

THE ANTS OF THE GENUS *MYRMICA* (HYMENOPTERA, FORMICIDAE) FROM BALTIC AND SAXONIAN AMBER (LATE EOCENE)

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INTRODUCTION

IN THE course of ongoing revision of the ant genus *Myrmica* Latreille, 1804, we located, in the collections of the Russian and Polish Academies of Sciences, pieces of Baltic Amber (Late Eocene, ca. 40 Ma; earlier this amber was considered to be Oligocene, e.g., see Wheeler, 1915; Larsson, 1978; Bolton, 1995; Dlussky, 1997), that each contained a fossilized specimen of *Myrmica*. We were also fortunate to be given access to a piece of Saxonian Amber (the same age as Baltic Amber) from the collection of Manfred Kutscher that contained three specimens of *Myrmica*. Four of the specimens belong to two new species. We describe these below, placing them in context with extant species, and we re-appraise all previously described fossil *Myrmica*, providing a key to the identification of the five extinct “true” *Myrmica* species.

Until now, seventeen extinct ant species have been ascribed to the genus *Myrmica* (Heer, 1850, 1867; Mayr, 1868b; Novak, 1878; Meunier, 1915): four species from the Late Eocene and Oligocene (ca. 40–35 Ma) and thirteen from the Miocene (ca. 25 Ma). However, only one of these species, *M. longispinosa* Mayr, 1868b found in Baltic Amber, indisputably belongs to the genus. All other fossil “*Myrmica*” species belong to other genera. The high number of misidentifications is not surprising because most species were described a long time ago from impressions in rock. Such fossils are very difficult to interpret and identify correctly, even with considerable experience and a good knowledge of recent ant taxonomy.

Three species, *M. pusilla* Heer, 1850, *M. duisburgi* Mayr, 1868b, and *M. rugiceps* Heer, 1850 were formally transferred to other genera by Handlirsch (1907), Wheeler (1915) and Assmann (1970) respectively (see also Mayr, 1867; Bolton, 1995), and one name (*M. bicolor* Heer, 1867) was considered to be a junior synonym of *M. tertiaria* Heer, 1850 (Dalla Torre, 1893). *Myrmica archaica* Meunier, 1915 was described from one male, but based on the original description and especially on the photo of the impression (Meunier, 1915, pl. 22, fig. 2) this species almost certainly belongs to the genus *Aphaenogaster* Mayr, 1853. The specimen determined at the same time by Meunier as *Myrmica* sp. (loc. cit., pl. 22, fig. 3) is not a myrmicine and, to our mind, most probably belongs to the genus *Camponotus* Mayr, 1861 (Formicidae). Wheeler (1915) transferred *M. duisburgi* to his newly described monotypic genus *Agroecomyrmex*, which well differs from *Myrmica*, especially by the presence of antennal scrobes on the head of workers and queens. All of Heer's (1850) “*Myrmica*” species were described before Mayr's (1855, 1861, etc.) rearrangement of the generic taxonomy of the family Formicidae and we entirely agree with Mayr's (1867) opinion that all previously described fossil “*Myrmica*” species either do not belong to this genus, or the specimens were in such a poor condition that the author had not been able to make an adequate description for proper taxonomic treatment. The same applies to *M. nebulosa* Novak, 1878. Consequently, we propose formally that *M. aemula* Heer, 1850, *M. angusticollis* Heer, 1850, *M. breinii* Heer, 1850, *M. jurinei* Heer, 1850, *M. macrocephala* Heer, 1850, *M. molassica* Heer, 1850, *M. obsoleta* Heer, 1850, *M. tertiaria*, *M. concinna*

Heer, 1867, *M. venusta* Heer, 1867 and *M. nebulosa* should be considered as unidentifiable taxa, *incertae sedis* in *Myrmica*.

Wheeler (1915) also described the genus *Nothomyrmica* emphasizing its similarity to *Myrmica*, from which it differs by only a single feature (considered very important at that time)—the lack of spurs on the middle and hind tibiae of workers. It contained only the four species placed there by Wheeler: *N. intermedia* Wheeler, *N. rudis* (Mayr, 1868b), *N. petiolata* (Mayr, 1868b) and *N. rugosostriata* (Mayr, 1868b); the latter three were first described in the genus *Macromischa* Roger, 1863 (now a synonym of *Temnothorax* Mayr, 1861; see Bolton, 1995, 2003).

Since many extant *Myrmica* species are known to have reduced tibial spurs, or even completely lack them, the feature of reduced tibial spurs is considered much less diagnostic nowadays (Bolton, 1988a; Radchenko and Elmes, 2003). In our opinion, genus *Nothomyrmica* is quite heterogenic and artificially joins unrelated species (including some *Myrmica*) having one common feature—the absence of spurs on the hind and middle tibia. *Nothomyrmica intermedia* and *N. rudis* are very similar to *M. longispinosa* and all three closely resemble living species from the *M. ritae*-group (Radchenko, 1994; Radchenko and Elmes, 2001b). Therefore, we formally transfer *N. intermedia* and *N. rudis* to the genus *Myrmica*; *N. rugosostriata* is transferred to the newly described extinct genus *Eocenomyrma* Dlussky and Radchenko, 2006, and *N. petiolata* is transferred to the genus *Temnothorax* Mayr (Dlussky and Radchenko, 2006).

Below we have revised all extinct species indisputably belonging to the genus *Myrmica*, described two new species, provided a key for their identification, and discussed the possible paths of *Myrmica* evolution.

MATERIAL AND METHODS

In total we investigated five *Myrmica* workers in three pieces of Late Eocene amber owned by the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN) (Baltic Amber), the Muzeum Ziemi of the Polish Academy of Sciences, Warsaw (MZPAN) (Baltic Amber) and the collection of Mr. Manfred Kutscher, Sassnitz, Rugen, Germany (three specimens in a piece of Saxonian Amber); Kutscher's type material is deposited in the Geological-Palaeontological Institute and Museum, Hamburg University, Germany (GPMHU). 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.

Not all features were easily visible and measurable on the examined specimens; therefore, we use a more restricted subset of morphometrics (accurate to 0.01mm) and indices than usual for our other publications on *Myrmica* (e.g., Radchenko and Elmes, 1998, 1999).

Measurements: HL (Head length)—length of head in dorsal view, measured in a straight line from the anterior point of median clypeal margin to mid-point of the occipital margin; HW (Head width)—maximum width of head in dorsal view behind the eyes; FW (Frons width)—minimum width of frons between the frontal carinae; FLW (Frontal lobes width)—maximum width between

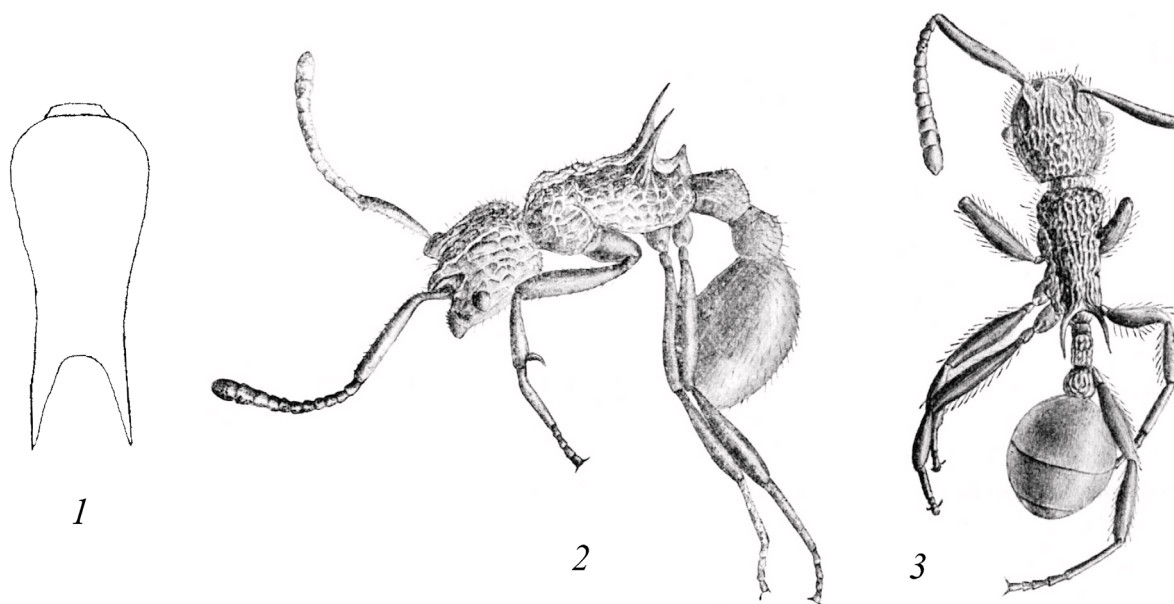


FIGURE 1—Drawings of fossil *Myrmica* species, workers. 1, *Myrmica longispinosa* Mayr, mesosoma in dorsal view (after Mayr, 1868b); 2, *M. rudis* (Mayr), body in dorso-lateral view (after Wheeler, 1915); 3, *M. intermedia* (Wheeler), body in dorsal view (after Wheeler, 1915).

external borders of the frontal lobes; SL (Scape length)—maximum straight-line length of antennal scape in lateral view; AL (Alitrunk length)—diagonal length of the alitrunk in lateral view, from the neck shield to the posterior margin of propodeal lobes; HTL (Hind tibia length)—length of tibia of hind leg; PNW (Pronotum width)—maximum width of pronotum in dorsal view; PL (Petiole length)—maximum length of petiole in dorsal view; ESL (Propodeal spine length)—maximum length of propodeal spine in lateral view; ESD (Propodeal spines distance)—distance between tips of propodeal spines in dorsal view.

Indices: CI (Cephalic index) = HL/HW; FI (Frontal index) = FW/HW; FLI (Frontal lobes index) = FLW/FW; SI₁ (Scape length index 1) = SL/HL; SI₂ (Scape length index 2) = SL/HW; ESLI (Propodeal spine length index) = ESL/HW; ESDI (Propodeal spines distance index) = ESD/ESL.

SYSTEMATIC PALEONTOLOGY

Family FORMICIDAE Latreille, 1809
Genus MYRMICA Latreille, 1804

Myrmica Latreille, 1804, p. 179; type species—*Formica rubra* Linnaeus, 1758, p. 580, by subsequent designation of Latreille, 1810, p. 437.
Nothomyrmica WHEELER, 1915, p. 60; type species—*Macromischa rudis* Mayr, 1868b, p. 85, fig. 85, by original designation; RADCHENKO, 1994, p. 48; BOLTON, 1995, p. 292, n. syn.

Notes.—For the diagnosis and full synonymy of the genus *Myrmica* see Bolton (1988a, 1995, 2003), Radchenko and Elmes (2003). Here, we have transferred two of the four *Nothomyrmica* species to the genus *Myrmica*, including type species of *Nothomyrmica*.

MYRMICA LONGISPINOSA Mayr, 1868b

Myrmica longispinosa MAYR, 1868b, worker, p. 87, fig. 86, Baltic Amber; WHEELER, 1915, p. 59; RADCHENKO, 1994, p. 48; BOLTON, 1995, p. 281.

Occurrence.—Kaliningrad Province of Russia, Baltic Amber.

Discussion.—Mayr (1868b) described this species based on a single worker from the Baltic Amber [“In der phys.-ökon. Ges. (i.e., Königsberg collection—our remark) 1 Stück (Nr. 40)”, loc. cit., p. 87]. Later Wheeler (1915) studied Mayr’s holotype and one additional unnumbered worker in the Königsberg collection

(Germany at that time, nowadays Kaliningrad in Russia). At present the holotype of *M. longispinosa* is absent from the Mayr’s collection in Naturhistorisches Museum Wien (Ponomarenko and Schultz, 1988). The Königsberg’s amber collection was apparently mostly lost during World War II, but a small part of it is preserved in the collection 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 *M. longispinosa* were found there (Perkovsky, personal commun., 2004). Hence, we believe that both Mayr’s holotype and Wheeler’s material belonging to this species are lost. The situation concerning the types of *M. rudis* and *M. intermedia* (see below) is the same and we believe them also to have been lost.

We have never seen any material belonging to this species. Based on Mayr’s original description and Wheeler’s comments, this species is characterized by: a coarse sculpture; the presence of a pectinate spur on the hind tibiae; a long antennal scape; long propodeal spines, which are directed backwards and are very feebly divergent, subparallel (in dorsal view). Unfortunately, Mayr’s drawing of this species is too schematic to be really helpful (see Fig. 1.1).

MYRMICA RUDIS (Mayr, 1868b) new combination

Macromischa rudis MAYR, 1868b, worker, p. 85, pl. 4, fig. 85, Baltic Amber; DALLA TORRE, 1893, p. 120; ANDRÉ, 1895, p. 82; HANDLIRSCH, 1907, p. 875.

Nothomyrmica rudis (Mayr, 1868b). WHEELER, 1915, p. 60, fig. 23; RADCHENKO, 1994, p. 48; BOLTON, 1995, p. 292.

Material examined.—One badly preserved worker, MZPAN, No. 1945/6, Baltic Amber.

Occurrence.—Kaliningrad Province of Russia and northwestern Poland, Baltic Amber.

Discussion.—The types of *M. rudis* are most probably lost (see above). Although, the specimen studied is in quite bad condition and the transparency of the piece of amber is poor, the general shape of the ant is visible, including the shape of petiole and propodeal spines that are directed upward and backward (characteristic for *M. rudis*, Fig. 1.2). However, at this time we think it would be unreasonable to designate this specimen as the neotype of *M. rudis*.

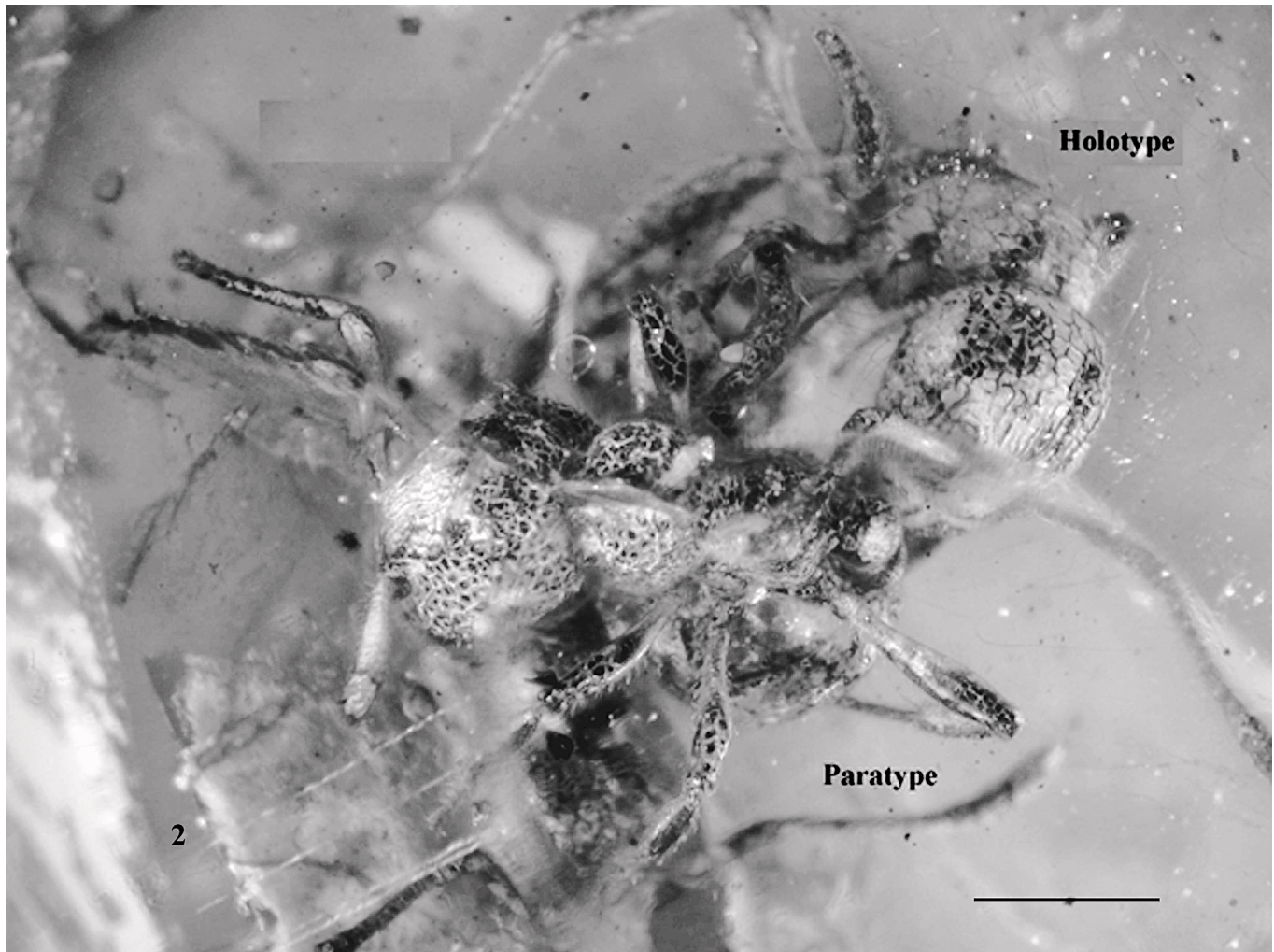


FIGURE 2—Microscopic photo of *Myrmica paradoxa* n. sp., workers, holotype (in antero-dorsal view) and paratype (in dorsal view) (GPMHU, No F-199, Saxonian Amber). Scale bar = 1 mm.

MYRMICA INTERMEDIA (Wheeler, 1915) new combination

Nothomyrmica intermedia WHEELER, 1915, worker, p. 61, fig. 24; RADCHENKO, 1994, p. 48; BOLTON, 1995, p. 292.

Occurrence.—Kaliningrad Province of Russia, Baltic Amber.

Discussion.—The holotype of *N. intermedia* is probably lost (see above) and we have never seen any material belonging to this species. Based on Wheeler's original description and drawing (see Fig. 1.3) this species is characterized by: a coarse sculpture; the absence of a spur on the hind tibiae; a long antennal scape; long propodeal spines, which directed mainly backwards and are very feebly divergent, subparallel (in dorsal view). Wheeler stressed that this species resembles *M. longispinosa* and differs from it mainly by the absence of spurs on the hind and middle tibiae.

MYRMICA PARADOXA n. sp.

Figures 2, 3

Diagnosis.—Propodeum with two denticles that are short, straight, wide, blunt at the apex, directed upward and slightly backward. Frontal carinae short, very weakly curved to merge with the rugae, which surround antennal sockets. Only anterior (lower) part of frons with longitudinal rugae, remaining part of head dorsum with dense but not coarse reticulation. Whole alitrunk and waist with reticulation. Hind tibiae with conspicuous pectinate spur.

Description.—Head longer than broad, with convex sides and occipital margin, and broadly rounded, barely marked occipital corners. Eyes of moderate size, not prominent laterally, situated approximately at the midlength of lateral margins of head. Anterior clypeal margin very broadly rounded, not prominent, shallowly notched medially, with pair of long median setae and fringe of shorter setae on the anterior margin (similar to that of other *Myrmica* species). Antennae twelve-segmented and with distinct three-segmented club, second to ninth funicular joints distinctly longer than broad. Antennal scape relatively long, at least reaching or slightly surpassing the occipital margin of head, gradually curved at the base, without any trace of lobe or carina.

Alitrunk short, wide, and robust. Promesonotum feebly convex (in lateral view) and in dorsal view with broadly rounded antero-lateral corners, distinctly narrowing posteriorly (approximately twice wider anteriorly than posteriorly), without any trace of a promesonotal suture. Metanotal groove distinct, abrupt but not very deep. Dorsal surface of propodeum subequal to its declivity (= posterior surface), propodeal lobes not sharply pointed, at most bluntly angulated at the apex. Petiole with relatively short but distinct peduncle, its node quite massive, with rounded dorsum. Postpetiole subglobular and lower than petiole (in lateral view).

Body with rather abundant, suberect to erect, moderately long, thin, pointed hairs. Antennal scape with subdecumbent to suberect hairs; hind tibiae and femora with short subdecumbent hairs, but with longer suberect hairs on the inner margin of femora.

Etymology.—The species named for its paradoxical combination of features.

Material examined.—Three workers (holotype and paratypes in the same piece of amber), GPMHU, No F-199, Germany, Saxonian Amber.

Measurements (mm) and indices.—Holotype: HW 1.12, FW 0.42, FLW 0.50, SL 0.99, AL 1.57, PNW 0.95; FI 0.38, FLI 1.20, SI₁ 0.89. Paratype

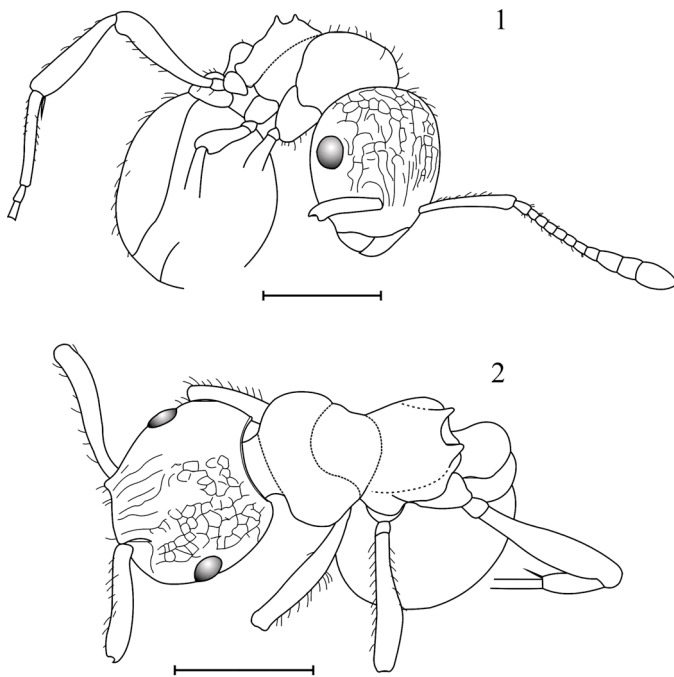


FIGURE 3—Explanatory drawings of *Myrmica paradoxa* n. sp., workers, made based on original photos. 1, holotype, in antero-dorsal view; 2, paratype, in dorsal view (GPMHU, No F-199, Saxonian Amber); sculpture of the alitrunk is omitted. Scale bars = 1 mm.

specimen one: HL 1.27, SL 0.92, HTL 0.87; SI₁ 0.73. Paratype specimen two: PL 0.46. Body length is ca. 6 mm.

Discussion.—*Myrmica paradoxa* n. sp. well differs from any other known modern or fossil *Myrmica* species, especially by the very short propodeal denticles: such a shape of propodeal armature is peculiar, unknown in any modern or other fossil *Myrmica* species. It is paradoxical because on one hand it is characterized by features that are quite normal for the genus *Myrmica*, but on the other hand, others that are not known from any other *Myrmica* species. Thus, while it has a sculpture and shape of the head, pilosity of the body, shape of petiole and postpetiole and a distinct pectinate spurs on the hind tibiae that are typically *Myrmica*, its very well marked three-jointed antennal club and the generally short and robust alitrunk with the short blunt propodeal denticles are atypical. No other extant *Myrmica* species has such a short dorsal surface of the propodeum relative to the posterior surface (the propodeal declivity) and only the unusual queens of *Myrmica luteola* Kupyanskaya, 1990 have short propodeal denticles. Unfortunately, the maxillary and labial palps, which can be diagnostic of certain genera, are invisible. We consider that most probably, *M. paradoxa* represents an extinct lineage within the genus.

MYRMICA EOCENICA n. sp.
Figures 4, 5

Diagnosis.—Propodeum with very long, straight propodeal spines, that are directed backwards, strongly divergent (in dorsal view). Frontal carinae very weakly curved, not curving outwards, merging with the rugae, which run backwards to the occipital margin of the head. Body with coarse sculpture. Hind tibiae with conspicuous pectinate spur.

Description.—Head distinctly longer than broad, with convex sides, straight occipital margin, and narrowly rounded occipital corners. Eyes relatively small, convex, situated approximately at the midlength of lateral margins of head. Anterior clypeal margin narrowly convex, but not prominent, without notch, with pair of long median setae and fringe of shorter setae on the anterior margin (similar to that of other *Myrmica* species). Frons wide; frontal lobes slightly extended, quite narrow and pointed at the apex. Antennae twelve-segmented and with three (possibly four?)-segmented club, funicular joints second to eighth distinctly longer than broad. Antennal scape long, surpassing occipital margin of head, very feebly curved at the base, without

any trace of lobe or carina. Frons between frontal carinae with only three coarse longitudinal, slightly sinuous rugae, which reach occipital margin; its lower (anterior) part between frontal lobes with four additional short longitudinal rugae, which extend only to the level of the eyes; upper (rear) part of frons and remainder part of head dorsum with coarse reticulation. Antennal sockets deep and surround by at least one coarse ruga. Clypeus with coarse longitudinal rugosity.

Alitrunk relatively long and slender. Promesonotum somewhat flattened (in lateral view), with narrowly rounded antero-lateral corners and with trace of promesonotal suture (in dorsal view). Metanotal groove distinct, but not very deep. Dorsal surface of propodeum somewhat longer than posterior one, propodeal lobes sharply pointed at the apex. Petiole with long peduncle, its node low and long, with weakly convex dorsum, postpetiole fig-shaped (in dorsal view). Whole alitrunk with coarse reticulation, only propodeal dorsum seems to be also having short longitudinal rugae (the last feature is not clearly visible in the investigated specimen). Petiolar node with longitudinally-concentric rugae, its dorsum also with moderate (not coarse) reticulation, postpetiole in dorsal view with longitudinal rugae.

Body with a few, suberect to erect, thin, pointed hairs. Antennal scape, hind tibiae and femora with sparse subdecumbent, quite long hairs; inner margin of femora has longer suberect hairs.

Etymology.—The species named after geological epoch when the type specimen was trapped in amber.

Material examined.—One worker, holotype, PIN, 964/479, Kaliningrad Province of Russia, Baltic Amber.

Measurements (mm) and indices.—HL 1.11, HW 0.95, FW 0.41, FLW 0.52, SL 1.06, AL 1.34, ESL 0.63, ESD 0.62, HTL 0.91; CI 1.16, FI 0.43, FLI 1.28, SI₁ 0.96, SI₂ 1.12, ESLI 0.66, ESDI 0.98. Body length ca. 6.5 mm.

Discussion.—*Myrmica eocenica* n. sp. is similar to all the previously described *Myrmica* species from Baltic Amber. Unfortunately, types of all others appear to be lost (see above), so this comparison is based solely on Mayr's and Wheeler's original descriptions and drawings.

It differs from *M. longispinosa* by its sharply pointed apically propodeal lobes, by the strongly divergent propodeal spines (compare Figs. 1.1 and 4, 5), and by its somewhat longer body (> 6 mm vs. ca. 5 mm). Compared to the former "*Nothomyrmica*" species, it differs by its well developed pectinate spurs on the hind tibiae; though this feature may be not so distinctive at the generic level (see above), it is usually more constant at the species level. It clearly differs from *M. rudis* by the shape of the propodeal spines and petiole: in *M. rudis* the spines are somewhat curved and directed backward and upward while its petiole has a much shorter peduncle and subtriangular node (compare Figs. 1.2 and 4, 5). *Myrmica eocenica* most resembles *M. intermedia* by the shape and sculpture of its body but, apart from the tibial spurs, it also differs by its straight and strongly divergent propodeal spines (compare Figs. 1.3 and 4, 5), and body length (> 6 mm vs. 4.7 mm). Generally, *M. eocenica* is very similar to living species of the *ritae*-group of *Myrmica* (see Radchenko, 1994; Radchenko and Elmes, 1998, 2001b) and almost certainly should be placed in this group (see discussion below).

A KEY FOR IDENTIFICATION OF MYRMICA SPECIES FOUND IN
LATE EOCENE AMBER

- 1 Propodeum with short, blunt teeth; head and alitrunk with fine reticulation; hind tibiae with distinct spur (Figs. 2, 3) *M. paradoxa* n. sp.
- Propodeum with long spines (Figs. 1, 4, 5); head and alitrunk with very coarse sinuous rugosity and reticulation (Figs. 1.2, 1.3, 4, 5); hind tibiae with or without spurs 2
- 2(1) Propodeal spines directed backward and upward, slightly curved down at the apex (Fig. 1.2); hind tibia without spur *M. rudis* (Mayr)
- Propodeal spines directed backward, straight or slightly curved inward (in dorsal view) (Figs. 1.1, 1.3, 4, 5); hind tibiae with or without spurs 3
- 3(2) Propodeal spines straight, strongly divergent (in dorsal view) (Figs. 4, 5); hind tibiae with spur; larger species, body length ca. 6.5 mm *M. eocenica* n. sp.
- Propodeal spines subparallel, not divergent (in dorsal view) (Fig. 1.1, 1.3); hind tibiae with or without spurs; smaller species, body length ca. 5 mm or less 4
- 4(3) Hind tibiae with spurs. Propodeal lobes rounded, not sharply pointed apically *M. longispinosa* Mayr
- Hind tibiae without spurs. Propodeal lobes sharply pointed apically *M. intermedia* (Wheeler)



FIGURE 4—Microscopic photo of *Myrmica eocenica* n. sp., worker, holotype, in dorso-lateral view (PIN, 964/479, Baltic Amber). Scale bar = 1 mm.

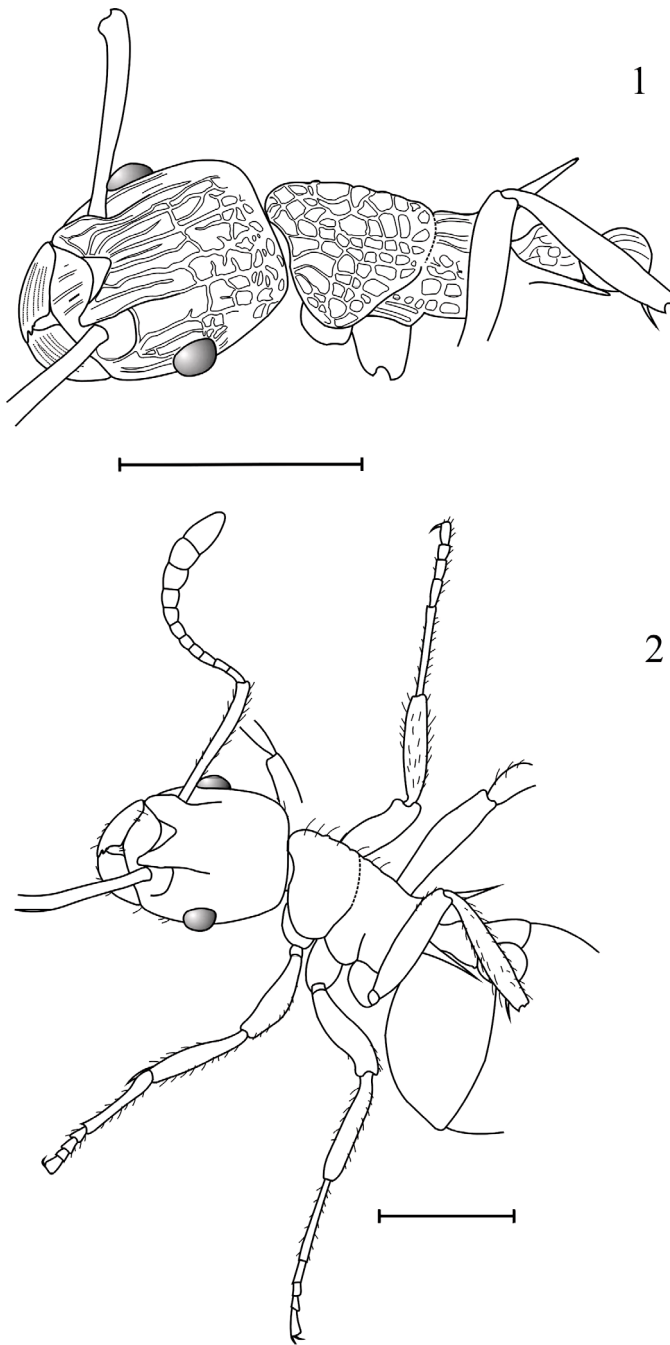


FIGURE 5—Explanatory drawings of *Myrmica eocenica* n. sp., made based on original photos; worker, holotype. 1, in dorsal view; 2, in dorso-lateral view (PIN, 964/479, Baltic Amber); sculpture on Fig. 5.2 is omitted. Scale bars = 1 mm.

DISCUSSION

Most authors consider the tribe Myrmicini (comprising *Myrmica*, *Manica* Jurine, 1807, *Eutetramorium* Emery, 1899, *Hylomyrma* Forel, 1912, *Pogonomyrmex* Mayr, 1868a and *Secostruma* Bolton, 1988b) to be the most basal morphologically in the subfamily Myrmicinae, based on the plesiomorphic state of features, such as the structure of the mesosoma with well defined sutures, six-jointed maxillary and four-jointed labial palps, and the presence of pectinate spurs on the mid and hind tibia. A recent molecular phylogeny of ants (Moreau et al., 2006) suggests that subfamily Myrmicinae arose more than 100 Ma prior to a huge diversification of ants that the authors believe was related to the

evolution of angiosperm plants. By the Late Cretaceous (about 80 Ma) the subfamily already comprised five or so, distinct (“old”) lineages and most of the modern genera were established during the next 35 million years before the start of the Eocene. Interestingly, they found that the three studied representatives from tribe Myrmicini fall in two of the “old” lineages: *Myrmica* and *Eutetramorium* are in one, while *Pogonomyrmex* is in another that includes *Messor* Forel, 1890 and *Aphaenogaster* (both latter genera belong to the tribe Pheidolini). When an even more detailed molecular phylogeny is made, the tribe Myrmicini will probably have to be revised.

Radchenko and Elmes (2001b) suggested that the ancestral Myrmicini were probably most similar to modern *Myrmica*, or perhaps *Manica*, because the other four genera possess many derived features (see Bolton, 2003 and literature cited therein). They had considered that any resemblance between *Messor* and *Pogonomyrmex* was solely due to convergent evolution, but the Moreau et al. study (loc. cit.) suggests otherwise. Despite *Manica* species appearing to have more plesiomorphic features, e.g., a full complement of mesosomal sutures with some large specimens having a rudimentary scutellum, filiform antennal funiculus in males, Radchenko and Elmes (2001b) believed *Manica* and *Myrmica* most probably derived from a common ancestor at about the same time. Unfortunately Moreau et al. (2006) did not sample *Manica* species, but the general thrust of their results support that idea. Furthermore, if both genera arose 60–70 Ma during a burst of ant diversification and before North America was completely separated from Eurasia, it would explain both the modern distribution of *Manica* (restricted to North America except for two species) and the general dissimilarity between North American and Eurasian *Myrmica* species-groups.

Four of the five known fossil *Myrmica* species are very similar to modern *ritae*-group species. These species are usually considered as basal in relation to the extant forms (Radchenko, 1994; Radchenko and Elmes, 2001b; and above). They are very poorly represented in collections and were considered to be unusual and rare until recent studies showed that they are relatively numerous and common in certain subtropical forests on mountains in the extreme southeastern part of the Palaearctic and in the north of the Oriental Regions (Radchenko and Elmes, 1998, 1999, 2001a, 2001b; Radchenko et al., 2001). Some species are superficially very similar to *Aphaenogaster* (tribe Pheidolini) and are frequently misidentified as such (see Radchenko and Elmes, 1998) but we believe that this is genuine convergence similar to, for example, that between *Cataglyphis* Förster, 1850 (tribe Formicini) and *Myrmecocystus* Wesmael, 1838 (tribe Lasiini). Weber (1950) also noted that *M. ritae* Emery, 1889 and related species have similar characteristics to some tropical species of *Aphaenogaster* and therefore suggested that they might have similar habits, such as a more arboreal way of life than is normal for *Myrmica*. Indeed, recent field studies of some *ritae*-group species (G. W. Elmes, A. Schulz, and K. Eguchi, personal commun., 2003) suggest that some species might live and forage entirely on trees.

We suggest that the putative ancestor of modern *Myrmica* lived in the warm early Eocene forests and by the late Eocene had given rise to *M. ritae*-like species and other unusual forms, such as the extinct *M. paradoxa* n. sp. or extant *M. mirabilis* Elmes and Radchenko, 1998. While it is possible that the ancestors of most other modern *Myrmica* species-groups had by this time already developed a greater cold tolerance and had penetrated the more northerly temperate forest zone, it is unlikely because there is a total absence of *Myrmica* specimens in the Oligocene and Miocene deposits of Eurasia that are associated with temperate conditions, despite the presence of quite a rich ant fauna, including several *Aphaenogaster* species that are morphologically and ecologically similar to *Myrmica* (Théobald, 1937; Dlussky, 1981; Zhang,

1989). More probably, ancestor(s) of the different modern species-groups remained restricted to the warmer Eocene forests, co-existing with *M. ritae*-like species. Given our current understanding of the available fossil records and the paucity of fossil *Myrmica*, represented by only a few specimens found in amber deposits, we suggest that at the end of the Eocene, *Myrmica* species might have been generally rare with restricted distributions. Yet, some of the early *Myrmica* species survived the ecological trauma of the post-Eocene cooling and adapted to the cooler habitats.

Unfortunately, there are no data on the Pliocene ant fauna of Eurasia to indicate how adaptive radiation proceeded to the extent that *Myrmica* is now one of the dominant ant genera of the temperate Holarctic, whether measured in terms of the number of species, colonies or individuals. Indubitably, isolation due to alternating glacial ages of the last millions of years played an important role in subsequent speciation. On the other hand, typical *ritae*-group species and a few other basal forms, for example *M. mirabilis* (rather similar to *Manica* in the general shape of the body, but in other features clearly *Myrmica*), were confined to forests on high mountains in subtropical South and Southeast Asia, where many species of plant and animal found in late Eocene amber still persist (Larsson, 1978).

It is interesting that most extant *Myrmica* species with apparently basal morphological features are generally found in southern mountain systems. There are numerous unusual and endemic *Myrmica* species, including presumably basal forms, in the southwestern Himalayas, which were isolated from the rest of the *Myrmica* fauna at some time in the late Miocene – early Pliocene. We have found some similar atypical *Myrmica* in the mountains of Turkey (Elmes et al., 2002) and few unusual species have been described from the southern mountains of the USA (see also Radchenko and Elmes 2001b). Almost certainly, more rare, basal forms of *Myrmica* remain to be discovered in the southern mountains of North America. It would not surprise us if species similar to *M. ritae* were discovered on high mountains in Mexico, since Tertiary flora and fauna have persisted in the Americas because migration in response to climate change is facilitated by the north-south orientation of mountain systems.

The morphology of the fossil *Myrmica*, discussed above, suggest that female castes of the ancestral species probably had long, gently curved antennal scape, with no thickening or lobes. A short scape in males is plesiomorphic evolutionary condition for all ants (Dlussky, 1983; Dlussky and Fedoseeva, 1988); therefore the males of the ancestral *Myrmica* species probably had short antennal scapes. This is the case in most *ritae*-group species for which this character is known (Radchenko and Elmes, 1998). The two morphological features that are most important in defining modern species-groups (sharply angled antennal scape of the female castes and longer antennal scape among males, see Radchenko and Elmes, 2001b) probably derived from the ancestral form during the adaptive radiation of *Myrmica* following the post-Eocene cooling.

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