worker, F-170, is deposited in the private collection of Manfred Kutscher, Sassnitz, Rugen, Germany; 1 worker, MZ 20234 [together with *Dolichoderus tertiarius* (Mayr, 1868) and *Monomorium* sp. in the same piece of amber], Poland.

Diagnosis.—Total length ca. 4 mm. This species is characterised by the following apomorphies: frontal carinae are short, very weakly curved and merge with the rugae, which surround antennal sockets, frons extremely wide, frontal lobes not extended laterally; mesosoma long, constricted behind, so that propodeum much narrower than promesonotum, metanotal groove deep but wide and not abrupt, promesonotal suture marked; pronotum (seen from above) delineated by the distinct carina in front and laterally; propodeal spines of moderate length, wide and stout, slightly curved downwards apically, directed backward, and very feebly divergent (seen from above); petiole distinctly longer than high, with long peduncle, petiolar node with rounded dorsum, without dorsal plate; head dorsum with not coarse, longitudinal, subparallel, slightly sinuous rugae, without reticulation; mesosoma, petiole and postpetiole with longitudinal, slightly sinuous rugosity, without reticulation.

Eocenomyrma rugosostriata clearly differs from *E. elegantula* by its much coarser rugosity and lack of the reticulation on the head and mesosoma. Superficially it resembles *E. electrina* and *E. orthospina*, but differs from both by a much wider frons (FI 0.48–0.52 *versus* 0.39–0.42), by the narrower, not extended, frontal lobes (FLI <1.15 *versus* >1.20), by the lack of reticulation on the head and mesosoma dorsum, by the mesosoma constricted behind, so that propodeum much narrower than promesonotum. Additionally, it differs from *E. orthospina* by its distinctly downward-curved apically propodeal spines.

Remarks.—Mayr (1868: 84) described this species based on two workers from the Baltic Amber ["In der physikalischökonomischen Gesellschaft (Königsberg) 1 Stück (Nr. 218), in Coll. Künow (Justizrath, Deutschland) 1 Stück (Nr. 15)"], and attributed it to the genus *Macromischa* Roger, 1863

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Fig. 4. Myrmicine ant *Eocenomyrma rugosostriata* (Mayr, 1868), the neotype worker, ZMHU F-191, from the Saxonian Amber, late Eocene. **A.** Photograph in dorso-lateral view. **B**, **C**. Explanatory drawings, based on the original photographs; in dorso-lateral view (**B**), and mesosoma, waist, and gaster in lateral view (**C**).

(now a synonym of *Temnothorax* Mayr, 1861; see Bolton 2003). Later Wheeler (1915) transferred *M. rugosostriata* into his newly described genus, *Nothomyrmica*. He studied the queen and 10 workers (including one Mayr's syntype), preserved in Königsberg's (Germany at that time, nowadays Kaliningrad in Russia) collection, described the queen and provided drawing of the worker (not of the Mayr's syntype). At present the types of *E. rugosostriata* are absent in the Mayr's collection in Naturhistorisches Museum Wien (Ponomarenko and Schultz 1988). The most part of the Königsberg's collection was apparently lost during the World War II, but a small part of it is preserved nowadays in the collec-

tion of the Institut und Museum für Geologie und Paläontologie der Universität Göttingen (Germany). Based on the database of the fossils of Göttingen's Museum no specimens of *E. rugosostriata* can be found there (Eugeny Perkovsky, personal communication 2004). Moreover, all our efforts to discover anything on the fate of the Künow's personal collection were unsuccessful.

Therefore, we believe that both Mayr's types and Wheeler's material, belonging to this species, are lost, and we formally redescribe *E. rugosostriata* and designate the neotype (worker) of this species (see above). The neotype specimen wholly corresponds with the Mayr's and Wheeler's descriptions and drawing. Two other specimens investigated by us, are in much poorer condition, but certainly belong to this species.

Stratigraphic and geographic range.—Saxonian and Baltic ambers, late Eocene.

A Key for the identification of *Eocenomyrma* species:

- 1 Mesosoma with longitudinal, slightly sinuous rugosity (Fig. 4) *E. rugosostriata* (Mayr, 1868)
- Mesosoma at least partly with reticulation (Figs. 1–3)
- 2(1) Whole head dorsum and mesosoma with fine reticulation; petiolar node long, with distinctly flattened dorsum (Fig. 3) *E. elegantula* sp. nov.

- Propodeal spines massive, widened at the base, slightly curved downward apically, directed mainly backward; petiole with much shorter peduncle (PI 1.27) (Fig. 2)
 E. electrina sp. nov.

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