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; Novák, 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 (1893), Wheeler (1915) and Assmann (1868b), and we re-appraise all previously described fossil Myrmica, providing a key to the identification of the five extinct “true” Myrmica species.

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 Ziem 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 (Frongs width)—minimum width of frongs between the frontal carinae; FLW (Frontal lobes width)—maximum width between

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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; PNV (Pronotum width)—maximum width of pronotum in dorsal view; PL (Pettiole 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/FW; FLI (Frontal lobes index) = FLW/FW; SI (Scape length index 1) = SL/HL; SI (Scape length index 2) = SL/HW; ESLI (Propodeal spine length index) = ESL/HW; ESDL (Propodeal spines distance index) = ESL/ESL.

SYSTEMATIC PALEONTOLOGY

Family Formicidae Latreille, 1809

Genus Myrmica Latreille, 1804


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


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.-ökön. 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 Myrmica 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 Myrmica 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 Myrmica 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; Dall’Ara 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 Myrmica 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 Myrmica rudis, Fig. 1.2). However, at this time we think it would be unreasonable to designate this specimen as the neotype of Myrmica rudis.

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).
**Myrmica intermedia** (Wheeler, 1915) new combination


**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 anterio-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, SI 0.89. Paratype...
Description.—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 pectinate spur. Presence of such a form is very unusual 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, Myrmica paradoxa represents an extinct lineage within the genus.

Material examined.—One worker, holotype, PIN, 964/479, Kalingrad Province of Russia, Baltic Amber. Measurements (mm) and indices.—HL 1.11, HW 0.95, FL 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, SI, 0.96, SI, 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 titubal spurs, it also differs by its strongly divergent propodeal spines (compare Figs. 1.3 and 4, 5), and body length (> 4.7 mm). Generally, M. eocenica is very similar to living species of the rite-group of Myrmica (see Radchenko, 1994; Radchenko and Elmès, 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. 2(1) 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(2) Propodeal spines directed backward and upward, slightly curved down at the apex (Fig. 1.2); hind tibiae without spur .......................... M. rudis (Mayr) 3 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 4 Propodeal spines straight, strongly divergent (in dorsal view) (Figs. 1, 4, 5); hind tibiae with spurs; larger species, body length ca. 6.5 mm ................................. M. eocenica n. sp. 4(2) 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 5 Hind tibiae without spurs. Propodeal lobes sharply pointed apically .................................................. M. longispinosa Mayr 6 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.
Most authors consider the tribe Myrmicini (comprising Myrmica, Manica Jurine, 1807, Eutetramorium Emery, 1899, Hyalomyrmex 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 palpes, 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 Myrmicininae 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 riteae-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 Catacliphis Förster, 1850 (tribe Formicinae) and Myrmecocystus Wesmael, 1838 (tribe Lasiini). Weber (1950) also noted that M. riteae 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 riteae-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. riteae-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,
Eurasia to indicate how adaptive radiation proceeded to the extent that Myrmica is now one of the dominant ant genera of the temperate Holartic, 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 rite-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. riteae 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 pleisomorphic evolutionary condition for all ants (Dlussky, 1983; Dlussky and Fedoseeva, 1988); therefore the males of the ancestral Myrmica species probably had short antenal scapes. This is the case in most riteae-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.

References


PALEONTOLOGICAL NOTES


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