

MYRMICA ANTS (HYMENOPTERA: FORMICIDAE) IN LATE EOCENE EUROPEAN AMBERS

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Abstract.— The genus *Myrmica* Latreille, 1804 from late Eocene European ambers is revised. The neotypes for *M. longispinosa* Mayr, 1868, *M. rudis* (Wheeler, 1915) and *M. intermedia* (Wheeler, 1915) are designated; four new species, *Myrmica electrina* sp. nov., *M. dictyosa* sp. nov., *Myrmica damzeni* sp. nov. and *Myrmica saxonica* sp. nov. are described; *M. rudis* and *M. intermedia* are recorded for Rovno amber for the first time. A key to identification of amber *Myrmica* species is compiled. *Myrmica* in mentioned ambers is the second species rich myrmicine genus. Only *M. longispinosa* can be assigned to the *ritae*-group; other ‘*ritae*-like’ species have either some putative plesiomorphies compared to this group, or putative apomorphy. *M. electrina* and *M. saxonica* are well distinguished from species of the *ritae*-group, but they are distinct from all extant *Myrmica* species and cannot be assigned to any modern species-groups. *M. schaeferi* Jessen, 2020 and *M. nungesseri* Jessen, 2020 from late Oligocene deposits fit well into the modern *rugosa* species group. It can be assumed that the putative ancestor of modern *Myrmica* lived in the warm forests of the early or middle Eocene, and by the late Eocene had already given rise to *M. ritae*-like species and other forms, and in the Oligocene species of the *rugosa*-group evolved.



Key words.— New species, *Myrmica electrina*, *M. dictyosa*, *M. damzeni*, *M. saxonica*, neotypes, palaeontology, evolution, taxonomy, key to identification

INTRODUCTION

The genus *Myrmica* Latreille, 1804 includes 187 modern species (Bolton 2023), 159 of which are known from the Old World (Radchenko and Elmes 2010, Bharti *et al.* 2016). They are distributed mainly in the Palaearctic and Nearctic, but many species are also found in the mountains of the Oriental Region (Himalayas, Taiwan, Southern China, Vietnam, Burma, Thailand and Indonesia) and the Neotropics (Mexico) (Radchenko and Elmes 2010).

Until the beginning of the 20th century, 17 extinct ant species were assigned to the genus *Myrmica*,

but only one of them, *M. longispinosa* Mayr, 1868 from Baltic amber (Priabonian age, 37.8–33.9 Ma), indisputably belongs to this genus. All other fossil ‘*Myrmica*’ species were later transferred to other genera or considered *incertae sedis* within Myrmicinae Lepeletier, 1835 (Wheeler 1915, Radchenko *et al.* 2007, Radchenko and Elmes 2010, Dlussky and Putyatina 2014, Fischer *et al.* 2014).

Wheeler (1915) established a new genus *Nothomyrmica*, transferred *Macromischa rudis* Mayr, 1868 (the type species of *Nothomyrmica*), *M. rugosostriata* Mayr, 1868 and *M. petiolata* Mayr, 1868 into it, and described the new species, *N. intermedia*

Wheeler, 1915. Radchenko and Dlussky (2006) transferred *N. petiolata* to *Temnothorax* Mayr, 1861, and *N. rugosostriata* to the new genus *Eocenomyrma* Radchenko et Dlussky, 2006. A year later, Radchenko *et al.* (2007) synonymized *Nothomyrmica* with *Myrmica*, transferred *N. rudis* and *N. intermedia* to the latter genus and described two new *Myrmica* species from Baltic and Bitterfeld (= Saxonian) ambers. Thus, five 'true' extinct *Myrmica* species were known by the end of 2000th, but two more *Myrmica* species have been recently described from the late Oligocene deposits (24.8–24.6 Ma) of Enspel (Germany) (Jessen 2020).

In total, only 23 *Myrmica* specimens have been found in Baltic, Bitterfeld and Danish ambers to date (Mayr 1868, André 1895, Wheeler 1915, Radchenko *et al.* 2007, Dlussky and Rasnitsyn 2009, Radchenko and Elmes 2010), which is about 0.1% of all known ant specimens. I recently obtained 12 more *Myrmica* specimens, both of the previously described species and the four new species described below. This makes *Myrmica* one of the most species rich Myrmicinae genera in late Eocene European ambers and it is second only to *Temnothorax* with six described and 12 as yet undescribed species (Radchenko, in preparation).

Three *Myrmica* species, described by Mayr (1868) and Wheeler (1915) (e.g. *M. longispinosa*, *M. rudis* and *M. intermedia*), were originally found in pieces of Baltic amber, preserved at that time in the collection of the Königliche Bernsteinsammlung des Geologischen Instituts of Königsberg ("In der phys.-ökon. Ges." according to Mayr 1868). Moreover, *M. longispinosa* and *M. intermedia* were described based on a single specimen each, and *M. rudis* – based on one specimen from the Königsberg's collection and another from the private collection of Dr. Sommerfeldt from Königsberg.

The current location of the Sommerfeldt's collection is unknown, if it survives anywhere at all. The Königsberg's amber collection, apparently, was mostly lost during the World War II, but at present a small part of it is preserved in the collection of the Institut und Museum für Geologie und Paläontologie der Universität Göttingen (Germany). Unfortunately, according to the database of fossil ants of the Göttingen Museum, neither the types nor any other *Myrmica* specimens studied by André (1895), Wheeler (1915) or Carpenter (1927) were found there. The type specimens of *M. longispinosa* and *M. rudis* are also absent from the Mayr's collection at the Naturhistorisches Museum Wien (Ponomarenko and Schultz 1988).

Therefore, both the Mayr's types and the Wheeler's material, belonging to the mentioned species, I consider lost, and designate the neotypes of *M. longispinosa*, *M. rudis* and *M. intermedia*. In addition, *M. rudis* and *M. intermedia* are also recorded for Rovno amber (Ukraine) for the first time. Below I also

describe *Myrmica electrina* sp. nov. from Baltic and Rovno ambers, *M. dictyosa* sp. nov. and *M. damzeni* sp. nov. from Baltic amber, and *M. saxonica* sp. nov. from Bitterfeld amber.

MATERIAL AND METHODS

In the course of this revision I examined 12 *Myrmica* specimens (workers), belonging to four previously described species and to four new species from Baltic, Danish, Bitterfeld and Rovno ambers. The type specimens are deposited in the following Institutions and Museums:

- SIZK – Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev, Ukraine;
- ZMUC – Zoological Museum of the University of Copenhagen, Denmark;
- LIB – Leibniz Institute for the Analysis of Biodiversity Change, Hamburg (collection of Carsten Gröhn, CCGG – former of the University of Hamburg; former Geological-Palaeontological Institute and Museum, Hamburg University), Germany;
- MAGU – Museum of Amber Inclusions of Gdańsk University, Poland;
- HMB – Humboldt Museum, Berlin, Germany;
- GZG.BST – Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen, Germany;
- PIN – Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia;
- CJDL – private collection of Jonas Damzen, Lithuania;
- CMKHU – private collection of M. Khomych, Ukraine.

The original photographs were taken with a Leica Z16 APO microscope equipped with a Leica DFC 450 camera and processed by LAS Core software, and with a Canon 90D camera, equipped with a macrolens Canon MPE-65 mm and processed with the Helicon Focus.

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

- HL – maximum length of the head in dorsal view, measured in a straight line from the anterior-most point of clypeus to the mid-point of occipital margin;
- HW – maximum width of the head in dorsal view behind (above) the eyes;
- SL – maximum length of the scape measured in a straight line from its apex to the articulation with the condylar bulb;

- FW – minimum width of the frons between the frontal carinae;
- FLW – maximum distance between outer borders of the frontal lobes;
- OL – maximum diameter (= length) of the eye;
- GL – length of the genae, measured from the anterior margin of the eyes to the articulation with the mandible;
- MdL – length of the mandible, measured from its tip to articulation with the head;
- ML – diagonal length of the mesosoma (seen in profile) from the anterior end of the neck shield to the posterior margin of the propodeal lobes;
- MH – height of the mesosoma, measured from the upper level of promesonotum perpendicularly to the level of lower margin of mesopleuron;
- PNW – maximum width of the pronotum from above;
- PL – maximum length of the petiole, measured from the posterodorsal margin of the petiole to the articulation with the propodeum;
- 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 lowest point of the petiole;
- PPL – maximum length of the postpetiole in dorsal view between its visible anterior and posterior margins;
- PPW – maximum width of the postpetiole in dorsal view;
- PPH – maximum height of the postpetiole in profile from the uppermost to the lowermost point, measured perpendicularly to the tergo-sternal suture;
- ESL – maximum length of the propodeal spine in profile, measured along the spine from its tip to the deepest point of the propodeal constriction at the base of the spine;
- ESD – distance between the tips of propodeal spine in dorsal view;
- HTL – maximum length of the metatibia.

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

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

A review of previously described species

Myrmica paradoxa Radchenko, Dlussky et Elmes, 2007 (Fig. 1, A, B; Tables 1, 2)

Myrmica paradoxa Radchenko, Dlussky and Elmes, 2007: 1496, Figs 2, 3, w, Bitterfeld amber; Radchenko and Elmes 2010: 654.

Locality. Germany, Saxony-Anhalt, Bitterfeld amber, late Eocene, Priabonian age, 37.8–33.9 Ma.

Diagnosis. Metatibiae with conspicuous pectinate spurs; eyes located approximately at midlength of sides of head; antennal scape gradually and feebly curved at base, funiculus with conspicuous 3-segmented club; frontal carinae short, very weakly curved and merge with rugae, which surround antennal sockets; only anterior part of frons with longitudinal rugae, remaining part of head dorsum with dense, but not coarse reticulation; mesosoma and waist with not coarse reticulation; propodeum with two short, wide, blunt denticles, directed upward and slightly backward.

Description – see Radchenko *et al.* 2007.

Material examined. Three workers (holotype and two paratypes), complete specimens in the same piece of amber, No. F-199 (GZG.BST.27.199, coll. of M. Kutchner) (GZG.BST).

Etymology. Named for its paradoxical combination of features.

Notes. *Myrmica paradoxa* is characterized by a rather unusual combination of characters for this genus: on the one hand, the shape of the head and waist, the sculpture of the body and the character of the pilosity, distinct pectinate spurs on the metatibiae are quite normal for *Myrmica*, while, on the other hand, a short and robust mesosoma with short blunt propodeal denticles are atypical. On the whole, in general appearance it quite resembles species of the genus *Manica* Jurine, 1807, but the latter have five-segmented funicular club and multidentate mandible with at least 12 teeth on the masticatory margin (Wheeler G. and Wheeler J. 1970). Recent record of the first fossil *Manica* species from Baltic amber confirms this characteristic (Zharkov *et al.* 2023). Nevertheless, a final opinion on the exact taxonomic position of *M. paradoxa* requires additional study of the type specimens using modern technique (e.g., micro-computed tomography).

Comparative diagnosis. *Myrmica paradoxa* is well distinguished from all other fossil *Myrmica* species by short blunt propodeal denticles (instead of spines), and a three-segmented funicular club.

Myrmica longispinosa Mayr, 1868
(Fig. 1, C–E; Tables 1, 2)

Myrmica longispinosa Mayr, 1868: 87, pl. IV, fig. 86, w, Baltic Amber; Wheeler 1915: 59; Dalla Torre 1893: 112; Handlirsch 1907: 874; Burnham 1978: 110; Radchenko 1994: 48; Bolton 1995: 281; Dlussky 1997: 625; Radchenko *et al.* 2007: 1495; Radchenko and Elmes 2010: 654; Bolton 2023 (Website).

Locality. Poland, Baltic amber, late Eocene, Priabonian age, 37.8–33.9 Ma.

Diagnosis. Meso- and metatibiae with conspicuous pectinate spurs; head, mesosoma and waist coarsely

sculptured; upper lateroventral corners of head somewhat pointed; eyes located approximately at midlength of sides of head; scape gradually, but quite strongly curved at base, without any angle, lobe or carina (similar to modern *M. sulcinodis* Nylander, 1846); mesosoma long and low; petiole long and low; propodeal spines directed mainly backward (seen in profile) and very slightly divergent (seen from above).

Redescription of workers. Body length ca. 5 mm. Head width in studied specimens cannot be measured properly, but nevertheless head elongated, with almost

straight sides, feebly convex occipital margin and widely rounded occipital corners; its posterior margin surrounded by distinct ridge ('collar') and its upper lateroventral corners somewhat pointed. Anterior clypeal margin convex, not pointed and with medial notch. Width of frontal carinae and frontal lobes cannot be measured properly, but carinae feebly curved, merging with rugae that extend to posterior third of head dorsum, they do not curve outwards and do not merge with rugae that surround antennal sockets; frons quite wide. Frontal lobes moderately extended and raised up

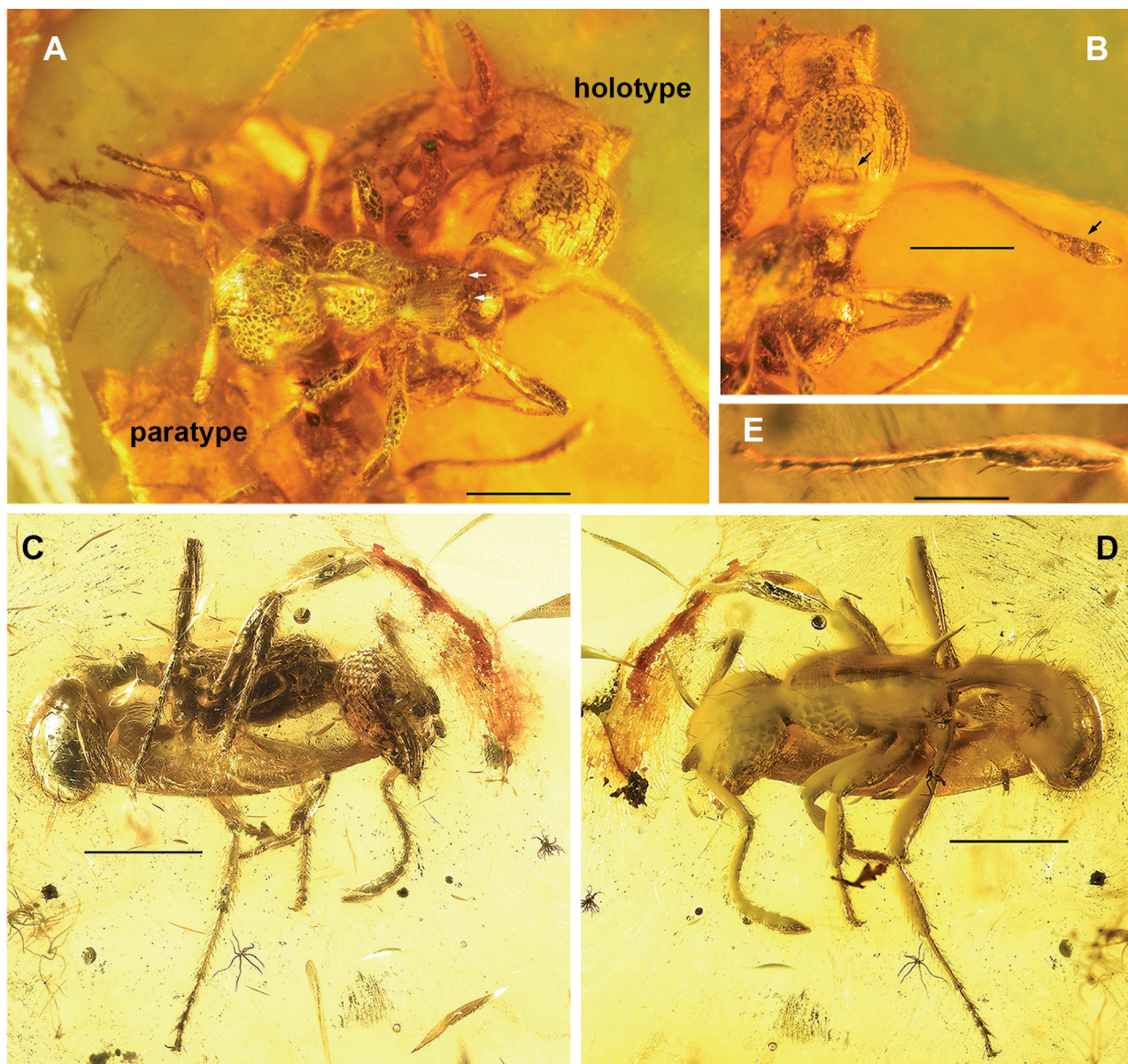


Figure 1. *Myrmica paradoxa* Radchenko, Dlussky et Elmes, 2007, workers: (A) holotype and paratype, general view (arrows indicate propodeal teeth); (B) holotype, head and antenna (arrows indicate shape of frontal carina and 3-segmented funicular club); *Myrmica longispinosa* Mayr, 1868, worker, neotype: (C) body, right side lateral view; (D) body, left side dorso-lateral view; (E) hind tibia. Scale bars: A–D – 1 mm, E – 0.5 mm.

Table 1. Measurement of the *Myrmica* species from late Eocene European ambers (in mm).

No	species	status	HL	HW	FW	FLW	SL	OL	GL	MdL	ML	MH
GZG.BST.27.199	<i>paradoxa</i>	holotype		1.12	0.42	0.50	0.99				1.57	
GZG.BST.27.199	<i>paradoxa</i>	paratype	1.27				0.92					
GZG.BST.27.199	<i>paradoxa</i>	paratype										
JDC 8606	<i>longispinosa</i>	neotype	1.01				0.87	0.20	0.25	0.62	1.85	0.49
JDC 6810	<i>longispinosa</i>		0.98				0.88	0.18	0.23	0.60	1.76	0.46
JDC 8482	<i>rudis</i>	neotype	1.25	1.07	0.42	0.47	1.22	0.23	0.23	0.57	1.98	0.68
KH F-256	<i>rudis</i>		1.30	1.09			1.27	0.26	0.26		2.03	0.70
JDC 9268	<i>intermedia</i>	neotype	1.22				1.14	0.18	0.20	0.62	1.72	0.57
F-650	<i>intermedia</i>		1.43	1.14	0.55	0.65	1.25	0.23	0.26	0.68	2.13	0.73
GPIH 4942	<i>intermedia</i>		1.37	1.09	0.51	0.61	1.17	0.23	0.26	0.66	1.91	
964/479	<i>eocenica</i>	holotype	1.11	0.95	0.41	0.52	1.06				1.34	
K-7581	<i>electrina</i>	holotype	1.20	1.07			1.20	0.23	0.30	0.62	1.92	0.78
JDC 5627	<i>electrina</i>	paratype	1.14	1.01	0.42	0.55	1.13	0.22	0.29	0.59	1.56	0.62
472. WK 79	<i>dictyosa</i>	holotype		1.07	0.52	0.60	1.09	0.21	0.21		1.77	
JDC 9928	<i>damzeni</i>	holotype	1.04				1.01	0.18	0.23		1.64	0.55
7/216	<i>saxonica</i>	holotype	1.25	1.09	0.42	0.48		0.23	0.31	0.57	1.69	0.75

Table 1. Extended.

No	species	status	PNW	PL	PH	PW	PPL	PPH	PPW	ESL	ESD	HTL
GZG.BST.27.199	<i>paradoxa</i>	holotype	0.95									
GZG.BST.27.199	<i>paradoxa</i>	paratype										0.87
GZG.BST.27.199	<i>paradoxa</i>	paratype		0.46								
JDC 8606	<i>longispinosa</i>	neotype		0.55	0.33		0.36	0.36		0.59	0.48	0.98
JDC 6810	<i>longispinosa</i>			0.55	0.35		0.35	0.34		0.59		0.95
JDC 8482	<i>rudis</i>	neotype	0.57	0.68	0.36	0.21	0.42	0.43	0.31	0.83	0.81	0.99
KH F-256	<i>rudis</i>		0.62	0.75	0.42	0.26	0.42	0.44	0.36	0.78	0.75	1.04
JDC 9268	<i>intermedia</i>	neotype	0.55	0.57	0.35	0.18	0.33	0.38	0.23	0.61	0.51	0.96
F-650	<i>intermedia</i>		0.87	0.70	0.44		0.49	0.57		0.68	0.52	1.25
GPIH 4942	<i>intermedia</i>		0.79	0.60		0.36	0.39		0.47	0.59	0.42	0.98
964/479	<i>eocenica</i>	holotype								0.63	0.62	0.91
K-7581	<i>electrina</i>	holotype		0.70	0.55		0.49	0.60		0.70		1.01
JDC 5627	<i>electrina</i>	paratype	0.53	0.59	0.46		0.43	0.46		0.64	0.56	0.96
472. WK 79	<i>dictyosa</i>	holotype	0.70							0.57	0.62	0.99
JDC 9928	<i>damzeni</i>	holotype	0.52	0.49	0.31		0.29	0.34		0.47	0.42	0.88
7/216	<i>saxonica</i>	holotype	0.60	0.42	0.34	0.26	0.36	0.36	0.31	0.47	0.52	0.99

vertically. Scape quite long, ca. 0.9 times as head length. Funiculus with not well-defined 4-segmented club. Eyes of medium size, located approximately at midlength of sides of head, genae 1.27–1.29 times as long as maximum diameter of eyes. Mandibles with five sharp teeth, apical tooth the longest.

Mesosoma long and low, 3.7–3.8 times as long as height, with moderately convex promesonotal dorsum

(seen in profile), promesonotal suture marked, while not deep and narrow (seen from above); metanotal groove very shallow (seen in profile); dorsal surface of propodeum nearly flat, not longer than posterior one; propodeal lobes not projecting apically, but pointed. Propodeal spines long, ca. 0.6 times as long as head, widened at base, almost straight, directed backward and slightly upward at an angle less than 40° (seen in

profile), very slightly divergent (seen from above) and sharply pointed. Petiole quite long and low, 1.56–1.68 times as long as height and > 0.5 times as long as head; petiolar node quite long, its anterior surface concave and steep, its dorsum somewhat flattened. Postpetiole fig-shaped (seen from above), its length subequal to height, its anterior surface not steep, feebly convex, node dorsum narrowly rounded (seen in profile).

Whole body (except gaster) coarsely sculptured. Only anterior (lower) part of frons with sinuous longitudinal rugae, remainder parts of head dorsum with reticulation. Clypeus with almost straight longitudinal rugae, mandibles with longitudinal rugae. Promesonotum with reticulation, mesopleura, propodeum and waist with longitudinal rugae. Body surface between rugae appears smooth and quite shiny. Gaster smooth and shiny.

Occipital margin and sides of head with quite abundant subdecumbent to suberect hairs; mesosoma, waist and gaster with erect to suberect hairs; antennal scape and legs with subdecumbent hairs. No decumbent pilosity.

Gynes and males unknown.

Material examined. Neotype worker (designated here), complete specimen, Baltic amber, No. JDC 8606 (SIZK); worker, complete specimen, Baltic amber, No. JDC 6810 (CJDL).

Etymology. From a combination of the Latin words *longus* = long, and *spinosa* = thorny, to described the obviously long propodeal spines.

Notes. Wheeler (1915) studied the Mayr's holotype specimen and an unnumbered additional worker from the Königsberg's collection, but added very little to Mayr's description.

According to Mayr's description, the most important diagnostic features of this species are the following: meso- and metatibiae with distinct pectinate spurs; head and mesosoma with very coarse sculpture; antennal scape strongly, but gradually curved at the base; propodeal spines long, directed mostly backward and slightly divergent (seen from above). Unfortunately, Mayr's drawing of this species is too schematic to be helpful (Mayr 1868, Fig. 86).

The neotype specimen of *M. longispinosa* designated here corresponds well to the original description with one exception: Mayr noted that the propodeal lobes of the holotype specimen are not pointed apically, while they are pointed in the neotype. Since the most of the holotype specimen was covered with a white film, the shape of the propodeal lobes was probably not clearly visible (see also Mayr 1868; Wheeler 1915).

Comparative diagnosis. *Myrmica longispinosa* differs from *M. dictyosa* sp. nov. by the presence of pectinate spurs on the meso- and metatibiae and by the longitudinally rugosed mesopleura, propodeum and waist (vs. completely coarsely reticulated mesosoma in

the latter). It is distinguished from *M. electrina* sp. nov. and *M. saxonica* sp. nov. by the long and slender mesosoma ($ML/MH > 3.5$) and long and low petiole ($PL/PH > 1.50$) vs. shorter and more robust mesosoma and short and high petiole in the latter species ($ML/MH \leq 2.50$, $PL/PH < 1.30$). In general appearance, *M. longispinosa* resembles *M. eocenica* Radchenko, Dlussky et Elmes, 2007, *M. rudis*, *M. intermedia* and *M. damzeni* sp. nov., but differs from all of them (except *M. eocenica*) by the presence of pectinate spurs on the meso- and metatibiae. It differs from *M. eocenica* in having very weakly diverging propodeal spines (vs. strongly divergent ones) and a gradually but rather strongly curved scape at the base (vs. the very weakly curved scape in the latter species). In *M. rudis* and *M. intermedia*, the eyes are located in front of the midlength of the sides of the head, while in *M. longispinosa* they are located approximately at the midlength of the sides of the head; moreover, the propodeal spines of *M. rudis* are directed more upwards and distinctly divergent. From *M. damzeni* sp. nov. it is well distinguished by a much more abundant erect or suberect pilosity on the body and appendages, vs. very sparse scattered thin suberect hairs on the body and very sparse thin decumbent hairs on the appendages.

Myrmica rudis (Mayr, 1868) (Fig. 2, A–C; Tables 1, 2)

Macromischa rudis Mayr, 1868: 85, pl. IV, fig. 85, w, Baltic Amber; Dalla Torre 1893: 120; André 1895: 82; Handlirsch 1907: 875; Burnham 1978: 110.

Nothomyrmica rudis: Wheeler 1915: 60, fig. 23; Carpenter 1927: 31; Radchenko 1994: 48; Bolton 1995: 292; Dlussky 1997: 625.

Myrmica rudis: Radchenko et al. 2007: 1495; Radchenko and Elmes 2010: 655, 744; Bolton 2023 (Website).

Localities. Poland, Baltic amber (neotype worker); Ukraine, Rivne Prov., Volodymyrets Distr., Rovno amber; both late Eocene, Priabonian age, 37.8–33.9 Ma.

Diagnosis. Meso- and metatibiae without spur; head, mesosoma and waist coarsely sculptured; upper lateroventral corners of head somewhat pointed; eyes located distinctly in front of midlength of sides of head; scape gradually, but quite strongly curved at base, without any angle, lobe or carina; mesosoma long and low; petiole very long and low; propodeal spines directed backward and upward at an angle ca. 45° (seen in profile) and distinctly divergent (seen from above).

Redescription of workers. Body length 5.6–5.9 mm. Head elongate-oval, ca. 1.2 times as long as wide, with convex sides, nearly straight occipital margin and steeply rounded occipital corners; its posterior margin surrounded by distinct ridge ('collar') and its upper lateroventral corners somewhat pointed. Anterior clypeal margin convex, not pointed and not-notched medially. Frontal carinae feebly curved, merging with

rugae that extend to posterior third of head dorsum, they do not curve outwards and do not merge with rugae that surround antennal sockets; frons quite wide, ca. 0.4 times as head width. Frontal lobes slightly extended and raised up vertically. Scape long, subequal to head length. Funiculus with moderately defined 4-segmented club. Eyes of medium size, their maximum diameter equal to length of genae. Mandibles with long apical tooth, twice shorter preapical one and 5 minor denticles.

Mesosoma long and low, nearly 3 times as long as height, with very feebly convex promesonotal dorsum (seen in profile), promesonotal suture visible and quite deep and wide (seen from above); metanotal groove very shallow (seen in profile); dorsal surface of propodeum nearly flat, distinctly longer than posterior one; propodeal lobes projecting apically and sharply pointed. Propodeal spines very long, 0.60–0.67 times as long as head, widened at base, almost straight, directed backward and upward at an angle ca. 45° (seen in

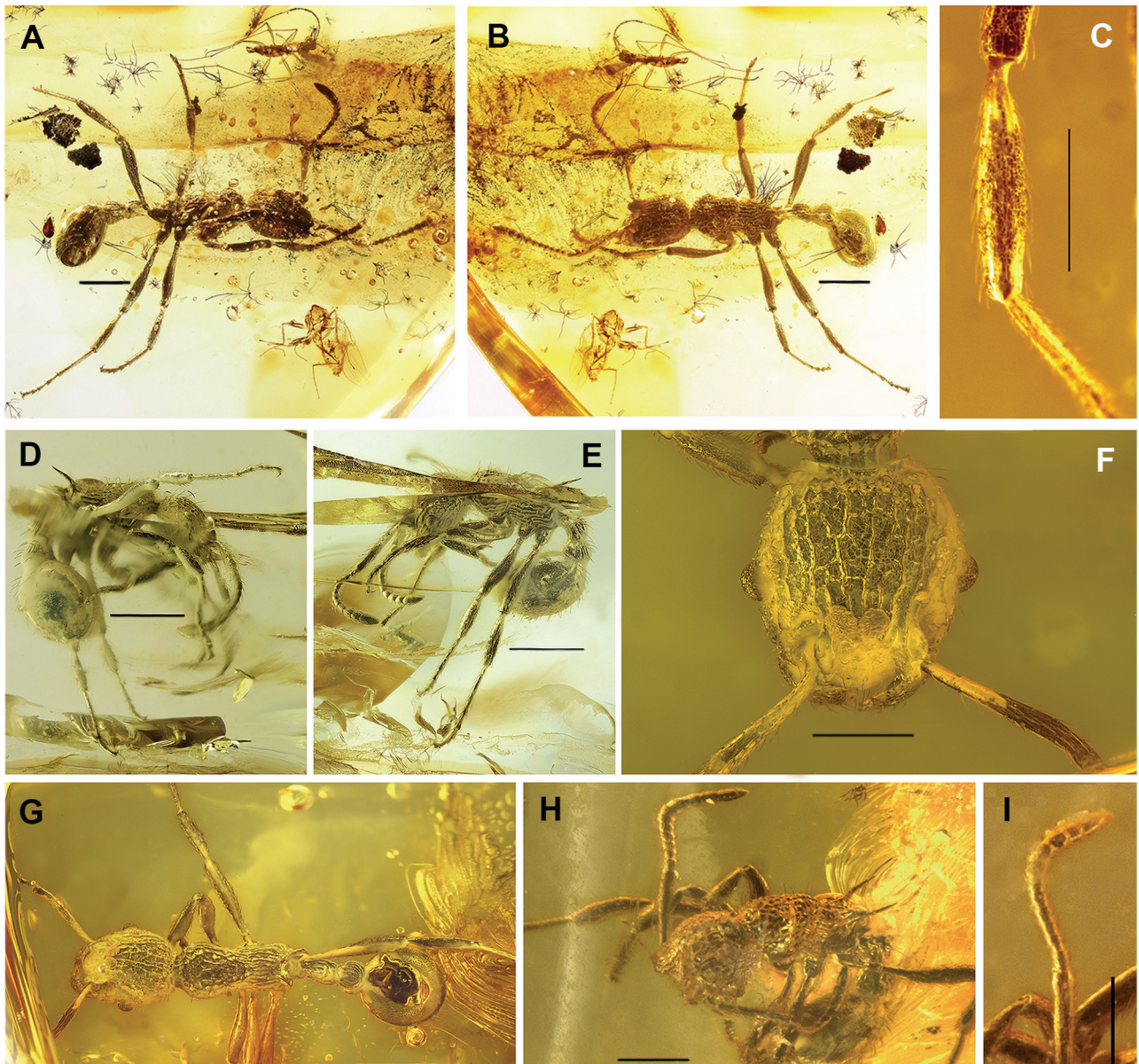


Figure 2. *Myrmica rudis* (Mayr, 1868), worker, neotype: (A) body, right side lateral view; (B) body, left side dorso-lateral view; (C) hind tibia; *Myrmica intermedia* (Wheeler, 1915), workers: neotype (D) body, left side lateral view; (E) body, right side dorso-lateral view; specimen GPIH 4942: (F) head, dorsal view; (G) body, dorsal view; specimen F-650: (H) body, dorso-lateral view; (I) antenna. Scale bars: A, B, D, E, G–I – 1 mm, C, F – 0.5 mm.

profile), distinctly divergent (seen from above) and sharply pointed. Petiole long, low and narrow, 1.81–1.86 times as long as height, > 0.5 times as long as head; petiolar node not very long, its anterior surface concave and steep, its dorsum convex and gradually sloping posteriorly. Postpetiole fig-shaped (seen from above), 1.4–1.5 times as wide as petiole, slightly higher than length, its anterior surface not steep, feebly convex, node dorsum narrowly rounded (seen in profile).

Whole body (except gaster) coarsely sculptured. Frons with six sinuous longitudinal rugae between frontal carinae level with the eyes, remainder parts of head dorsum with reticulation; ventral surface of head with six transversally-concentric rugae. Clypeus with almost straight longitudinal rugae, mandibles with less coarse longitudinal rugae. Promesonotum, mesopleura and sides of propodeum reticulated; propodeal dorsum with sinuous longitudinal rugae; surface between propodeal spines transversally rugosed; posterior surface of propodeum between propodeal spines smooth and shiny. Petiole with sinuous longitudinal rugae and reticulation, postpetiole with straight longitudinally-concentric rugosity. Body surface between rugae with superficial reticulation, not smooth. Gaster smooth and shiny.

Occipital margin and sides of head with quite abundant subdecumbent to suberect hairs; mesosoma, waist and gaster with erect to suberect hairs; antennal scape and legs with subdecumbent hairs. No decumbent pilosity.

Gynes and males unknown.

Material examined. Neotype worker (designated here), complete specimen, Baltic amber, No. JDC 8482 (SIZK); worker, complete specimen (badly preserved), Baltic amber, No. 1945/6 (MZPAN); worker, complete specimen (mostly covered by whitish film), Rovno amber, No. F-256 (CMKHU).

Etymology. From the Latin word *rudis*, probably in its sense of being ‘coarse’ or ‘rough’, to indicate its very coarse body sculpture.

Notes. This species was originally assigned to the genus *Macromisha* Roger, 1863 (now junior synonym of *Temnothorax*), then it was transferred by Wheeler (1915) to the established by him extinct genus *Nothomyrmica*, and finally was transferred to *Myrmica* by Radchenko *et al.* (2007).

Mayr (1868) described *M. rudis* based on two workers from Baltic amber, but later André (1895), Wheeler (1915), Carpenter (1927) and Radchenko *et al.* (2007) studied 13 more specimens of this species from Baltic amber. Taking into account current data (see Material examined, above), the total number of found specimens of this species is 17, which is twice as many as the number of specimens of all other species of amber *Myrmica* combined. Moreover, one of these specimens was first discovered in Rovno amber.

The designated neotype specimen of *M. rudis* agrees well with the original description of this species, further Wheeler’s (1915) comments and an excellent drawing (*loc. cit.*, Fig. 23).

Comparative diagnosis. For differences from *M. longispinosa*, see above. In *M. dictyosa* the entire mesosoma is very coarsely reticulate, while in *M. rudis* at least the propodeal dorsum has sinuous longitudinal rugae. Like *M. longispinosa*, *M. rudis* differs from *M. electrina* sp. nov. and *M. saxonica* sp. nov. by the longer and more slender mesosoma and long and low petiole. By the eyes located in front of midlength of sides of head, it resembles *M. intermedia* and differs from *M. eocenica* and *M. damzeni* sp. nov. In addition, it is distinguished from *M. eocenica* by the absence of spurs on the meso- and metatibiae and by the scape more strongly curved at the base, and from *M. damzeni* sp. nov. – by a much more abundant erect or suberect pilosity on the body and appendages and longer propodeal spines ($ESL/HL \geq 0.60$ vs. 0.45). It differs from *M. intermedia* by the somewhat longer propodeal spines, directed backward and upward at an angle ca. 45° and more divergent.

Myrmica intermedia (Wheeler, 1915)

(Fig. 2, D–I; Tables 1, 2)

Nothomyrmica intermedia Wheeler, 1915: 61, fig. 24, w, Baltic amber; Burnham 1978: 110; Radchenko 1994: 48; Dlussky 1997: 625; Bolton 1995: 292.

Myrmica intermedia: Radchenko *et al.* 2007: 1496; Radchenko and Elmes 2010: 653; Bolton 2023 (Web site).

Localities. Poland, Baltic amber; Ukraine, Rivne Prov., Rovno amber; both late Eocene, Priabonian age, 37.8–33.9 Ma.

Diagnosis. Meso- and metatibiae without spur; head, mesosoma and waist coarsely sculptured; upper lateroventral corners of head slightly pointed; eyes located somewhat in front of midlength of sides of head; scape gradually, but quite strongly curved at base, without any angle, lobe or carina; mesosoma long and low; petiole long and low; propodeal spines directed mainly backward (seen in profile) and very slightly divergent (seen from above).

Redescription of workers. Body length 4.9–6.4 mm. Head elongate, 1.25 times as long as wide, with feebly convex sides, almost straight occipital margin and widely rounded occipital corners; its posterior margin surrounded by distinct ridge (‘collar’) and its upper lateroventral corners somewhat pointed. Anterior clypeal margin almost straight, not pointed and not-notched medially. Frontal carinae feebly curved, merging with rugae that extend to posterior third of head dorsum, they do not curve outwards and do not merge with rugae that surround antennal sockets; frons wide,

Table 2. Morphometric indices of the *Myrmica* species from late Eocene European ambers.

No	species	status	HL/HW	SL/HL	SL/HW	FW/HW	FLW/FW	OL/HL	GL/OL	MdL/HL	ML/MH	ML/PNW
GZG.BST.27.199	<i>paradoxa</i>	holotype			0.89	0.38	1.20					
GZG.BST.27.199	<i>paradoxa</i>	paratype		0.73								
GZG.BST.27.199	<i>paradoxa</i>	paratype										
JDC 8606	<i>longispinosa</i>	neotype		0.86				0.19	1.27	0.62	3.74	
JDC 6810	<i>longispinosa</i>			0.90				0.19	1.29	0.61	3.85	
JDC 8482	<i>rudis</i>	neotype	1.17	0.98	1.15	0.39	1.13	0.19	1.00	0.46	2.92	3.45
KH F-256	<i>rudis</i>		1.19	0.98	1.17			0.20	1.00		2.89	3.25
JDC 9268	<i>intermedia</i>	neotype		0.93				0.15	1.07	0.51	3.00	3.14
F-650	<i>intermedia</i>		1.25	0.87	1.09	0.47	1.19	0.16	1.11	0.47	2.93	2.45
GPIH 4942	<i>intermedia</i>		1.25	0.86	1.07	0.46	1.21	0.17	1.11	0.49		2.41
964/479	<i>eocenica</i>	holotype	1.16	0.96	1.12	0.43	1.28					
K-7581	<i>electrina</i>	holotype	1.12	1.00	1.12			0.20	1.27	0.52	2.47	
JDC 5627	<i>electrina</i>	paratype	1.13	0.99	1.12	0.41	1.31	0.19	1.29	0.51	2.50	2.93
472. WK 79	<i>dictyosa</i>	holotype			1.02	0.49	1.15		1.00			2.52
JDC 9928	<i>damzeni</i>	holotype		0.98				0.18	1.29		3.00	3.15
7/216	<i>saxonica</i>	holotype	1.14			0.38	1.13	0.19	1.33	0.46	2.24	2.83

Table 2. Extended.

No	species	status	PL/PH	PL/HL	PL/HW	PW/HW	PPL/PPH	PPW/PW	ESL/HW	ESL/HL	ESD/ESL
GZG.BST.27.199	<i>paradoxa</i>	holotype									
GZG.BST.27.199	<i>paradoxa</i>	paratype									
GZG.BST.27.199	<i>paradoxa</i>	paratype									
JDC 8606	<i>longispinosa</i>	neotype	1.68	0.54			1.00			0.58	0.82
JDC 6810	<i>longispinosa</i>		1.56	0.56			1.04			0.60	
JDC 8482	<i>rudis</i>	neotype	1.86	0.54	0.63	0.20	0.97	1.50	0.78	0.67	0.97
KH F-256	<i>rudis</i>		1.81	0.58	0.69	0.23	0.94	1.40	0.71	0.60	0.97
JDC 9268	<i>intermedia</i>	neotype	1.63	0.47			0.86	1.29		0.50	0.83
F-650	<i>intermedia</i>		1.59	0.49	0.61		0.86		0.59	0.47	0.77
GPIH 4942	<i>intermedia</i>			0.44		0.33		1.29	0.54	0.43	0.71
964/479	<i>eocenica</i>	holotype								0.66	0.98
K-7581	<i>electrina</i>	holotype	1.29	0.58			0.83			0.59	
JDC 5627	<i>electrina</i>	paratype	1.29	0.51	0.58		0.94		0.63	0.56	0.88
472. WK 79	<i>dictyosa</i>	holotype							0.54		1.09
JDC 9928	<i>damzeni</i>	holotype	1.58	0.48			0.85			0.45	0.89
7/216	<i>saxonica</i>	holotype	1.23	0.33	0.38	0.25	1.00	1.20	0.43	0.38	1.11

0.46–0.47 times as wide as head. Frontal lobes moderately extended, ca. 1.2 times as wide as frons and raised up vertically. Scape long, 0.86–0.93 times as long as head. Funiculus with 4-segmented club. Eyes quite small and convex, located somewhat in front of mid-length of sides of head, genae ca. 1.1 times as long as maximum diameter of eyes. Mandibles with long apical tooth, somewhat shorter preapical one and 4 minor denticles. Palp formula 6, 4.

Mesosoma long and low, ca. 3 times as long as height, with feebly convex promesonotal dorsum (seen in profile), promesonotal suture indistinct (seen from above); metanotal groove distinct, though not very deep (seen in profile); dorsal surface of propodeum nearly flat, subequal in length to posterior one; propodeal lobes projecting apically and sharply pointed. Propodeal spines long, 0.43–0.50 times as long as head, widened at base, thin, almost straight, directed backward and somewhat

upward at an angle ca. 40° (seen in profile), very slightly diverging (seen from above) and sharply pointed. Petiole quite long, and low, ca. 1.6 times as long as height, 0.44–0.49 times as long as head; petiolar node not long, its anterior surface concave and steep, node dorsum rounded, posterior surface steep. Postpetiole fig-shaped (seen from above), 1.3 times as wide as petiole, higher than length, its anterior surface quite steep, feebly convex, with narrowly rounded dorsum (seen in profile).

Whole body (except gaster) coarsely sculptured. Frons with six sinuous longitudinal rugae between frontal carinae level with the eyes, remainder parts of head dorsum with reticulation; ventral surface of head with 5–6 less coarse transversally-concentric rugae. Clypeus with not coarse straight longitudinal rugae, mandibles with not coarse longitudinal rugae. Promesonotal dorsum and sides of propodeum reticulated; mesopleura and propodeum with sinuous longitudinal rugae; surface between propodeal spines transversally rugulose. Petiole with sinuous longitudinal rugae and reticulation, postpetiole with straight longitudinally-concentric rugosity. Body surface between rugae smooth. Gaster smooth and shiny.

Whole body with numerous, quite long, thin suberect hairs, scape and legs with abundant hairs, outstanding at an angle ca. 30°. No decumbent pilosity.

Gynes and males unknown.

Material examined. Neotype worker (designated here), complete specimen, Baltic amber, No. JDC 9268 (SIZK); worker, complete specimen, Baltic amber, No. GPIH 4942, (CCGG 6790) (AntWeb CASENT0917563); worker, complete specimen, Rovno amber, F-650 (CMKHU).

Etymology. From the word intermediate, derived from the Latin prefix *inter* = between, and *media* = in the middle; Wheeler (1915: 61) wrote: “Closely resembling *N. rudis* and almost intermediate between this form and *Myrmica longispinosa* in many particulars”.

Notes. Until now, only the holotype specimen was known, but I found two more workers (including the neotype) from Baltic amber, and one was found for the first time from Rovno amber.

The designated neotype and two other specimens redescribed above agree well with the original description and drawing of *M. intermedia* (Wheeler 1915, Fig. 24). It is important that in one of the examined specimens, the maxillary and labial palps are clearly visible and are 6- and 4-segmented, respectively. This fact confirms our previous proposal to transfer *M. intermedia* to the genus *Myrmica* (Radchenko *et al.* 2007), despite the absence of spurs on the meso- and metatibiae.

Comparative diagnosis. For differences from *M. longispinosa* and *M. rudis*, see above. It differs

from *M. dictyosa* by the mesopleura and propodeum with sinuous longitudinal rugae, while in the latter species the entire mesosoma is very coarsely reticulate. Like *M. longispinosa* and *M. rudis*, *M. intermedia* differs from *M. electrina* sp. nov. and *M. saxonica* sp. nov. by the longer and more slender mesosoma and long and low petiole. By the eyes located in front of midlength of sides of head, it differs from *M. eocenica* and *M. damzeni* sp. nov. In addition, it is distinguished from *M. eocenica* by the absence of spurs on the meso- and metatibiae and by the much less divergent propodeal spines, and from *M. damzeni* sp. nov. – by a much more abundant erect or suberect pilosity on the body and appendages.

Myrmica eocenica Radchenko, Dlussky et Elmes, 2007 (Fig. 3, A, B; Tables 1, 2)

Myrmica eocenica Radchenko, Dlussky et Elmes, 2007: 1497, Figs 4, 5, w, Baltic amber; Radchenko and Elmes 2010: 653; Bolton 2023 (Web site).

Localities. Russia, Kaliningrad Prov., Baltic amber; Denmark, Scandinavian amber; both late Eocene, Priabonian age, 37.8–33.9 Ma.

Diagnosis. Meso- and metatibiae with pectinate spur; head, mesosoma and waist coarsely sculptured; upper lateroventral corners of head somewhat pointed; eyes located approximately at midlength of sides of head; scape very feebly curved at base [similar to modern *M. rubra* (Linnaeus, 1758)]; mesosoma long and low; petiole long and low; propodeal spines directed mainly backward (seen in profile) and strongly divergent (seen from above).

Description – see Radchenko *et al.* 2007.

Material examined. Holotype worker, complete specimen, Baltic amber, No. 964/479 (PIN); worker, complete specimen, Baltic amber, No. JDC 10573 (CJDL); worker, complete specimen, Scandinavian amber, No. 381, leg. B. V. Henningsen, 1-1-1966 (ZMUC).

Etymology. Named for the Eocene Epoch, when the type specimen was trapped in amber, the name Eocene means dawn of the recent period, is derived from the Greek *εοσ* (eos), = sunrise and *κοινος* (koinos) = recent.

Notes. *Myrmica eocenica* was originally described based on a single worker from Baltic amber, and later I found two workers belonging to this species in Baltic and Scandinavian ambers.

Comparative diagnosis. For differences from *M. longispinosa*, *M. rudis* and *M. intermedia* see above. *Myrmica eocenica* differs from *M. electrina*, *M. dictyosa* and *M. damzeni* by the presence of spurs on the meso- and metatibiae. In additions, in *M. dictyosa* the entire mesosoma is very coarsely reticulate, while in *M. eocenica* the propodeal dorsum has

sinuous longitudinal rugae; form *M. damzeni* sp. nov. it differs by a more abundant erect or suberect pilosity on the body and especially on appendages, and from *M. electrina* – by the shape of propodeal spines, which are straight and strongly divergent in *M. eocenica* vs. curved down along their length and weakly divergent. Finally, *M. saxonica* differs from the latter by the not pointed upper lateroventral corners of the head and by shorter propodeal spines that are strongly widened at the base, massive and somewhat curved inwards.

Description of new species

Myrmica electrina sp. nov.

(Fig. 3, C–E, Tables 1, 2)

Localities. Ukraine, Rivne Prov., Rovno amber; Poland, Baltic amber; both late Eocene, Priabonian age, 37.8–33.9 Ma.

Diagnosis. Meso- and metatibiae without spur; head, mesosoma and waist coarsely sculptured; upper

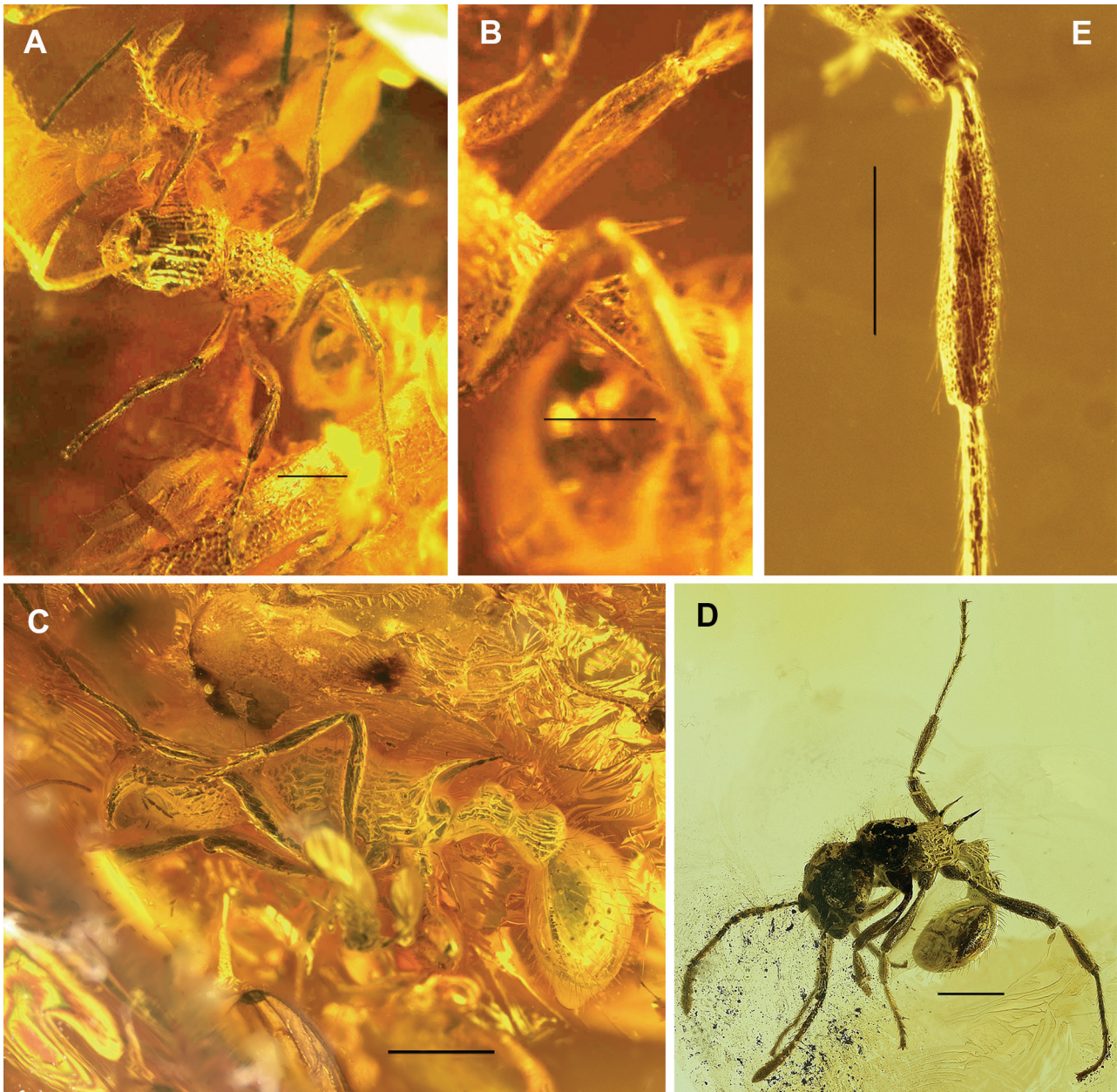


Figure 3. *Myrmica eocenica* Radchenko, Dlussky et Elmes, 2007, worker, holotype: (A) body, dorso-lateral view; (B) propodeal spines, dorsal view; *Myrmica electrina* sp. nov., workers: (C) holotype, body, lateral view; paratype (D) body, dorso-lateral view; (E) hind tibia. Scale bars:

A, C, G – 1 mm, B, E – 0.5 mm.

lateroventral corners of head somewhat pointed; eyes located approximately at midlength of sides of head; scape very feebly curved at base [similar to modern *M. rubra* (Linnaeus, 1758)], without any angle, lobe or carina; mesosoma relatively short; petiole rather long, but high; propodeal spines directed mainly backward (seen in profile), curved down along their length and slightly divergent (seen from above).

Description of workers. Body length 5.2–6.2 mm. Head comparatively slightly elongate, 1.12–1.13 times as head width, with feebly convex sides, broadly rounded occipital corners and straight occipital margin; its posterior margin surrounded by distinct ridge ('collar') and its upper lateroventral corners somewhat pointed. Anterior clypeal margin convex, not pointed and not-notched medially. Frontal carinae feebly curved, merging with rugae that extend to posterior third of head dorsum, they do not curve outwards and do not merge with rugae that surround antennal sockets; frons wide, 0.41 times as wide as head. Frontal lobes moderately extended, not raised up vertically. Scape long, subequal to head length. Funiculus with 4-segmented club. Eyes of medium size and convex, located approximately at midlength of sides of head, genae 1.27–1.29 times as long as maximum diameter of eyes. Mandibles with long apical tooth, somewhat shorter preapical one and 4–5 minor denticles.

Mesosoma relatively short, ca. 2.5 times as long as height, with moderately convex promesonotal dorsum, promesonotal suture dorsally indistinct (seen from above); metanotal groove distinct, though not very deep (seen in profile); dorsal surface of propodeum nearly flat, subequal in length to posterior one; propodeal lobes projecting apically and sharply pointed. Propodeal spines very long, 0.56–0.59 times as long as head, widened at base, curved down along their length, directed backward and somewhat upward at an angle ca. 40° (seen in profile), slightly divergent (seen from above) and sharply pointed. Petiole comparatively high (compare to related species), ca. 1.3 times as long as height, petiolar node short, its anterior surface concave and steep, node dorsum rounded, posterior surface steep; postpetiole fig-shaped (seen from above), higher than length, its anterior surface not steep, feebly convex, node dorsum narrowly rounded (seen in profile).

Whole body (except gaster) coarsely sculptured. Lower part of frons with six sinuous longitudinal rugae between frontal carinae level with the eyes, remainder parts of head dorsum with reticulation. Clypeus and mandibles with not coarse straight longitudinal rugae. Only anterior part of pronotum with reticulation, remainder part of pronotum, mesonotum, propodeum and petiole with sinuous longitudinal rugae, postpetiole with straight longitudinally-concentric rugae. Body surface between rugae with very fine superficial microsculpture, though appears shiny.

Whole body with quite abundant erect to suberect hairs. Scape and legs with subdecumbent pilosity.

Gynes and males unknown.

Material examined. Holotype worker, complete specimen, Rovno amber, No. K-7581 (SIZK); paratype worker, complete specimen, Baltic amber, No. JDC 5627 (CJDL).

Etymology. From the Greek word *ήλεκτρο* (electron) = amber, to indicate that this species was found in amber.

Comparative diagnosis. For differences from *M. longispinosa*, *M. rudis*, *M. intermedia* and *M. eocenica* see above. It is clearly distinguished from *M. dictyosa* sp. nov. by the mostly coarsely sinuously longitudinally rugosed mesosoma and waist, but the entire mesosoma is coarsely reticulate in the latter species. *M. electrina* well differs from *M. damzeni* by the shorter and more robust mesosoma and shorter and higher petiole (ML/MH \leq 2.50, PL/PH 1.29 vs. ML/MH 3.00, PL/PH 1.58 in the latter). *M. saxonica* differs from *M. electrina* by the pectinate spurs on the metatibiae, not pointed upper lateroventral corners of the head, the distinctly shorter propodeal spines, which are strongly widened at the base, massive and somewhat curved inwards, and by the less coarse body sculpture.

Myrmica dictyosa sp. nov.

(Fig. 4, A, B; Tables 1, 2)

Localities. Poland, Baltic amber, late Eocene, Priabonian age, 37.8–33.9 Ma.

Diagnosis. Meso- and metatibiae without spur; head dorsum and mesosoma with very coarse reticulation, only lower part of frons with short coarse longitudinal rugae; upper lateroventral corners of head somewhat pointed; eyes located distinctly in front of midlength of sides of head; scape gradually, but quite strongly curved at base, without any angle, lobe or carina; mesosoma long and narrow; propodeal spines directed mainly backward (seen in profile) and strongly divergent (seen from above).

Description of worker. Body length ca. 5.8 mm. Head length does not properly measurable, but head appears moderately elongate, with distinctly convex sides, broadly rounded occipital corners and straight occipital margin; its posterior margin surrounded by distinct ridge ('collar') and its upper lateroventral corners somewhat pointed. Clypeus obscured in specimen. Frontal carinae feebly curved, merging with rugae that extend to posterior third of head dorsum, they do not curve outwards and do not merge with rugae that surround antennal sockets; frons wide, frontal lobes slightly extended, 1.15 times as wide as frons and raised up vertically. Scape quite long, surpassing

occipital margin, subequal to head width. Funiculus with 4-segmented club. Eyes of medium size, located distinctly in front of midlength of sides of head, their maximum diameter equal to length of genae. Mandibles with long apical tooth, somewhat shorter preapical one and 4 sharp smaller denticles.

Mesosoma long and narrow, with very feebly convex promesonotal dorsum, promesonotal suture indistinct; metanotal groove shallow; propodeal lobes not pointed apically, at most slightly angulated. Propodeal spines long, somewhat widened at base, sharply pointed, slightly curved down along their length (seen in profile). Petiole and postpetiole mostly destroyed (cut when piece amber was polished), but petiole appears quite long and postpetiole fig-shaped (seen from above).

Whole head dorsum and mesosoma with very coarse reticulation, only lower part of frons between frontal carinae with five short coarse longitudinal rugae. Mandibles with coarse longitudinal rugae. Surface between sculpture with very fine superficial microsculpture, but appears shiny. Gaster smooth and shiny.

Head margins, mesosoma and gaster with not abundant, relatively short suberect to subdecumbent hairs. Scape and legs with subdecumbent hairs. No decumbent pilosity.

Gynes and males unknown.

Material examined. Holotype worker, complete specimen, Baltic amber, No. 472, WK 79 (MAGU).

Etymology. From the Greek word *δίχτυον* (dictyo) = net, to indicate its reticulated body sculpture.

Comparative diagnosis. For differences from *M. longispinosa*, *M. rudis*, *M. intermedia*, *M. eoecnica* and *M. electrina* see above. *Myrmica dictyosa* well distinguished from *M. damzeni* and *M. saxonica* by the entirely reticulated mesosoma. In addition, *M. saxonica* has pectinate spurs on the metatibia, not pointed upper lateroventral corners of the head, and shorter propodeal spines that are strongly widened at the base, massive and somewhat curved inwards. The scape in *M. damzeni* is less strongly curved at the base. The eyes of both latter species are located approximately at the midlength of the sides of the head, while in *M. dictyosa* they are located in front of the midlength of the sides of the head.

***Myrmica damzeni* sp. nov.**

(Fig. 4, C; Tables 1, 2)

Localities. Poland, Baltic amber, late Eocene, Priabonian age, 37.8–33.9 Ma.

Diagnosis. Meso- and metatibiae without spur; eyes located approximately at midlength of sides of head; scape gradually and not strongly curved at base,

without any angle, lobe or carina (similar to modern *M. gallieni* Bondroit, 1920); mesosoma long and low; petiole long and low; propodeal spines directed mainly backward (seen in profile) and feebly divergent (seen from above).

Description of worker. Body length 4.7 mm. Head width does not properly measurable, but head appears elongate, with moderately convex sides, straight occipital margin and widely rounded occipital corners; its posterior margin surrounded by distinct ridge ('collar') and its upper lateroventral corners somewhat pointed. Clypeus and mandibles obscured. Frontal carinae feebly curved, merging with rugae that extend to posterior third of head dorsum, they do not curve outwards and do not merge with rugae that surround antennal sockets. Frontal lobes moderately extended. Scape long, subequal to head length. Funiculus with 4-segmented club. Eyes of medium size, located approximately at midlength of sides of head, genae 1.29 times as long as maximum diameter of eyes. Mandibles obscured.

Mesosoma long and low, 3 times as long as height, with distinctly convex promesonotal dorsum (seen in profile), promesonotal suture dorsally well marked (seen from above); metanotal groove quite deep (seen in profile); dorsal surface of propodeum convex, subequal in length to posterior one; propodeal lobes narrowly rounded apically. Propodeal spines relatively short, 0.45 times as head length, widened at base, thin, straight, directed backward and slightly upward at an angle < 30° (seen in profile), feebly divergent (seen from above) and sharply pointed. Petiole quite long and low, ca. 1.6 times as long as height and ca. 0.5 times as long as head; petiolar node relatively short, its anterior surface concave and not steep, node dorsum rounded, posterior surface gradually sloping backward. Postpetiole subglobular, higher than length, its anterior surface quite steep, feebly convex, node dorsum widely rounded (seen in profile).

Head, mesosoma and waist not very coarsely sculptured. Head dorsum sinuously longitudinally rugulose, only temples and vertex with reticulation. Promesonotal dorsum and sides of pronotum sinuously longitudinally rugulose, only anterior part of pronotal dorsum with reticulation, mesopleura and whole propodeum with not coarse longitudinal rugosity; surface between propodeal spines transversally rugulose; posterior surface of propodeum smooth and shiny. Petiole and postpetiole with short sinuous longitudinal rugae and reticulation. Body surface between rugae with fine superficial reticulation. Gaster smooth and shiny.

Body with very sparse scattered thin suberect hairs, in general, specimen appears practically hairless; scape and legs with very sparse thin decumbent hairs.

Gynes and males unknown.

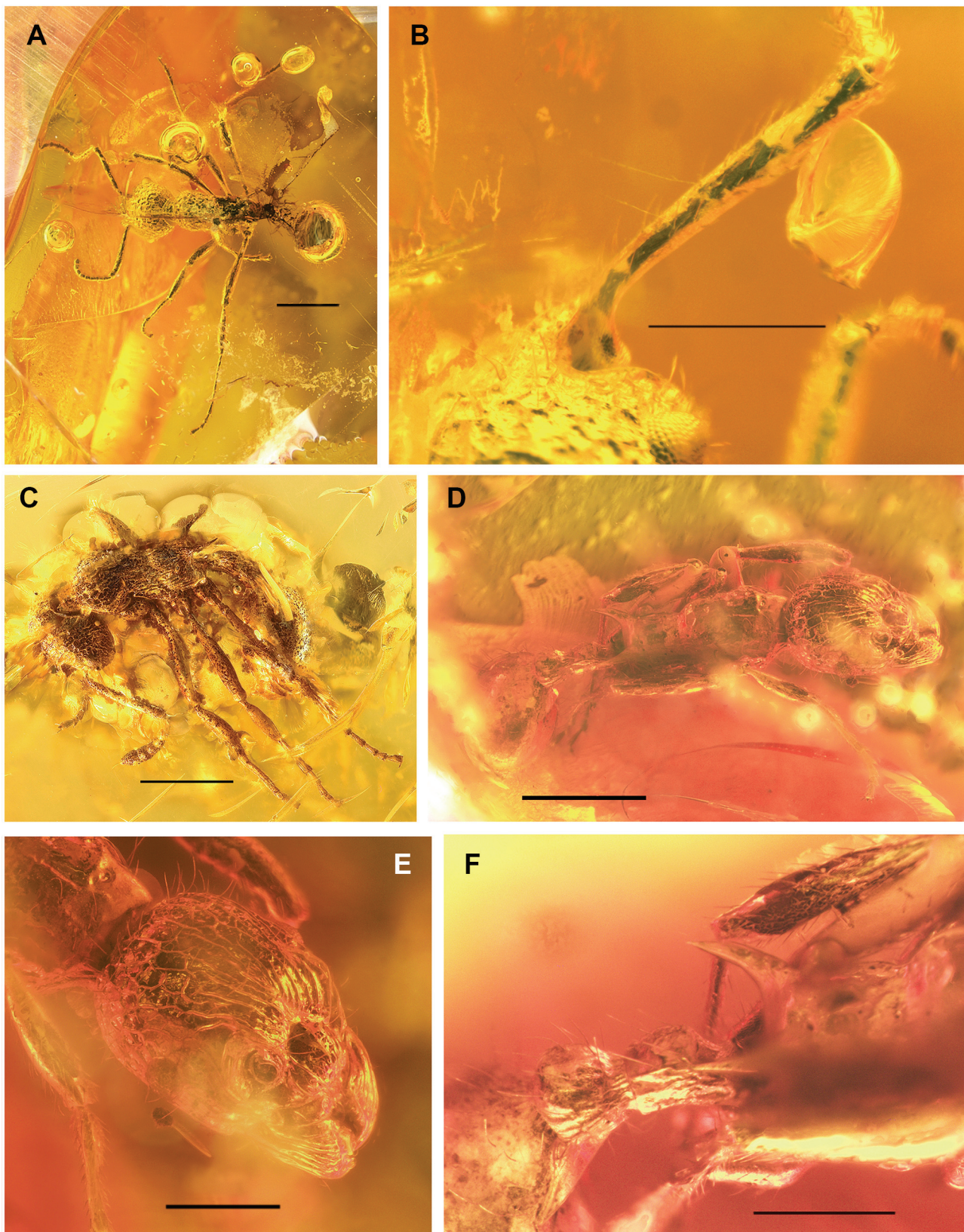


Figure 4. *Myrmica dictyosa* sp. nov., worker, holotype: (A) body, dorsal view; (B) scape; *Myrmica damzeni* sp. nov., worker, holotype: (C) body, lateral view; *Myrmica saronica* sp. nov., worker, holotype: (D) body, dorsal view; (E) head, dorso-lateral view; (F) waist and propodeum, dorso-lateral view. Scale bars: A, C, D – 1 mm, B, E, F – 0.5 mm.

Material examined. Holotype worker, complete specimen, Baltic amber, No. JDC 9928 (SIZK).

Etymology. The species dedicated to Mr. Jonas Damzen (Lithuania), who found and generously presented the holotype specimen to SIZK collection.

Comparative diagnosis. For differences from *M. longispinosa*, *M. rudis*, *M. intermedia*, *M. eoecenica*, *M. electrina* and *M. dictyosa* see above. *Myrmica damzeni* is clearly distinguished from *M. saxonica* by the absence of tibial spurs, the longer petiole, pointed upper lateroventral corners of the head, and by the shape of the propodeal spines, which are thin and straight, but massive and somewhat curved inward in *M. saxonica*.

***Myrmica saxonica* sp. nov.**

(Fig. 4, D–F; Tables 1, 2)

Localities. Germany, Saxony-Anhalt, Bitterfeld amber, late Eocene, Priabonian age, 37.8–33.9 Ma.

Diagnosis. At least metatibiae with pectinate spur; head, mesosoma and waist not coarsely sculptured; upper lateroventral corners of head not pointed; eyes located somewhat behind midlength of sides of head; antennae missing on specimen; mesosoma relatively short; petiole relatively short and high; propodeal spines relatively short, strongly widened at base, massive, directed backward and upward at an angle ca. 40° (seen in profile), somewhat curved inward and divergent (seen from above).

Description of worker. Body length 5.1 mm. Head comparatively slightly elongate, 1.14 times as head width, with feebly convex sides, broadly rounded occipital corners and slightly convex occipital margin; its posterior margin surrounded by weakly developed ridge ('collar'). Anterior clypeal margin convex, not pointed and not-notched medially. Frontal carinae feebly curved, merging with rugae that extend to posterior third of head dorsum, they do not curve outwards and do not merge with rugae that surround antennal sockets; frons quite wide, 0.38 times as head width. Frontal lobes slightly extended, not raised up vertically. Eyes of medium size, not convex, located somewhat behind midlength of sides of head, genae 1.33 times as long as maximum diameter of eyes. Mandibles with long apical tooth, somewhat shorter preapical one and 5 minor denticles.

Mesosoma relatively short, ca. 2.7 times as long as height, with moderately convex promesonotal dorsum, promesonotal suture dorsally indistinct (seen from above); metanotal groove quite deep and wide (seen in profile); dorsal surface of propodeum weakly convex, subequal in length to posterior one; propodeal lobes projecting apically and pointed. Petiole short and high, 1.23 times as long as height and 0.33 times as long as

head, petiolar node short, its anterior surface concave and steep, node dorsum rounded and gradually sloping posteriorly; postpetiole subglobular (seen from above), its length equal to height, anterior surface quite steep, feebly convex, node dorsum narrowly rounded (seen in profile). Metatibiae with pectinate or at least barbulate spurs, right mesotibia absent, left one hidden due to position of specimen.

Head, mesosoma and waist not coarsely sculptured. Frons with about ten somewhat sinuous longitudinal rugae, remainder part of head dorsum with reticulation; clypeus with a few straight longitudinal rugae, mandible longitudinally rugose. Promesonotal dorsum and sides of pronotum with reticulation, mesopleura and whole propodeum with sinuous longitudinal rugosity; posterior surface of propodeum smooth and shiny. Petiole longitudinally rugoso-reticulate, postpetiole longitudinally rugulose. Body surface between rugae appears smooth and shiny. Gaster smooth and shiny.

Whole body with quite abundant erect to suberect hairs. Tibiae with subdecumbent pilosity, tarsi with subdecumbent to suberect bristle-like pilosity.

Gynes and males unknown.

Material examined. Holotype worker, complete specimen, Bitterfeld amber, No. 7/216 (HMB).

Etymology. Named after Saxony-Anhalt, the region in Germany where Bitterfeld amber was collected.

Comparative diagnosis. For differences from all other *Myrmica* species see above. For the separation of all species see also Key to their identification, below.

Key to identifications of *Myrmica* species from late Eocene European ambers (workers)

1. Propodeum with short, blunt teeth; head and mesosoma with not coarse reticulation; frontal carinae merge with rugae, which surround antennal sockets; antennal funiculus with 3-segmented club (Fig. 1, A, B). Meso- and metatibiae with pectinate spurs *M. paradoxa* Radchenko *et al.*
- . Propodeum with long spines; head and mesosoma with much coarser rugosity and/or reticulation (Figs 1, C, D; 2, A, B, D–H; 3, A, C, D; 4, A, C–F). Frontal carinae merge with rugae that extend to posterior third of head dorsum, they do not curve outwards and do not merge with rugae that surround antennal sockets (Figs 2, F; 3, A; 4, E). Antennal funiculus with 4-segmented club (Figs. 1, C, D; 2, A, B, D, E, H, I; 3, A, D; 4, A, C). Meso- and metatibiae with or without spurs **2**
2. Entire mesosoma reticulated; propodeal spines directed mainly backward and strongly divergent (ESD/ESL 1.09) (Fig. 4, A). Meso- and metatibiae without spurs. Eyes located in front of midlength of

- sides of head (GL/OL 1.00). Scape gradually, but quite strongly curved at base (Fig. 4, B) *M. dictyosa* sp. nov.
- At least propodeal dorsum (often also sides of mesosoma) with longitudinal rugae (Figs 1, C, D; 2, A, B, D, E, G, H; 3, A, C, D; 4, C, D). Meso- and metatibiae with or without spurs. Position of eyes, shape of scape and propodeal spines varied 3
 - 3. Mesosoma relatively short and robust (ML/MH ≤ 2.50); petiole relative short and high (PL/PH < 1.30) (Figs. 3, C, D; 4, D, F) 4
 - Mesosoma long and slender (ML/MH > 2.85); petiole long and low (PL/PH > 1.50) (Figs 1, C, D; 2, A, B, D, E, G, H; 3, A; 4, C) 5
 - 4. Meso- and metatibiae without spurs (Fig. 3, E). Head, mesosoma and waist very coarsely sculptured; propodeal spines longer (ESL/HL > 0.55), curved down along their length and weakly divergent (ESD/ESL < 0.90) (Fig. 3, C, D) *M. electrina* sp. nov.
 - At least metatibiae with pectinate (or at least barbulate) spurs. Head, mesosoma and waist finely sculptured; propodeal spines shorter (ESL/HL 0.38), strongly widened at base, massive, somewhat curved inward and distinctly divergent (ESD/ESL 1.11) (Fig. 4, D-F) *M. saxonica* sp. nov.
 - 5. Eyes located in front of midlength of sides of head (GL/OL < 1.15) (Fig. 2, A, B, D, E). Meso- and metatibiae without spurs (Fig. 2, C) 6
 - Eyes located at midlength of sides of head (GL/OL > 1.25) (Figs 1, C, D; 3, A; 4, C). Meso- and metatibiae with or without spurs 7
 - 6. Propodeal spines somewhat longer (ESL/HL ≥ 0.60), directed backward and upward at an angle ca. 45° and strongly divergent (ESD/ESL > 0.95) (Fig. 2, A, B) *M. rudis* (Mayr)
 - Propodeal spines somewhat shorter (ESL/HL ≤ 0.50), directed mainly backward at an angle ca. 40° and weakly divergent (ESD/ESL < 0.85) (Fig. 2, D, E) *M. intermedia* Wheeler
 - 7. Meso- and metatibiae without spurs. Propodeal spines somewhat shorter (ESL/HL 0.45); body with very sparse scattered thin suberect hairs, appears almost hairless; scape and legs with sparse thin decumbent hairs (Fig. 4, C) ... *M. damzeni* sp. nov.
 - Meso- and metatibiae with pectinate spur (Fig. 1, E). Propodeal spines longer (ESL/HL > 0.55); body with numerous erect to suberect hairs; scape and legs with abundant suberect hairs (Figs 1, C, D; 3, A) ... 8
 - 8. Propodeal spines weakly divergent (ESD/ESL < 0.85) (Fig. 1, D). Scape gradually but quite strongly curved at base (similar to *M. sulcinodis*) *M. longispinosa* Mayr
 - Propodeal spines strongly divergent (ESD/ESL > 0.95) (Fig. 3, B). Scape very feebly curved at base (similar to *M. rubra*) *M. eocenica* Radchenko et al.

DISCUSSION

Myrmica is the type genus of the subfamily Myrmicinae and, accordingly, of the tribe Myrmicini. Forel (1891) first considered Myrmicini as a tribe in this subfamily, attributing to it the vast majority of the Myrmicinae genera, except those he assigned to the tribes Attini Smith, 1858 with five genera, and Cryptocerini Smith, 1853 with two genera (now a junior synonym of Attini). Subsequently, various authors interpreted the composition of this tribe in different ways (Emery 1921; Bolton 1976; Dlussky and Fedoseeva 1988; Bolton 2003; Dlussky and Radchenko 2009; Jansen and Savolainen 2010), and, in the end, four genera were assigned to it: the modern *Myrmica* and *Manica* and extinct *Proto-myrmica* Dlussky et Radchenko, 2009 and *Plesio-myrmex* Dlussky et Radchenko, 2009 from late Eocene European ambers (Ward et al. 2015).

Based on morphological features, the tribe Myrmicini was traditionally considered by all authors to be 'primitive', ancestral to other Myrmicinae. Already Emery (1921) placed this tribe at the base of his "genealogical tree" of the subfamily Myrmicinae; Wheeler G. and Wheeler J. (1970: 131) emphasized that *Myrmica* and *Manica* are "among the least specialized genera in the Myrmicinae"; Bolton (2003) defined Myrmicini based solely on workers plesiomorphies. Finally, Ward et al. (2015) based on molecular genetic data first pointed out that the tribe Myrmicini (i.e. *Myrmica*+*Manica*) form a sister clade to all other Myrmicinae.

Thus, among all known species of Myrmicinae, only representatives of this tribe have 6-segmented maxillary and 4-segmented labial palps (plesiomorphic state for the entire family Formicidae); have an unmodified structure of the head, mandibles, mesosoma and waist; antennae are 12-segmented with a moderately defined 3-5-segmented club; meso- and metatibiae usually with well developed pectinate spurs, while spurs can be reduced to varying degrees or absent altogether. Workers of *Manica* seem to possess even more 'primitive' features than *Myrmica*, e.g. a complete set of mesosomal sutures, and some large specimens have a rudimentary scutellum (Wheeler G. and Wheeler J. 1970, Radchenko and Elmes 2001, Radchenko et al. 2007).

Males of the Myrmicini genera are also characterized by a set of plesiomorphies, combined with several apomorphic states of features. They have 6-segmented maxillary and 4-segmented labial palps, 13-segmented antennae (rarely 12-segmented in some, usually socially-parasitic *Myrmica* species) with a weakly developed 3-5-segmented club or without it; scutum with well developed notauli; mandibles with a well defined masticatory margin, having a set of distinct sharp teeth (see also Radchenko and Dlussky 2009).

The Myrmicinae as a whole is the most taxonomically diverse ant subfamily both now and in the past, with about 150 modern genera and over 7,000 species, and 41 extinct genera with about 190 species are known (Bolton 2023, Radchenko 2023).

Dlussky *et al.* (2004) described a new genus and species *Afromyrma petrosa* Dlussky, Brothers et Rasnitsyn, 2004 from the Turonian (ca. 91 Ma) mudstone deposits in Orapa (Botswana), considering it to be the oldest representative of the subfamily Myrmicinae. However, various authors have questioned this attribution (Wilson and Hölldobler 2005, Archibald *et al.* 2006), and Boudinot *et al.* (2022) formally excluded *Afromyrma* from Myrmicinae, placed it *incertae sedis* in the crown Formicidae and clustered it with Myrmeciinae.

Thus, the genera, undoubtedly belonging to Myrmicinae, were found from early (Ypresian, 56.0–47.8 Ma) and middle Eocene (Bartonian-Lutetian, 47.8–40.0 Ma) deposits of North America, Europe, China, India and Australia (Wilson 1985, Poinar *et al.* 1999, Dlussky and Rasnitsyn 2002, Hong 2002, Rust *et al.* 2010, Aria *et al.* 2011, Dlussky and Wedmann 2012, LaPolla *et al.* 2013, Dlussky and Perfilieva 2014, LaPolla and Greenwalt 2015, Radchenko and Perkovsky 2016, Stilwell *et al.* 2020). All of them belong to both modern and extinct genera, but none of these genera belongs to the tribe Myrmicini. Some of the fossil genera appear to be quite specialized morphologically, but species from extant genera appear rather primitive compared to modern ones. At the same time, representatives of the tribe Myrmicini (both *Myrmica* and *Manica*) are first encountered since the late Eocene, in particular, in European ambers (Mayr 1868, Wheeler 1915, Radchenko *et al.* 2007, Dlussky and Radchenko 2009, Zharkov *et al.* 2022). Based on molecular genetic data, the estimated crown age of the tribe Myrmicini is from ca. 45 Ma (Lutetian) to ca. 52 Ma (Ypresian), and the crown age of the genus *Myrmica* appears ca. 41 Ma (Jansen *et al.* 2010, Ward *et al.* 2015), which is quite consistent with paleontological data.

Radchenko and Elmes (2010) recognized 17 species groups and 10 species with unique autapomorphies in Old World *Myrmica* based on morphological characters, primarily the shape of the scape in female castes, and its length in males. Importantly, the molecular studies of Jansen *et al.* (2009, 2010) confirmed that almost all of proposed species groups are monophyletic, and the *ritae*- and *rugosa* groups are ancestral to *Myrmica* (see also Radchenko 1994, Radchenko and Elmes 2001, Radchenko *et al.* 2007).

The female castes of the two mentioned groups have a scape gently curved at the base, without any traces of a lobe or carina; their frontal carinae merge with rugae reaching to the occipital margin, they do not curve outwards and do not merge with the rugae

surrounding the antennal sockets; the frontal lobes are slightly curved and the frons is wide. In addition, species of the *ritae*-group have a very long scape, which is subequal to or even longer than the head; their anterior clypeal margin slightly convex and distinctly notched medially (in species of the *rugosa*-group it is convex and prominent, without medial notch); posterior head margin with narrow collar-like ridge and posteroventral angles of the head are prominent; the petiole is very long and low ($PL/PH > 1.35$, often > 2.0); the postpetiole is fig-shaped (seen from above); the propodeal spines very long and the propodeal lobes sharply pointed apically; finally, meso- and metatibiae in species of both groups with well developed pectinate spurs.

Usually it is quite easy to recognize species from the *ritae*-group, because their overall appearance, particularly their elongated petiole, fig-shaped postpetiole, very long propodeal spines and relatively long appendages are quite distinct from other *Myrmica* species. Consequently, Radchenko *et al.* (2007) noted that the known fossil *Myrmica* species (with exception of the enigmatic *M. paradoxa*) are very similar to modern species of the *ritae*-group.

However, among the previously and newly described *Myrmica* species from late Eocene European ambers, only *M. longispinosa* has a complete set of characteristic features of the *ritae*-group, while other species lack at least one diagnostic character. Thus, in all other species, the anterior clypeal margin is without notch (in *M. dictyosa* and *M. damzeni* clypeus is obscured); *M. rudis*, *M. intermedia*, *M. electrina*, *M. dictyosa* and *M. damzeni* have no spur on the meso- and metatibiae; the propodeal lobes narrowly rounded apically and not pointed in *M. damzeni* and *M. dictyosa*; the lateroventral corners of the head in *M. dictyosa* are not pointed; finally, the petiole is relatively high and short in *M. electrina* and *M. saxonica*.

Thus, only *M. longispinosa* can be assigned with certainty to the modern *ritae*-group, but other ‘*ritae*-like’ species have either some putative plesiomorphies compared to this group (not-notched anterior clypeal margin or non-pointed apically propodeal lobes) or even putative apomorphy (completely reduced meso- and metatibial spurs). In addition, *M. electrina* and *M. saxonica* are well distinguished from the *ritae*-group species by their relatively short and high petiole, as well as a shorter and more robust mesosoma. However, they are morphologically distinct from all known extant *Myrmica* species and I cannot assign them to any modern species-groups. So, in all these species one can observe various paths of morphological radiation of *Myrmica* in the Eocene, when quite morphologically diverse species already existed.

In general, the *Myrmica* fauna in late Eocene European ambers was relatively very rich compared to

other myrmicine species: nine species were found, second only to *Temnothorax* with six described and 12 as yet undescribed species (Radchenko, in preparation), or ca. 11% of the total number of amber Myrmicinae species. Interestingly, the number of modern *Myrmica* species is only 2.6% of all myrmicines.

It seems quite important the discovery of two new *Myrmica* species, *M. schaeferi* Jessen, 2020 and *M. nungesseri* Jessen, 2020, in the Oligocene deposits (24.8–24.6 Ma) of Enspel (Germany) (Jessen 2020). Firstly, this is the first and last record of the fossil *Myrmica* since the Eocene. Second, both described species morphologically fit well into the modern *rugosa*-group. This supports the idea that *ritae*- and *rugosa*-groups are ancestral to the rest of the modern *Myrmica* (Jansen *et al.* 2010, Radchenko and Elmes 2010).

It can be assumed that the putative ancestor of modern *Myrmica* lived in the warm forests of the early or middle Eocene, and by the late Eocene gave rise to *M. ritae*-like species and other forms, such as *M. paradoxa*, *M. electrina* and *M. saxonica*, and then, in the Oligocene, species from the *rugosa*-group evolved. Based on what little is known about the ecology of species from the *ritae*- and *rugosa*-groups, they appear to forage more readily in small trees and shrubs compared to the other major *Myrmica* lineages (that gave rise to *scabrinodis*-, *lobicornis*- or *schencki*-group species), which have many 'more derived' morphological features (in particular, the shape of the scape) that may be associated with a 'ground foraging' lifestyle and expansion to open areas. Most likely the further adaptive radiation of *Myrmica* species was associated with the cooling and aridization of the climate that started since late Eocene (Westerhold *et al.* 2020) and the appearance and further expansion of open grassy areas in the temperate zone of the Earth in the Miocene.

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