



## BILOBOMYRMA NEW GENUS, A NEW EXTINCT ANT GENUS (HYMENOPTERA, FORMICIDAE) FROM THE LATE EOCENE EUROPEAN AMBERS

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**ABSTRACT**—A new fossil ant genus, *Bilobomyrma* new genus, and two new species are described based on males from the late Eocene Rovno (*B. ukrainica* n. sp.) and Baltic (*B. baltica* n. sp.) ambers. We tentatively place this genus in the myrmicine tribe Formicoxenini. *Bilobomyrma* is characterized by its 13-segmented antennae without an apical club; by the short scape, which is subequal to the length of the first and second funicular segments together; by the shape of the second funicular segment, which is distinctly longer than the any other funicular segment except for the apical one; by the presence of notauli on the scutum; by the absence of spurs on the middle and hind tibiae. At the same time, *Bilobomyrma* differs from other myrmicine genera by the peculiar shape of its clypeus, having a strongly incised medially, bilobed anterior margin, and its forewing venation: the wings have three closed cells—*mcu*, *1+2r* and *3r*; the cell *3r* is very short, only twice as long as its width; the distal section of veins *RS* and *M* diverge from the cell *1+2r* separately.

### INTRODUCTION

THE ANTS of the late Eocene European (ca. 37 Ma) ambers are very well studied. Currently, more than 17,000 ant specimens, belonging to more than 170 species from 64 genera and 12 subfamilies, have been examined from these ambers (Dlussky and Rasnitsyn, 2009; Radchenko and Dlussky, 2012). The materials from Baltic Amber are the richest and best studied and include about 75 percent of all ant specimens found in the European late Eocene ambers. In addition, quite rich materials that include more than 60 ant species from about 30 genera have been collected from the Rovno Amber (western Ukraine) during the last decade (Perkovsky et al., 2007; Dlussky and Rasnitsyn, 2009).

Until recently the diversity of the subfamily Myrmicinae in European ambers seemed to be comparatively low: only 21 species from 13 genera were known. Furthermore, no new myrmicine genera or even species were described from the European late Eocene ambers after Wheeler's (1915) monographic revision of the ants of Baltic Amber until the beginning of twenty-first century. However, during the last decade we have had the opportunity to investigate the rich new amber collections from the Baltic, Bitterfeldian (=Saxonian), Scandinavian (=Danish), and Rovno ambers. As a result, we described few new species from several ant subfamilies, including Myrmicinae, and even described five new myrmicine genera (Dlussky, 2002a, 2002b, 2008a, 2008b, 2009, 2010; Dlussky and Perkovsky, 2002; Dlussky and Radchenko, 2006 a, 2006b, 2009, 2011; Radchenko et al., 2007; Radchenko and Perkovsky, 2009; Radchenko and Dlussky, 2012).

Nowadays, Myrmicinae is the most taxonomically diverse subfamily containing 146 genera and more than 6,500 species, or approximately 50 percent of the total number of ant genera and >50 percent of species. For the purpose of comparison, three other largest ant groups are Formicinae: 17 percent of genera and ~20 percent of species; Dolichoderinae: 9 percent of genera and ~7 percent of species; and poneroid families: 15 percent of genera and ~10 percent of species (calculated from the data of Bolton, 2013).

In addition, representatives of the subfamily Myrmicinae are among the most numerous ants worldwide, dominating in many modern ecosystems. For example, Ward (2000) analyzed the composition of 110 Winkler samples collected from many localities in different regions (Nearctic, Neotropic, Malagasy, Australian, and Oriental) and showed the Myrmicinae to be the dominant subfamily in forest leaf litter, comprising approximately 55 percent of genera, approximately 65 percent of species and about 74 percent of specimens, whereas the combined totals for the Formicinae, Dolichoderinae and poneroids were about 41 percent, 34 percent, and 26 percent, respectively. On the other hand, the myrmecofauna of canopies in tropical forests is quite different, the dominant subfamilies being Formicinae and Dolichoderinae (Brühl et al., 1998; Wilson and Hölldobler, 2005).

A similar pattern is observed in the temperate zone. For example, in Europe the most diverse subfamily is also Myrmicinae, which includes 52 percent of ant genera and 60 percent of all species. More than 85 percent of all species inhabit soil, leaf litter or foraging in a grass level. About 80 percent of the species of Myrmicinae are also epigeaic, and only members of the genera *Crematogaster* Lund, partly *Temnothorax* Mayr and *Aphaenogaster* Mayr can be considered as typical arboreal dwellers. Even so, arboreal Myrmicinae reach approximately 70 percent of total number of the dendrobiontic ant species, but members of Formicinae and partly of Dolichoderinae clearly dominate in the canopies and tree trunks by the number of individuals (our unpublished data).

It is interesting that this balance of subfamilies was not always the case. Paleontological data demonstrate that for almost the entire evolutionary history of ants Myrmicinae took a subordinate position in the current territory of Eurasia and North America: the proportion of their individuals in all investigated Eocene and Oligocene deposits, as a rule, does not exceed 5 to 6 percent. Members of the subfamilies Dolichoderinae and Formicinae dominated throughout these epochs and the total proportion of their individuals reached up to 80 to 97 percent. The relative numbers of the Myrmicinae specimens became similar to the modern ones only in the middle Miocene (ca. 15

Ma) (Dlussky and Rasnitsyn, 2007; Dlussky and Wedmann, 2012).

A rather paradoxical situation exists in the late Eocene ambers of Europe. On the one hand, the proportion of Myrmicinae individuals is found to be low: in Baltic Amber, 2.1 percent; in Rovno Amber, 4.7 percent; in Bitterfeldian Amber, 6.0 percent; and in Danish Amber, 13.2 percent (it should be noted that that high proportion of Myrmicinae individuals in the latter two ambers may be somewhat artificially inflated due to the high number of specimens found of the extinct genus *Fallomyrma* Dlussky and Radchenko). On the other hand, Myrmicinae taxonomic diversity greatly exceeded that of the other subfamilies. Currently, 66 ant genera are known from these ambers, 25 (38%) belong to the subfamily Myrmicinae (including a new genus described below), whereas only 15 (23%) of genera are Formicinae, 10 (15%) are Dolichoderinae, and 10 (15%) belong to poneroid subfamilies (15% in each); the rest of the subfamilies contain only six genera (9%). Another detail also seems quite surprising: there is a high proportion of extinct genera in Myrmicinae: 11 of 25, or 48 percent. Moreover, almost all extinct myrmicine genera (except for, perhaps, *Promeranoplus* Wheeler) are highly specialized and could not be considered as the ancestors of any of the recent genera (see Dlussky and Radchenko, 2006a, 2006b, 2009; Radchenko and Dlussky, 2012). In the other major subfamilies the proportion of extinct genera is lower: six of 15 in Formicinae (40%), four of 10 in Dolichoderinae (40%), and three of 10 in poneroids (30%), although among six genera from the subfamilies Aneuretinae, Cerapachyinae, Myrmeciinae and Pseudomyrmecinae, known in these ambers, five genera are extinct.

It is also interesting to compare the proportion of genera found in the late Eocene European ambers and the total number of fossil genera of the world in relation to the amount of modern genera. Thus, the proportion of amber Myrmicinae genera is 17 percent (25 genera found in these ambers vs. 149 extant ones); Formicinae, 29 percent (15 vs. 51); Dolichoderinae, 36 percent (10 vs. 28); and poneroid subfamilies, 23 percent (10 vs. 44). The most interesting is that the ratio of all known fossil and extant Myrmicinae genera in the world is similar to that in the late Eocene amber of Europe, 20 percent (29 fossil genera vs. 149 extant ones), but in other subfamilies this pattern strongly differs: the proportion of fossil genera of Formicinae is 57 percent (29 vs. 51); of Dolichoderinae, 54 percent (15 vs. 28); and of poneroids, 34 percent (15 vs. 44 genera) (our unpublished data).

We propose the following hypothesis to explain this paradox. There is a good reason to believe that the Myrmicinae arose in the late Cretaceous (Turonian, ca. 90 Ma) in Africa (Dlussky et al., 2004; Dlussky, 2005; Dlussky and Rasnitsyn, 2007), and later on diverged at least until the early or middle Paleocene (ca. 60 Ma) in the same region. One can assume that during the early and middle Eocene (ca. 45–50 Ma) some species and genera migrated to the territory of present-day Europe. Most likely, this migration might take place on the trunks of fallen trees washed down rivers and then drifting across the Tethys Ocean, similar to that proposed for how ants more recently colonized many oceanic islands (Dlussky, 1990). Indirectly, this can be confirmed by the fact that the most Myrmicinae species in all modern ecosystems of Earth live in a leaf litter and a soil, whereas most of amber species probably were arboreal dwellers, or at least foraged on trees and so trapped in resin.

Workers of epigaic forms usually do not go up tree trunks, but during the nuptial flights winged gynes and males often climb up on trees before starting to fly. As a result, almost

exclusively, sexual forms of these species were trapped and then fossilized in amber. The proportion of winged individuals relative to their workers of the most numerous epigaic amber species *Nylanderia pygmaea* (Mayr) (Formicinae) and *Hypoponera atavia* (Mayr) (Ponerinae) to their workers are 98 percent and 94 percent, respectively. All poneroids, except for extinct *Electroponera* Wheeler and *Bradoponera* Mayr, represented also mainly by winged gynes and males. In Myrmicinae the situation is quite different: among 25 known genera, only three are represented exclusively by males: *Plesiomyrmex* Dlussky and Radchenko, *Protomyrmica* Dlussky and Radchenko and *Bilobomyrmex* (described in this paper), but in all the other genera workers and only sometimes winged sexuals (mostly males) are known.

We propose the following hypothesis for the evolutionary history of myrmicines. When the first myrmicines invaded the territory of the modern Europe, the adaptive zone of these ants had not yet been filled. This should lead to adaptive radiation and origin of new genera, which is what we observe in the late Eocene ambers. Perhaps this was the cause of the decreasing of the species diversity and relative abundance of poneroids in amber compared to mid-Eocene deposits of Messel (Dlussky and Wedmann, 2012). Thus we suggest that the set of new Myrmicinae taxa arose under conditions when ecological niches were empty and interspecific competition was comparatively low. However, later they could not successfully compete with the better adapted other Myrmicinae and perhaps members of other subfamilies, including representatives of extant genera, which penetrated to Europe (most probably, by the land from other parts of Eurasia), and so many of these less well adapted Myrmicinae genera went extinct.

The new myrmicine genus, *Bilobomyrma* n. gen. (mentioned above) and two new species, *Bilobomyrma ukrainica* n. sp. and *B. baltica* n. sp., are described below. We tentatively place this genus in the tribe Formicoxenini (sensu Bolton, 2003).

#### MATERIAL AND METHODS

We examined two pieces of amber, each containing one male. The piece with *Bilobomyrma ukrainica* from the Rovno Amber is deposited in the Shmalhausen Institute of Zoology of the Ukrainian national Academy of Sciences, Kiev, Ukraine (SIZK), and the piece with *B. baltica* from the Baltic Amber is in the Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (PIN).

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. The high quality color photos were made using the Leica MZ16 stereomicroscope, connected to the camera IC 3D.

Insects or other inclusions in some ambers (e.g., Sakhalin amber, Russia) are quite often plastically strongly distorted, but inclusions in the late Eocene European ambers normally are not deformed. The investigated specimens of both *B. ukrainica* and *B. baltica* are not distorted and remain preserved in good condition. However, not all features of the studied specimens were easily visible and measurable; hence we measured only visible details (accurate to 0.01 mm).

Abbreviations used for 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; OL (eye length), maximal diameter of eye; SL (scape length), maximum straight-line length of antennal scape seen in profile; PL (petiole length), maximum length of petiole

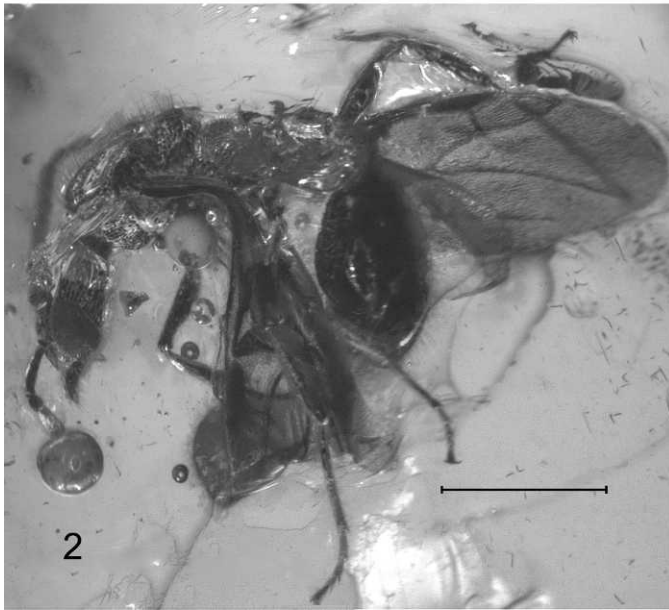
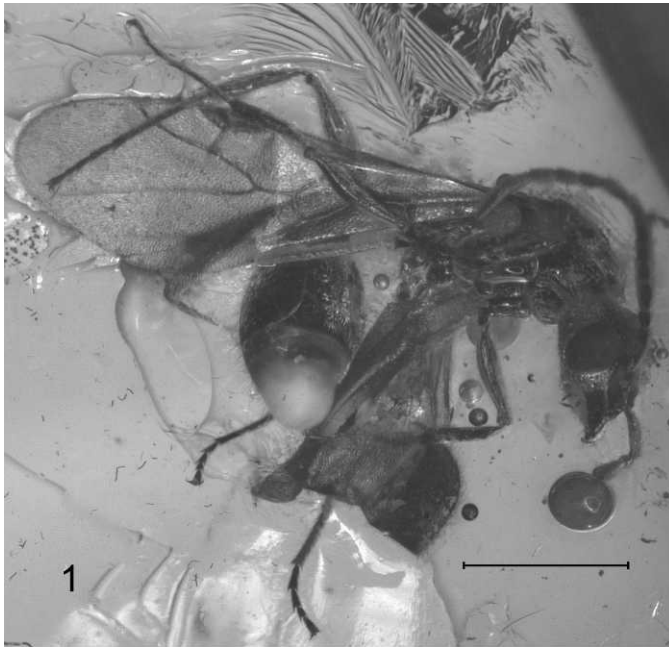


FIGURE 1—Microscopic photographs of *Bilobomyrma ukrainica* n. sp., male, holotype (SIZK, N. K-7656, Rovno Amber). 1, body, in lateral right-side view; 2, body, in lateral left-side view. Scale bars=1 mm.

from above; PH (petiole height), maximum height of petiole in profile; PPL (postpetiole length), maximum length of postpetiole from above; PPH (postpetiole height), maximum height of postpetiole in profile; AL (alitrunk length), diagonal length of the alitrunk (=mesosoma) seen in profile, from the anterior-upper margin of pronotum to the posterior margin of propodeal lobes; AH (alitrunk height), height of mesosoma, measured from the upper level of scutum perpendicularly to the level of lower margin of mesopleuron; SCL (scutum and scutellum length), maximum length of scutum+scutellum from above; SCW (scutum width), maximum width of scutum from above; HTL (hind tibia length), length of tibia of hind leg.

Abbreviations for indices: CI (cephalic index)=HL/HW; SI<sub>1</sub> (scape length index 1)=SL/HL; SI<sub>2</sub> (scape length index 2)=SL/

HW; OI (ocular index)=OL/HL; PI<sub>1</sub> (petiole index 1)=PL/HL; PI<sub>2</sub> (petiole index 2)=PL/PH; PPI<sub>1</sub> (postpetiole index 1)=PPL/HL; PPI<sub>2</sub> (postpetiole index 2)=PPL/PPH; AI (alitrunk index)=AL/AH; SCI (scutum index)=SCL/SCW.

#### SYSTEMATIC PALEONTOLOGY

Family FORMICIDAE Latreille, 1809  
Subfamily MYRMICINAE Lepeletier, 1835  
Genus BILOBOMYRMA new genus

*Type species.*—*Bilobomyrma ukrainica* n. sp., by present designation.

*Other species.*—*Bilobomyrma baltica* n. sp.

*Diagnosis.*—Anterior clypeal margin deeply incised medially, with two lateral lobes; median portion of clypeus distinctly elevated, rounded, without lateral and central longitudinal carinae. Forewing with closed cells *mcu*, *1+2r* and *3r*; cell *3r* is very short, approximately twice longer than width; distal section of veins *RS* and *M* diverge from cell *1+2r* separately. Antennae 13-segmented; scape relatively short, subequal to length of first and second funicular segments together; apical club indistinct; second funicular segment distinctly longer than all other funicular segments, except for apical one. Palp formula 4(5?), 3. Scutum with notauli. Middle and hind tibiae without spur.

*Etymology.*—Named after Latin prefix “-bi,” two, twice, binary, and Greek words “λοβος” (lobos), lobe, and “μυρμήγκι,” ant, to emphasize the structure of the anterior clypeal margin that has two distinct lobes.

*Occurrence.*—Rovno Amber (Ukraine) and Baltic Amber (Russia), late Eocene.

*Remarks.*—*Bilobomyrma* differs from all known both extinct and extant Myrmicinae genera by the following combination of features: the shape of clypeus, the peculiar wing venation, the elongate second funicular segment, combining with 13-segmented antennae without apical club, absence of the spur on middle and hind tibiae, etc. (for more details see Discussion, below).

#### BILOBOMYRMA UKRAINICA new species

Figures 1, 2

*Diagnosis.*—Sides of pronotum longitudinally rugulose, lower part of mesopleura with somewhat finer longitudinal rugulosity, sides of propodeum longitudinally rugose, while its dorsum transversally rugose. Postpetiole long (PPI<sub>1</sub>=0.48, PPI<sub>2</sub>=1.75), mesosoma short and high (AI=1.46). Head seems almost hairless.

*Description.*—Head distinctly longer than broad, with feebly convex sides and well-marked, quite narrowly rounded occipital corners, occipital margin feebly concave. Eyes very big, situated distinctly in front of mid-length of sides of head, their maximal diameter approximately twice smaller than head length. Ocelli very big. For shape of clypeus see generic diagnosis, above. Clypeus widely inserted between frontal carinae; frontal triangular well-marked, distinctly separated from clypeus by suture. Mandibles elongate-triangular, with well-developed masticatory margin; the latter with quite long apical tooth and four shorter sharp teeth. Scape somewhat shorter than first and second funicular segments together, second funicular segment elongate, 1.5 times longer than third one, approximately 1.5 times shorter than apical segment. Only three distal segments of maxillary palps and two distal segments of labial palps are visible, but based on length of visible parts of palps and their position, palp formula seems to be 4, 3 or even 5, 3 (see also description of *B. baltica*, below). Clypeus, frons and lateral parts of head longitudinally rugose, posterior part of head dorsum smooth. Head dorsum almost without hairs (at least they are concealed on the specimen). Scape with short decumbent pilosity.

Mesosoma relatively short, less than 1.5 times longer than its height; dorsal surface of propodeum somewhat shorter than its posterior (declivous) surface. Scutum moderately widened, less

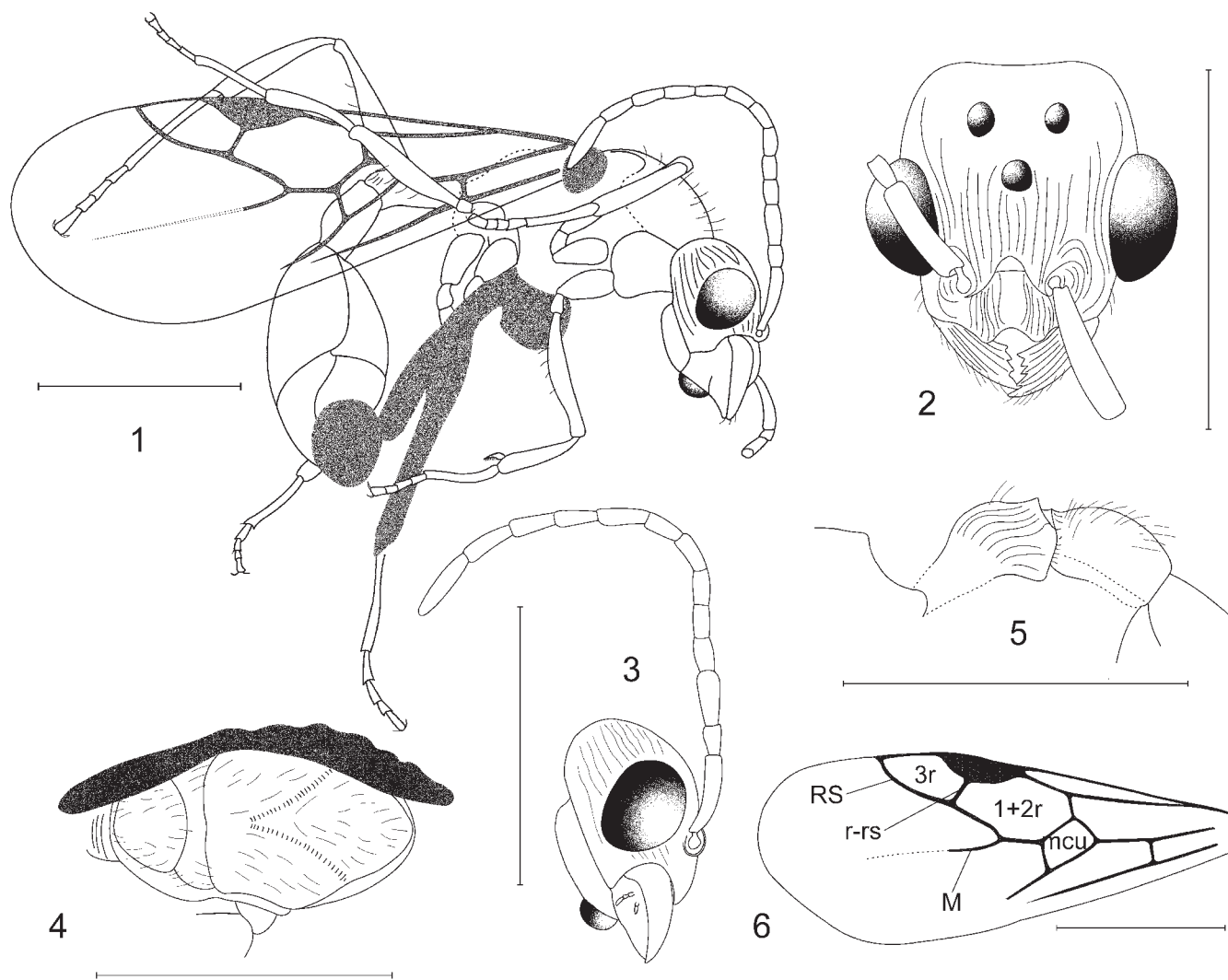


FIGURE 2—Explanatory line-drawings of *Bilobomyrma ukrainica* n. sp., male, holotype (SIZK, N. K-7656, Rovno Amber). 1, body, in lateral right-side view; 2, head, in dorsal view; 3, head and antenna, in anterior-lateral view; 4, scutum and scutellum, in dorsal view; 5, petiole and postpetiole, in lateral view; 6, forewing. Scale bars=1 mm.

than 1.5 times narrower than total length of scutum and scutellum. Sides of pronotum longitudinally rugulose, lower part of mesopleura with somewhat finer longitudinal rugulosity, sides of propodeum longitudinally rugose, its dorsum with transversal rugosity. Scutum and scutellum with abundant, quite long standing hairs, propodeum hairless. Petiole and especially postpetiole long and low, much longer than their height. Petiolar node with quite coarse longitudinal rugae, postpetiole smooth. Petiolar node with a few long hairs, postpetiole with numerous hairs. Legs quite long and slender; tibia with rather long subdecumbent pilosity; ventral surface of femora with sparse long erect hairs; tarsi with short decumbent pilosity.

Forewing venation (additionally to generic characteristics): pterostigma well developed; cell *3r* less than twice longer than width; cell *1+2r* big, approximately 1.7 times longer than width and 1.3 times longer than length of cell *3r*; cell *mcu* trapezoidal, 1.7 times longer than width.

Gaster smooth, with abundant long suberect to subdecumbent hairs. Pygidium and genitalia are concealed.

Workers and gynes unknown.

*Etymology*.—Named after Ukraine, the type locality of described species.

*Types*.—One male, holotype, complete specimen, N. K-7656 (SIZK).

*Occurrence*.—Rovno Province of Ukraine, Rovno Amber, late Eocene.

*Measurements*.—All measurements in mm. Body length approximately 4.3 mm; HL=0.77; HW=0.64; SL=0.27; OL=0.40; AL=1.44; AH=0.99; HTL=0.64; PL=0.40; PH=0.19; PPL=0.37; PPH=0.21; SCW=0.69; SCL=1.01. Indices: CI=1.21; SI<sub>1</sub>=0.34; SI<sub>2</sub>=0.42; OI=0.52; PI<sub>1</sub>=0.52; PI<sub>2</sub>=2.14; PPI<sub>1</sub>=0.48; PPI<sub>2</sub>=1.75; AI=1.46; SCI=1.46.

#### BILOBOMYRMA BALTICA new species

Figures 3, 4

*Diagnosis*.—Sides of pronotum mostly smooth, with only a few longitudinal rugae on its upper part, whole mesopleura and sides of propodeum smooth, only upper half of sides of propodeum and its dorsal surface longitudinally rugose. Postpetiole short (PPI<sub>1</sub>=0.33, PPI<sub>2</sub>=1.11), mesosoma long and low (AI=1.69). Head with many standing hairs.

*Description*.—Head width hardly measurable, but head seems distinctly longer than broad, with feebly convex sides and rounded occipital corners, occipital margin barely visible, while seems more or less straight or at most feebly concave. Eyes very



FIGURE 3—Microscopic photograph of *Bilobomyrma baltica* n. sp., male, holotype (PIN, N. 964/1274, Baltic Amber), body, in lateral view. Scale bar=1 mm.

big, situated distinctly in front of mid-length of sides of head, their maximal diameter twice smaller than head length. Ocelli very big. For shape of clypeus see generic diagnosis, above. Clypeus widely inserted between frontal carinae; frontal triangular well-marked, distinctly separated from clypeus by suture. Mandibles elongate-triangular, with well-developed masticatory margin; the latter with quite long apical tooth and four shorter sharp teeth. Scape somewhat longer than first and second funicular segments together, second funicular segment elongate, 1.75 times longer than third one, 1.5 times shorter than apical segment. Maxillary palps concealed, labial palps distinctly 3-segmented. Lateral parts of head longitudinally rugose, posterior part of head dorsum smooth; sculpture on clypeus and frons barely visible. Head dorsum with not abundant long standing hairs. Scape with short decumbent pilosity

Mesosoma relatively long, approximately 1.7 times longer than its height; dorsal surface of propodeum somewhat shorter than its posterior (declivous) surface. Sides of pronotum mostly smooth, a few longitudinal rugae present on its upper part; whole mesopleura smooth, as well as lower part of sides of propodeum, only upper half of sides of propodeum and its dorsal surface longitudinally rugose. Scutum and scutellum with abundant, quite long standing hairs, propodeum hairless. Petiole long and low, much longer than height, postpetiole distinctly shorter than petiole. Petiolar node with fine rugosity and striation, postpetiole smooth. Petiolar node and postpetiole with quite abundant standing hairs of various length. Legs quite long and slender; tibia with rather long subdecumbent pilosity; ventral surface of femora with long erect hairs; tarsi with short decumbent pilosity.

Forewing venation (additionally to generic characteristics): pterostigma well developed; cell *3r* approximately twice longer than width; cell *1+2r* big, approximately 1.9 times longer than width, subequal to length of cell *3r*; cell *mcu* trapezoidal, 1.7 times longer than width.

Gaster smooth, with abundant long suberect to subdecumbent hairs. Pygidium apically rounded, stipites of genitalia strongly curved inward apically.

Workers and gynes unknown.

*Etymology*.—Named after the Baltic region, the type locality of described species.

*Types*.—One male, holotype, complete specimen, N. 964/1274 (PIN).

*Occurrence*.—Kaliningrad Province of Russia, Baltic Amber, late Eocene.

*Measurements*.—All measurements in mm. Body length approximately 4.5 mm; HL=0.80; SL=0.30; OL=0.50; AL=1.31; AH=0.77; PL=0.43; PH=0.20; PPL=0.27; PPH=0.24. Indices: SI<sub>1</sub>=0.33; OI=0.50; PI<sub>1</sub>=0.53; PI<sub>2</sub>=2.13; PPI<sub>1</sub>=0.33; PPI<sub>2</sub>=1.11; AI=1.69.

*Remarks*.—*Bilobomyrma ukrainica* n. sp. and *B. baltica* n. sp. are quite similar in the general appearance and in many diagnostic features, including the peculiar shape of clypeus, the shape of head and eyes, the wing venation, etc. However, they differ from each other by the details of the body sculpture: the sides of pronotum in *B. ukrainica* are longitudinally rugulose, the lower part of mesopleura with somewhat finer longitudinal rugosity, the sides of propodeum are longitudinally rugose, while its dorsum is transversally rugose; the sides of pronotum in *B. baltica* are mostly smooth, with the only a few longitudinal rugae on its upper part, whole mesopleura and sides of propodeum smooth, only the upper half of sides of propodeum and its dorsal surface longitudinally rugose. Additionally, the postpetiole of *B. ukrainica* is distinctly longer than in *B. baltica* (PPI<sub>1</sub>=0.48, PPI<sub>2</sub>=1.75 vs. PPI<sub>1</sub>=0.33, PPI<sub>2</sub>=1.11), and mesosoma in the first species is relatively short (AI=1.46 vs. 1.69).

Although the pilosity of mesosoma of both species is similar, the head of *B. ukrainica* seems almost hairless, but that of *B. baltica* is quite hairy.

#### DISCUSSION

*Bilobomyrma* n. gen. possesses a set of primitive characters, combined with distinctly derived ones. The venation of the forewing is primitive: compared to the most of Myrmicinae genera the cell *3r* is closed, which is a common state for this feature in the most of the more primitive poneroid and myrmecoid subfamilies, as well as in the subfamilies Dolichoderinae and Formicinae. Moreover, the closed cell *3r* in *Bilobomyrma* is very short (only twice longer than its width) compared to its “typical condition” in various genera from the above mentioned subfamilies. We also consider as primitive the position of the distal section of vein *M* that diverges from cell *1+2r* much more proximally than the section *RS* (we consider the derived condition to be when the distal sections of vein *M* diverge from cell *1+2r* more distally, near the cross-vein *r-rs*, from the same nodule or at least very close to it).

Among all known Myrmicinae genera from the late Eocene ambers, only *Carebara* Westwood (now the senior synonym of *Oligomyrmex* Mayr) has comparable venation to that of *Bilobomyrma*, i.e., a closed cell *r3* and similar position of the section of vein *M*. However, cell *r3* of males of *Carebara* is of ‘normal’ length, being more than three times longer than the wide. Additionally, *Carebara* males very well differ from those of *Bilobomyrma* by having a differently shaped mesosoma, head and waist, by the absence of notauli, by the short second funicular segment and by many other features. We also consider the presence of notauli on the scutum, and the 13-segmented antennae with short scape and without apical club to be the primitive state for Myrmicinae.

At the same time, *Bilobomyrma* possess a set of derived characters. Thus, venation of forewing combines primitive characters mentioned above with the derived features, such as the lack of closed cells *rm* and *cua*, what is a derived state in the

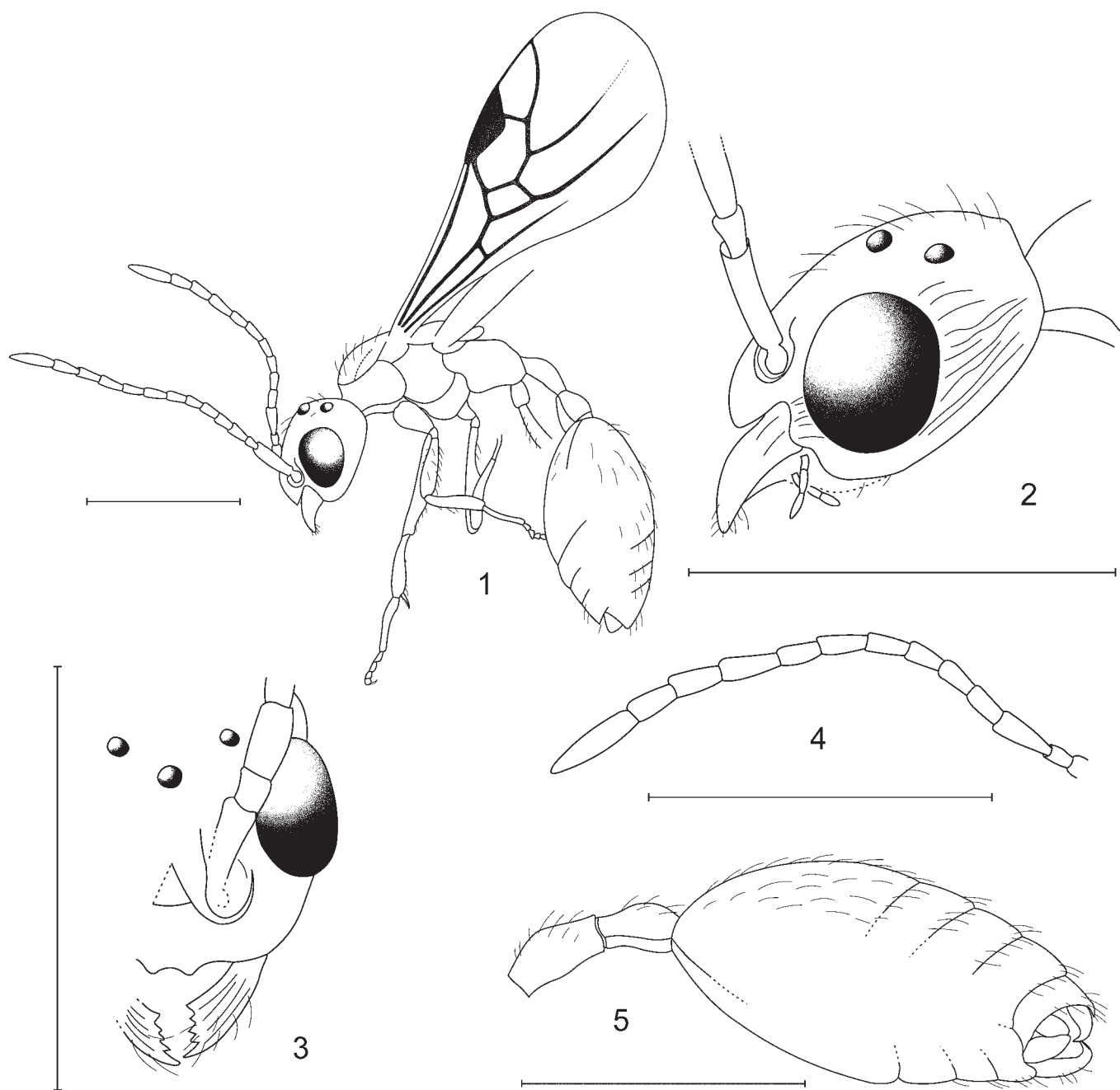


FIGURE 4—Explanatory line-drawings of *Bilobomyrma baltica* n. sp., male, holotype (PIN N. 964/1274, Baltic Amber). 1, body, in lateral view; 2, head, in lateral view; 3, visible part of head, in dorsal view; 4, antennal funiculus; 5, petiole, postpetiole and gaster, in lateral view. Scale bars=1 mm.

subfamily Myrmicinae and in the most of the other advanced ant subfamilies.

We consider the peculiar shape of clypeus with the strongly incised medially anterior margin that makes it looks distinctly bilobed anteriorly, to be autapomorphic in *Bilobomyrma*. Derived is also the shape of the median portion of clypeus that is distinctly elevated, while this portion lacks longitudinal lateral carinae—the synapomorphy of several tribes of Myrmicinae, including some extinct genera (e.g., see Bolton, 2003; Dlussky and Radchenko, 2006a, 2006b). Indisputably derived characters are the reduced number of maxillary and labial palps seen in *Bilobomyrma* (palp formula is 4[5?], 3) and lack of spurs on the middle and hind tibiae.

Thus we conclude that based on the combination of morphological features described and discussed above, *Bilobomyrma* is distinct from any known extinct or extant Myrmicinae genera. Also there seem to be no reasons to consider it as a direct ancestor of any of the Myrmicinae genera.

Data on male characters are scarce in the Bolton's (2003) synopsis and ant classification, but based on this we suggest that *Bilobomyrma* has some relatedness with the tribe Formicoxenini. Probably, it represents an extinct evolutionary branch having a common ancestor with the modern Formicoxenini.

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