

Ants of the Genus *Fallomyrma* Dlussky et Radchenko (Hymenoptera, Formicidae, Myrmicinae) from Late Eocene European Ambers

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Abstract—The extinct monotypic ant genus *Fallomyrma* was described by Dlussky and Radchenko in 2006 based on workers from Late Eocene Rovno (Ukraine), Scandinavian (Denmark), and Bitterfeld (Germany) ambers. Three new *Fallomyrma* species from the Rovno amber are here described based on workers: *F. anodontata* sp. nov., *F. marginata* sp. nov., and *F. robusta* sp. nov. A key to all known species of this genus is compiled. The quantity ratios (of the numbers of species and specimens) of *Fallomyrma* and other amber Myrmicinae genera are considered. The opinion of the autochthonous origin of the Rovno amber is confirmed.

Keywords: ants, new species, *Fallomyrma anodontata* sp. nov., *F. marginata* sp. nov., *F. robusta* sp. nov., Late Eocene, amber, Europe

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INTRODUCTION

Ants from Late Eocene ambers of Europe (Priabonian Stage, 33.9–37.8 Ma: *International Chronostratigraphic ...*, 2016) are most thoroughly studied among all known fossil myrmecofaunas irrespective of their age or sampling sites. These ambers are the Baltic amber (primarily the Kaliningrad Region of Russian Federation and Baltic coast of Poland); Scandinavian amber (=Danish; mainly from the coasts of Denmark); Bitterfeld (=Saxonian) amber (Germany, Saxony) and Rovno amber (Ukraine). From the first third of the 19th century to the present time, more than 17500 inclusions with ants belonging to almost 200 species of 70 genera of 12 subfamilies have been studied by various authors (Dlussky and Perkovsky, 2002; Dlussky, 2002, 2008a, 2008b, 2010; Dlussky and Radchenko, 2006a, 2006b, 2009, 2011; Radchenko et al., 2007; Dlussky and Rasnitsyn, 2009; Dlussky, 2009, 2011; Heterick and Shattuck, 2011; Dubovikoff, 2012; Radchenko and Dlussky, 2012, 2013a, 2013b, 2015; Dlussky and Dubovikoff, 2013; Dlussky et al., 2014; original unpublished data).

Before the 21st century, a total of 24 species of 12 genera of the subfamily Myrmicinae (according to the modern taxonomy and synonymy) had been described from the Baltic amber; moreover, new myr-

micine genera or even species had not been described after the publication of the monograph by Wheeler (1915) up to 2002. However, the study of additional material from various Late Eocene European ambers enabled us to describe 19 new fossil Myrmicinae species and six genera, and more than 30 new species and several new genera are expected to be described (Dlussky and Perkovsky, 2002; Dlussky and Radchenko, 2006a, 2006b, 2009, 2011; Radchenko et al., 2007; Radchenko and Perkovsky, 2009; Radchenko and Dlussky, 2012, 2013a, 2013b, 2015; original unpublished data). Thus, 77 species of 27 myrmicine genera (including not yet described taxa) are currently found in these ambers.

Fallomyrma transversa, the type species of the monotypic fossil ant genus *Fallomyrma*, was described based on 19 workers from the Rovno, Bitterfeld, and Scandinavian ambers (Dlussky and Radchenko, 2006a), but one paratype from the Rovno amber we presently exclude from the type series and assign it to *F. marginata* sp. nov. described below. After description of *F. transversa*, we have found 13 more workers of this species. In addition, we found four workers in the Rovno amber, which are referred to three new species described in the present paper: *F. anodontata* sp. nov., *F. marginata* sp. nov., and *F. robusta* sp. nov. The key to all known *Fallomyrma* species is provided below.

† Deceased.

MATERIAL AND METHODS

We studied a total of 39 specimens of *F. transversa* (including the holotype and 17 paratypes) (15 specimens from the Rovno amber, five from the Bitterfeld amber, and 19 from the Scandinavian amber), two specimens of *F. anodonta* sp. nov. in one piece of amber, two specimens of *F. marginata* sp. nov. in two pieces of amber, and one specimen of *F. robusta* sp. nov. (all new species are from the Rovno amber). The type specimens of the newly described species are stored in the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev (IZShK).

State of inclusions. All ants fossilized in amber are not distorted, their condition is satisfactory.

The photographs of type specimens were taken using a IC 3D digital camera fitted to a Leica MZ16 stereomicroscope; the figures were produced by redrawing the original photographs, with further improvement using software CorelDraw 13.

Measurements (accurate to 0.01 mm) and indices are as follows: (HL) maximum head length in dorsal view from the most anterior point of the clypeus to the midpoint of the occipital margin; (HW) maximum head width in dorsal view just behind (above) the eyes; (SL) maximum scape length in lateral view from the scape apex to articulation with the condylar bulb; (OL) maximum eye diameter; (ML-1) diagonal length of the mesosoma in lateral view from the articulation with the head to the posterior margin of the propodeal lobes; (ML-2) mesosoma length in dorsal view from the anterior end of the pronotum to the point of articulation with the petiole (if the mesosoma length in lateral view is impossible to measure); (MH) mesosoma height from the upper point of the promesonotum perpendicular to the level of the lower margin of the mesopleuron; (PnW) maximum pronotum width in dorsal view; (PL) petiole length in dorsal view from the posterodorsal margin of petiole to the articulation with propodeum; (PH) petiole height in lateral view; (PW) petiole width in dorsal view; (PPL) postpetiole length in dorsal view; (PPH) postpetiole height in lateral view from the upper to lower points measured perpendicular to the tergo-sternal suture; (PPW) postpetiole width in dorsal view; (HTL) hind tibia length; the total length is calculated as the sum of HL + ML + PL + PPL + gaster length.

The following indices were calculated based on the measurements listed above: CI = HL/HW, SI-1 = SL/HL, SI-2 = SL/HW, OI = OL/HL, MI = ML/MH, PI-1 = PL/HL, PI-2 = PL/PH, PPI-1 = PPL/HL, PPI-2 = PPL/PPH.

Since not all measurements of available specimens were possible to measure, we took the maximum possible measurements in each insect.

SYSTEMATIC PALEONTOLOGY

Subfamily Myrmicinae Lepeletier, 1835

Genus *Fallomyrma* Dlussky et Radchenko, 2006

Type species. *Fallomyrma transversa* Dlussky et Radchenko, 2006, by monotypy; Rovno, Bitterfeld, and Scandinavian ambers, Late Eocene.

Diagnosis. Workers monomorphic, body 2.5–4 mm long. Antennae 12-segmented, with distinct large three-segmented club longer than remaining funicular segments taken together; antennal scape relatively short, slightly curved at base, not reaching occipital margin. Eyes well developed, located somewhat lower (anteriorly) than midlength of lateral head margins. Ocelli absent. Frontal lobes widely spaced, so that central part of clypeus wedging in between these lobes wider than each lobe. Median portion of clypeus longitudinally concave, delineated laterally by longitudinal carinae; anterior clypeal margin widely and weakly medially concave, with two long setae. Masticatory margin of mandibles with six or seven teeth. Promesonotum distinctly narrowing posteriorly, subtrapezoidal, delineated markedly anteriorly and laterally by sharp ridge; its anterior margin convex (in dorsal view); dorsal and lateral surfaces of promesonotum positioned at right or even acute angle. Petiole with distinct cylindrical anterior part; its node high, with rounded dorsum. Middle and hind tibiae with one simple spur. Whole body smooth, without punctation or granulated sculpture; rugosity sometimes developed on various parts of head and mesosoma.

Queens and males unknown.

Species composition. In addition to the type species from Late Eocene European ambers (except for the Baltic amber), three new species from the Rovno amber described below.

Comparison. Based on the complex of morphological characters listed above, *Fallomyrma* differs from all known fossil myrmicine genera from the Late Eocene European ambers. *Fallomyrma* species are superficially similar to the extant Neotropical genus *Oxyepoecus* Santschi, 1926 in the shape of head, mesosoma, and petiole, but the antennae of workers of the latter genus are 11-segmented, the masticatory margin of the mandibles has only three teeth, and the frontal lobes are positioned closely, so that the central part of the clypeus, which wedges in between the frontal lobes is narrower than each lobe. We do not assume that these genera are related, most probably this similarity results from convergence.

Fallomyrma anodonta Radchenko et Dlussky, sp. nov.

Plate 5, figs. 1 and 2

Etymology. From the Greek οδοντος (teeth) and ον (without), meaning the absence of teeth on the propodeum.

Table 1. Measurements of body parts of newly described *Fallomyrma* species, mm

Measurements	<i>F. anodonta</i> sp. nov.		<i>F. marginata</i> sp. nov.		<i>F. robusta</i> sp. nov. holotype IZShK, no. K–2204
	holotype IZShK, no. K–24847	paratype IZShK, no. K–24847	holotype IZShK, no. K–24251	paratype IZShK, no. K–28–o	
HL	0.53	0.59	0.77	0.78	0.69
HW	0.32	0.37		0.65	0.72
SL	0.29	0.32	0.43	0.48	0.51
OL	0.13		0.17	0.18	0.19
ML-1	0.69		0.93	1.06	0.96
ML-2		0.75			
MH	0.29		0.40	0.42	
PnW	0.31	0.35		0.40	0.51
PL	0.21		0.36		0.32
PH	0.22		0.25		0.32
PW	0.13	0.16			0.26
PPL	0.15		0.2		0.21
PPH	0.17		0.21		
PPW	0.16	0.17			0.32
HTL	0.35	0.37	0.43	0.46	

For abbreviations, see MATERIAL AND METHODS.

Table 2. Morphometric indices calculated based on the measurements of various body parts of the newly described *Fallomyrma* species

Indices	<i>F. anodonta</i> sp. nov.		<i>F. marginata</i> sp. nov.		<i>F. robusta</i> sp. nov. holotype IZShK, no. K–2204
	holotype IZShK, no. K–24847	paratype IZShK, no. K–24847	holotype IZShK, no. K–24251	paratype IZShK, no. K–28–o	
CI	1.67	1.57		1.20	0.96
SI-1	0.55	0.55	0.55	0.62	0.74
SI-2	0.92	0.86		0.74	0.71
OI	0.24		0.22	0.23	0.28
MI	2.38		2.33	2.50	
PI-1	0.40		0.46		0.47
PI-2	0.96		1.37		1.00
PPI-1	0.29		0.31		0.30
PPI-2	0.89		1.13		

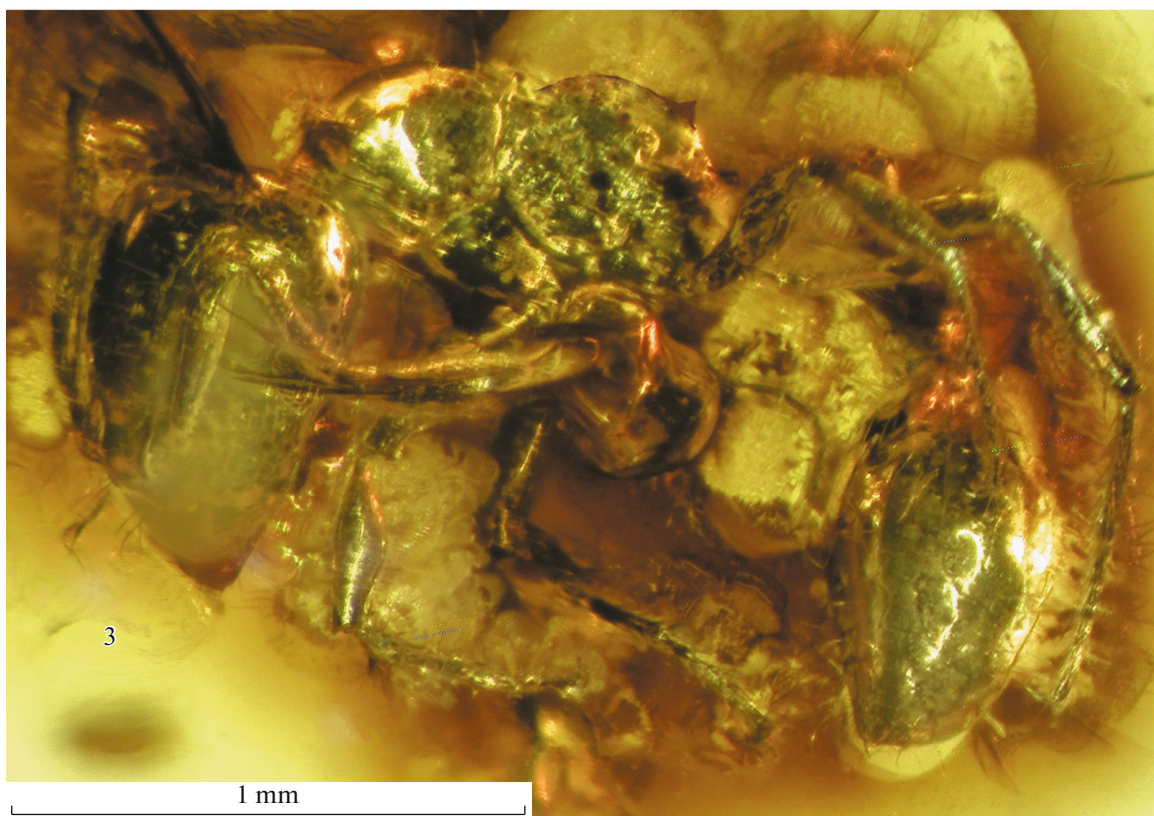
For abbreviations, see MATERIAL AND METHODS.

Holotype. IZShK, no. K–24847, worker; Rovno amber, Late Eocene.

Description (Figs. 1a–1c; Tables 1, 2). The head is rather narrow, more than 1.5 times longer than wide, with very weakly convex lateral sides, straight occipital margin, and narrowly rounded occipital corners. The clypeus structure corresponds to that of the generic diagnosis, but setae are indiscernible in the holotype and paratype. The maxillary palps are five-segmented, the labial palps are invisible. The number

of teeth on the masticatory margin of the mandibles is impossible to count.

The mesosoma is rather short; the promesonotum is arched convex; the metanotal groove is deep, abrupt and rather wide; the propodeum lacks teeth, only slightly angular at transition from horizontal to slightly sloping surface (in lateral view). The petiole with long peduncle; its node is high, somewhat longer than the petiole length. The postpetiole is globular, somewhat higher than long.



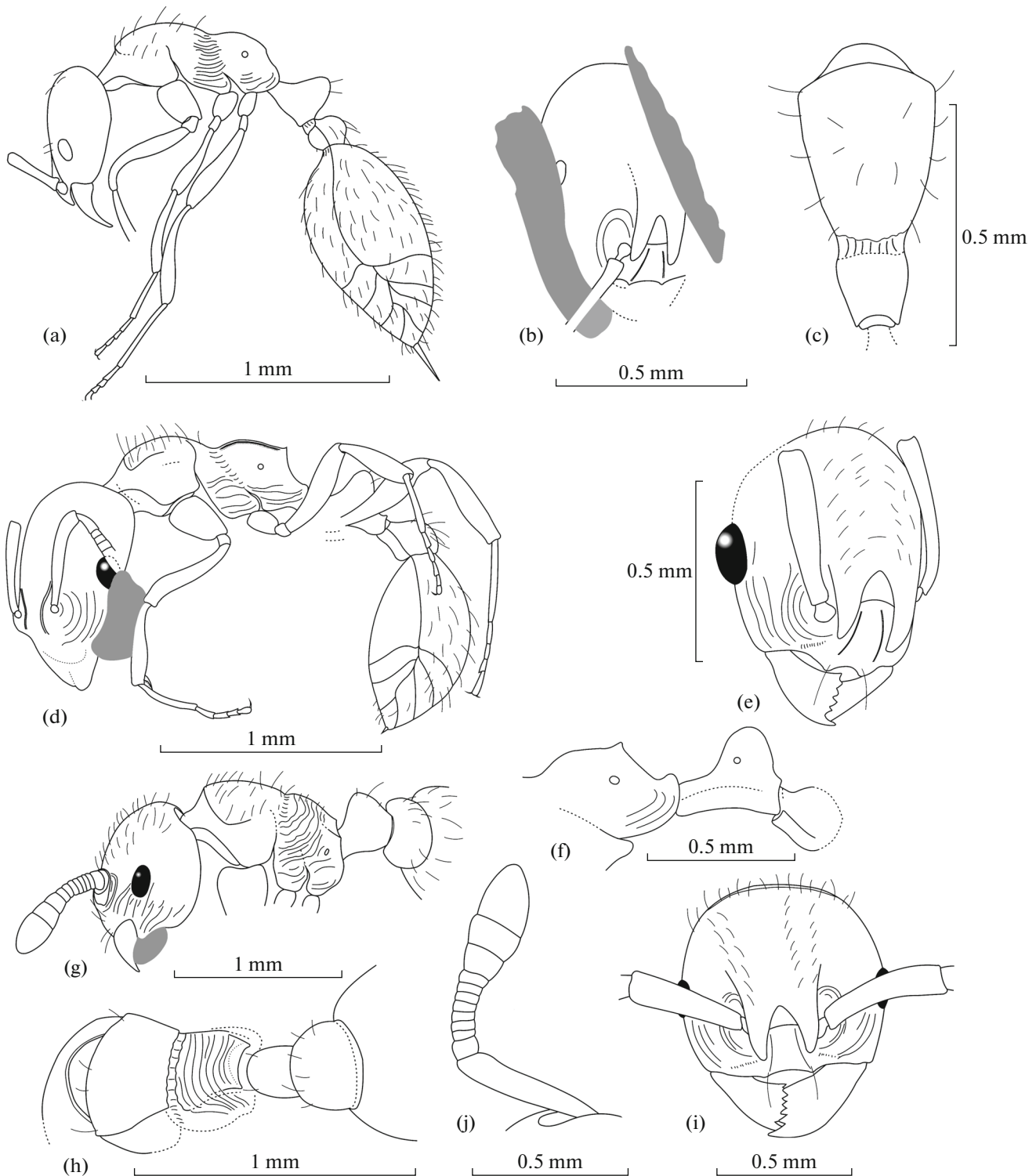


Fig. 1. Structural details of species of the genus *Fallomyrma*: (a–c) *F. anodonta* sp. nov., holotype IZShK, no. K–24847, worker: (a) body, lateral view; (b) head fragment, dorsal view; (c) mesosoma, dorsal view; (d–f) *F. marginata* sp. nov., holotype IZShK, no. K–24251, worker: (d) body, lateral view; (e) head, dorsal view; (f) propodeum and waist, lateral view; (g–j) *Fallomyrma robusta* sp. nov., holotype IZShK, no. K–2204, worker: (g) head, mesosoma, and waist, lateral view; (h) mesosoma and waist, dorsal view; (i) head, dorsal view; (j) antenna. Rovno amber; Late Eocene.

Explanation of Plate 5

Figs. 1–3. Photographs of species of the genus *Fallomyrma*: (1, 2) *F. anodonta* sp. nov., IZShK, no. K–24847, workers: (1) holotype; (2) paratype; (3) *F. marginata* sp. nov., holotype IZShK, no. K–24251, worker. Rovno amber; Late Eocene.

The body is smooth and shiny; short longitudinal, slightly sinuous rugae are only present on the mesopleura and the lower part of the propodeum sides. The mesosoma, waist, and gaster have long suberect setae, which are especially abundant on the gaster. The legs and antennal scape lack suberect setae (decumbent pubescence is also invisible).

Measurements, mm. Body length, about 2.5.

Comparison. *F. anodonta* differs from all known species of *Fallomyrma* in the absence of short pointed teeth on the propodeum, the longer head ($CI > 1.55$ versus < 1.35), and also in the smaller size (the body is about 2.5 mm long versus > 3 mm).

Material. Holotype and paratype IZShK, no. K-24847 (in the same piece of amber as the holotype).

Fallomyrma marginata Radchenko et Dlussky, sp. nov.

Plate 5, fig. 3

Fallomyrma transversa: Dlussky and Radchenko, 2006a: p. 156 (part., only paratype IZShK K-28-o).

Etymology. From the Latin *margino* (to border), meaning the presence of longitudinal lateral carinae on the upper surface of the propodeum.

Holotype. IZShK, no. K-24251, worker; Rovno amber, Late Eocene.

Description (Figs. 1d-1f; Tables 1, 2). The head is elongated oval, with slightly convex lateral sides and occipital margin and narrowly rounded occipital corners. The masticatory margin of the mandibles has six teeth.

The mesosoma is rather short; the promesonotum is arched convex; metanotal groove is deep, abrupt, and rather wide; the propodeum has short pointed teeth. The dorsal surface of the propodeum is delineated laterally by distinct longitudinal carinae. The petiole has a long peduncle, its node is high, but somewhat shorter than the petiole length. The postpetiole is globular, somewhat longer than high.

The body is smooth and shiny; only the genae, lower part of the mesopleurae, and propodeum sides have short longitudinal, slightly sinuous rugae. The mesosoma, waist, occipital head margin, and gaster have long suberect setae, which are especially abundant on the gaster. The legs and antennal scape lack standing setae (decumbent pubescence is also invisible).

Measurements, mm. Body length, 3.3-3.5.

Comparison. *F. marginata* differs from all known species of *Fallomyrma* in the presence of longitudinal carinae delineating laterally the dorsal surface of the propodeum. Additionally, it differs from *F. anodonta* in the presence of short pointed teeth on the propodeum, from *F. transversa* in the absence of transversal rugosity on the propodeal dorsum, from *F. robusta* in the more slender body and the distinctly longer head ($CI = 1.20$ versus 0.96).

Material. Holotype and paratype IZShK, K-28-o, worker; Rovno amber, Late Eocene (Dlussky and Radchenko, 2006a previously considered this specimen to be a paratype of *F. transversa*).

Fallomyrma robusta Radchenko et Dlussky, sp. nov.

Plate 6, figs. 1 and 2

Etymology. From the Latin *robustus* (strong, robust, powerful), as is characteristic of its habitus.

Holotype. IZShK, no. K-2204, worker; Rovno amber, Late Eocene.

Description (Figs. 1g-1i, 1i; Tables 1, 2). The head is slightly wider than long, oval, with strongly convex lateral sides, slightly convex occipital margin, and widely rounded occipital corners. The masticatory margin of the mandibles has six teeth.

The mesosoma is short, stout; the promesonotum is slightly arched convex; the metanotal groove is relatively shallow and rather wide; the propodeum has short, but distinct rectangular teeth. The petiole has a rather short peduncle; its node is as high as the petiole length. The postpetiole is globular.

The body is smooth and shiny, only the propodeum has transversal rugosity (similar to that of *F. transversa*) and genae have short longitudinal rugae. The mesosoma, petiole, head, and gaster have long suberect setae, which are especially abundant on the gaster. The legs and antennal scape lack suberect setae (decumbent pubescence is also invisible).

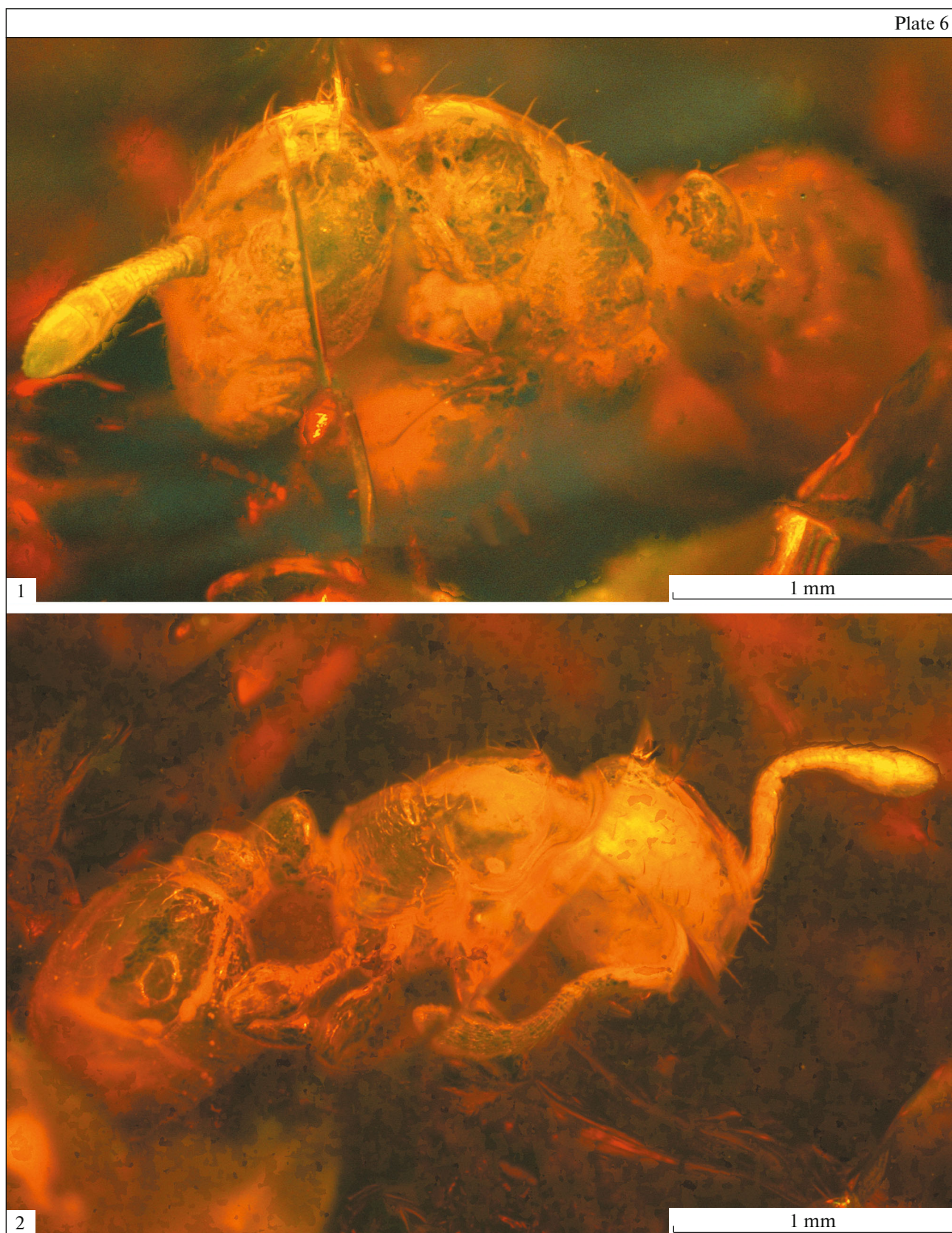
Measurements, mm. Body length is somewhat greater than 3.

Comparison. *F. robusta* is similar to *F. transversa* in the propodeum sculpture. It differs from all known species of *Fallomyrma* in the robust, stout body and the much shorter, slightly transversal head ($CI = 0.96$ versus ≥ 1.15).

Material. Holotype.

Key to Fallomyrma Species

1. Propodeum without teeth, only slightly angular (Pl. 5, figs. 1, 2; Fig. 1a).....*F. anodonta* sp. nov.
- Propodeum with teeth.....2
- 2 (1) Dorsal surface of propodeum delineated laterally by distinct longitudinal carinae, without transversal rugae (Pl. 5, fig. 3; Figs 1d, 1f).....*F. marginata* sp. nov.
- Dorsal surface of propodeum not delineated by distinct longitudinal carinae, with transversal rugae (Plate 6, figs. 1, 2; Figs. 1g, 1h).....3
- 3 (2) Head elongate, with slightly convex sides ($CI > 1.15$).....*F. transversa* Dlussky et Radchenko
- Head somewhat transversal, with strongly convex sides ($CI = 0.96$).....*F. robusta* sp. nov.



Explanation of Plate 6

Figs. 1 and 2. Photographs of *Fallomyrma robusta* sp. nov., holotype IZShK, no. K–2204, worker: (1) left lateral view; (2) right lateral view. Rovno amber; Late Eocene.

DISCUSSION

It is intriguing that representatives of the genus *Fallomyrma* have been found in coeval (Late Eocene) Rovno, Bitterfeld, and Scandinavian ambers, but have not in the Baltic amber. Taking into account the fact that the number of studied ant inclusions in the Baltic amber is at least five times greater than that of the three above ambers taken together (Wheeler, 1915; Dlussky and Rasnitsyn, 2009; our unpublished data), it is reasonably safe to suggest that the species of *Fallomyrma* did not inhabit the habitats where the Baltic amber was formed. At the same time, only one species of the studied genus, *F. transversa*, was found in all of three (Rovno, Bitterfeld, and Scandinavian) ambers, while three newly described species are only known in the Rovno amber. However, this is possibly accounted for by relative rarity compared to *F. transversa*.

It is noteworthy that *Fallomyrma* does not belong to the Myrmicinae genera particularly rich in species from Late Eocene European ambers. Taking into account species that are already present in collections, but have not yet been described, there are at least 15 species of *Temnothorax* Mayr, eight of *Myrmica* Latreille, seven of *Aphaenogaster* Mayr, five of *Monomorium* Mayr, five of *Eocenomyrma* Dlussky et Radchenko, four of *Carebara* Westwood, and four of *Fallomyrma*. That is, seven listed genera comprise more than half of all known species (78) of amber myrmicine ants and remaining 20 genera comprise from one to three species each. At the same time, *Fallomyrma* is among the genera of this subfamily represented by the greatest number of specimens. The richest in this parameter are the genera *Temnothorax* and *Monomorium* each represented by 100 or even more specimens; the next richest is *Fallomyrma* with 44 specimens; the genera *Aphaenogaster* and *Myrmica* comprise about 35 and 20 specimens, respectively.

It is plausible that small (2.5–4 mm long) *Fallomyrma* species, like amber *Temnothorax* and *Monomorium* of approximately the same size, were rather common representatives of the arboreal myrmecofauna, which built nests and fed in the tree crown. This probably explain the fact that myrmicine assemblages are distinctly dominated by representatives of three above-mentioned genera; they are almost twice as abundant as remaining 24 genera (more than 260 specimens versus about 140). Adding the genera *Aphaenogaster*, *Myrmica*, and *Carebara*, which are rather diverse and abundant, this ratio becomes even more evident: more than 330 specimens in the six genera versus 70 in remaining 21 genera.

Finally, the place of origin of various Late Eocene European ambers, in particular, Rovno and Baltic ambers, remains an important question. It was previously believed that the Rovno amber is redeposited Baltic amber (Katinas, 1971), but to date, it has become generally accepted by geologists that Rovno and Baltic ambers were formed independently at the

same geological time, but in different territories (Maidanovich and Makarenko, 1988; Kosmowska-Ceranowicz, 2012; Karlovich and Prokopets, 2014). The last statement is corroborated by the composition of the myrmecofauna and some other insect groups (Perkovsky et al., 2003, 2010; Dlussky and Rasnitsyn, 2009; Perkovsky, 2013; Ivanov et al., 2016). In our opinion, the distributional pattern, abundance of representatives of *Fallomyrma* in Rovno, Scandinavian, and Bitterfeld ambers, and complete absence of this genus in the Baltic amber are evidence of independent origin of Rovno and Baltic ambers.

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