ISSN 0031-0301, Paleontological Journal, 2008, Vol. 42, No. 5, pp. 500–513. © Pleiades Publishing, Ltd., 2008.
Original Russian Text © G.M. Dlussky, 2008, published in Paleontologicheskii Zhurnal, 2008, No. 5, pp. 45–59.

Ants of the Tribe Formicini (Hymenoptera, Formicidae) from Late Eocene Amber of Europe

G. M. Dlussky

Moscow State University, Moscow, 119899 Russia
e-mail: dlusskye@mail.ru

Received October 9, 2007

Abstract—The tribe Formicini (Formicinae) from the Late Eocene Baltic, Bitterfeld, Rovno, and Scandinavian ambers is revised. Ants are recorded for the first time from the Bitterfeld and Scandinavian ambers. Two new genera (*Cataglyphoides* gen. nov. and *Conoformica* gen. nov.) and six new species (*Cataglyphoides intermedius* sp. nov., *Conoformica bitterfeldiana* sp. nov., *Formica kutscheri* sp. nov., *F. palaeopolonica* sp. nov., *F. radchenkoi* sp. nov., *F. zherikhini* sp. nov.) are described. A new combination, *Cataglyphoides constrictus* (Mayr, 1868), comb. nov., is established. A lectotype of *Camponotus constrictus* Mayr, 1868 and a neotype of *Formica phaethusa* Wheeler, 1915 are designated. *Formica clymene* Wheeler, 1915 is recognized as a new synonym of *F. phaethusa* Wheeler, 1915. An identification key for workers of Formicini species from Late Eocene European ambers is provided.

DOI: 10.1134/S0031030108050055

Key words: ants, Formicini, Formicidae, Hymenoptera, Late Eocene, Europe, amber.

INTRODUCTION

Ants of the tribe Formicini of the subfamily Formicinae are the most conspicuous element of the Holarctic myrmecofauna. Members of the genus *Formica* are adapted to humid environments; *Alloformica* and *Proformica*, to semiarid zones; and *Cataglyphis*, to arid environments (Dlussky, 1981). Members of the genera *Polyergus* and *Rossomyrmex* are social parasites (slave-making ants), the former parasitizing various species of *Formica* , and the latter *Proformica.* Outside the Holarctic occur only few *Cataglyphis* species that penetrated into semiarid regions of South Africa, and one species of *Formica* in the mountains of Burma. In the Palearctic all genera of the tribe are found, whereas in the Nearctic only *Formica* and *Polyergus* occur. The adaptive zone of *Proformica* and *Cataglyphis* is occupied there by members of the genus *Myrmecocystus* Wesmael (Lasiini). Therefore, an early adaptive radiation of Formicini that resulted in the appearance of new genera undoubtedly occurred within the Palearctic. In this connection a study of the fossil history of the tribe, first of all of the fauna from Late Eocene European ambers, is especially interesting.

The first detailed revision of ants from Baltic amber was published by Mayr (1868) who described *Formica flori* and *Camponotus constrictus.* Wheeler (1915) transferred the latter species to the genus *Formica* and described *Formica* clymene, F. horrida, F. *phaethusa* and *F. strangulata.* In 1967 I published a revision of the genus *Formica* (Dlussky, 1967) where I described *F.* antiqua, F. baltica, F. *parvula* and *F. proformicoides* and suggested that *F. constricta* should be placed in the genus *Cataglyphis.* When preparing the revision I had no opportunity to examine types of the previously described species and relied on their descriptions and a small collection of amber ants kept in the Paleontological Institute, Russian Academy of Sciences. Therefore this paper contained several errors, partly corrected in subsequent publications (Dlussky, 1997, 2002).

In recent years I have studied large collections of ants from Baltic (Kaliningrad Region of Russia, Poland), Bitterfeld (Germany), Rovno (Ukraine), and Scandinavian (Denmark) ambers, including all existing types of Mayr and Wheeler. Altogether more than 5000 ant inclusions were studied, including 457 specimens of the tribe Formicini. The present paper forms part of the results of this study.

The collections studied are from the following institutions: Paleontological Institute, Russian Academy of Sciences, Moscow (PIN), Baltic amber; Institute of Zoology, National Academy of Sciences of Ukraine, Kiev (IZANU), Rovno amber; Museum Ziemi, Polska Akademia Nauk, Warsaw, Poland (MZ), Baltic amber; Natural History Museum, London (NHML), Baltic amber; Naturhistorische Museum in Wien (NHMW), types of Mayr from Baltic amber; Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen, Germany (GZG.BST), collection of Baltic amber, constituting a part of the collection formerly kept in Geologische Institut, Königsberg and described by Wheeler (1915), in which some Wheeler types[1] are preserved;

[1] In the list of specimens studied both new numbers (with index GZG.BST) and old numbers of Königsberg collection are given; in other places, only new numbers.

Humboldt Museum, Germany (HM), Bitterfeld amber; Zoological Museum of University Copenhagen (ZMUC), Scandinavian and Baltic ambers; personal collection of Carsten Gröhn, Glinde, Germany, settled to Humboldt Museum (CGC), the types of which are housed in the Geologisch-Paläontologischen Institut in Hamburg (GPIH), Baltic and Bitterfeld ambers; personal collection of Manfred Kutscher, Sassnitz, Rügen, Germany, bequeathed to Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen (MKC), Bitterfeld amber.

SYSTEMATIC PALEONTOLOGY

Subfamily Formicinae Latreille, 1802

Tribe Formicini Latreille, 1802

Diagnosis. Petiole one-segmented. Antennae in females and workers 12-segmented, in males, 13-segmented. Antennal insertion near posterior margin of clypeus. Ocelli in workers usually present. Propodeal spiracles situated at sides of propodeum, remote from line separating its lateral and posterior surfaces. Metapleural glands present. Hind coxae approximated. A transverse ridge present at base of first gastric sternite. Apex of gaster always with acidopore, surrounded with circlet of hairs. Forewing with closed cells 1+2r, 3r and mcu, free branches RS and M leaving cell 1+2r from common knot.

Composition. Bolton (2003) included in this tribe the genera *Alloformica* Dlussky (Recent), *Bajcaridris* Agosti (Recent), *Cataglyphis* Förster (Recent), *Formica* Linnaeus (Late Eocene–Recent), *Glaphyromyrmex* Wheeler (Late Eocene), *Polyergus* Latreille (Recent), *Proformica* Ruzsky (Recent), *Protoformica* Dlussky (Late Eocene), and *Rossomyrmex* Arnoldi (Recent). After reexamination of the holotype of *Glaphyromyrmex oligocenicus* Wheeler (type species of the genus) and two workers from the collection of MZ we revealed that in this species the hind coxae are broadly separated, as characteristic of the tribe Lasiini, so this genus should be excluded from the tribe Formicini. Additionally, the tribe comprises *Cataglyphoides* gen. nov. and *Conoformica* gen. nov. from Baltic and Bitterfeld ambers.

Genus *Cataglyphoides* Dlussky, gen. nov.

Etymology. From the generic name *Cataglyphis*.

Type species. *Camponotus constrictus* Mayr, 1868.

Diagnosis. Workers. Body slender, habitus resembling primitive members of the genus *Cataglyphis.* Head with distinct occipital angles. Ocelli forming obtuse triangle. Funicle segments elongate, 2nd–6th ones 1.5–2 times as long as wide. Apical tooth of mandible much longer than preapical one. Maxillary palps 6-segmented, long, with fourth segment elongate. Psammophore absent. Propodeal spiracles short-oval. Petiole nodule-shaped or with narrow thick scale.

Species composition. C. constrictus and *C. intermedius* sp. nov.

Comparison. Similar to *Cataglyphis* in general habitus, structure of mandibles (elongate apical tooth) and maxillary palps (elongate fourth segment), but distinct in the absence of psammophore and in short-oval propodeal spiracles (long and narrow in *Cataglyphis*).

Cataglyphoides constrictus (Mayr, 1868), comb. nov.

Camponotus constrictus: Mayr, 1868, p. 29, pl. I, fig. 11 (worker); Dalla Torre, 1893, p. 226; André, 1895, p. 82; Handlirsch, 1906–1908, p. 867; Ponomarenko and Schultz, 1988, p. 22.

Formica constricta (Mayr): Wheeler, 1915, pp. 128–130, fig. 61; Burnham, 1978, p. 115; Dlussky, 1997, p. 59.

Cataglyphis constrictus (Mayr): Dlussky, 1967, p. 85; Bolton, 1995, p. 135.

Lectotype (designated here). NHMW, no. 1984/31/137, worker with the label "ST *Camponotus constrictus* MAYR, 1868. Eozän, Baltischer Bernstein, Kollektion HANDLIRSCH, Syntypus zu MAYR 1868: 29"; Baltic amber; Late Eocene.

Description (Figs. 1a, 1b). Worker. Head length somewhat greater than width. Occipital margin slightly convex. Clypeus with anterior margin rounded, without median carina. Eyes oval, markedly displaced backwards; gena length 1.3 times the maximum eye diameter. Frontal carinae diverging, somewhat extended beyond middle of eyes. Scape projecting beyond occipital margin of head for more than one-half of its length. Funicle segments elongate, 1st–5th three times, distal ones (except for terminal one) about twice as long as wide. Mandibles with 6 or 7 teeth at molar margin. Apical tooth twice as long as preapical one, the latter only slightly longer than two preceding teeth. Maxillary palps reaching occipital foramen; third, fifth and sixth segments subequal, fourth 1.2–1.5 times as long as the others. In profile, mesonotum slightly raised above pronotum, mesopropodeal depression conspicuous, propodeum low and evenly rounded. Petiole with nodule and short anterior cylindrical part; petiole length somewhat smaller than height and greater than width. Entire body finely, superficially shagreened. Decumbent pubescence not visible in all specimens studied. Head with erect hairs on clypeus, frons (2 or 3 pairs), and near ocelli. Mesosoma, petiole and first two gastral tergites without erect hairs. Scape and legs with numerous semierect hairs.

Measurements (mm): specimen GZG.BST, no. 04173: mesosoma length, 3.3; head length, 2.25; specimen GZG.BST, no. 04172: mesosoma length, 3.75; specimen GZG.BST, no. 04167: mesosoma length, 3.8; head length, 2.5; maximal eye diameter, 0.67; scape length, 3.75; specimen GZG.BST, no. 04174: mesosoma length, 2.4; head length, 1.5; scape length, 1.75.

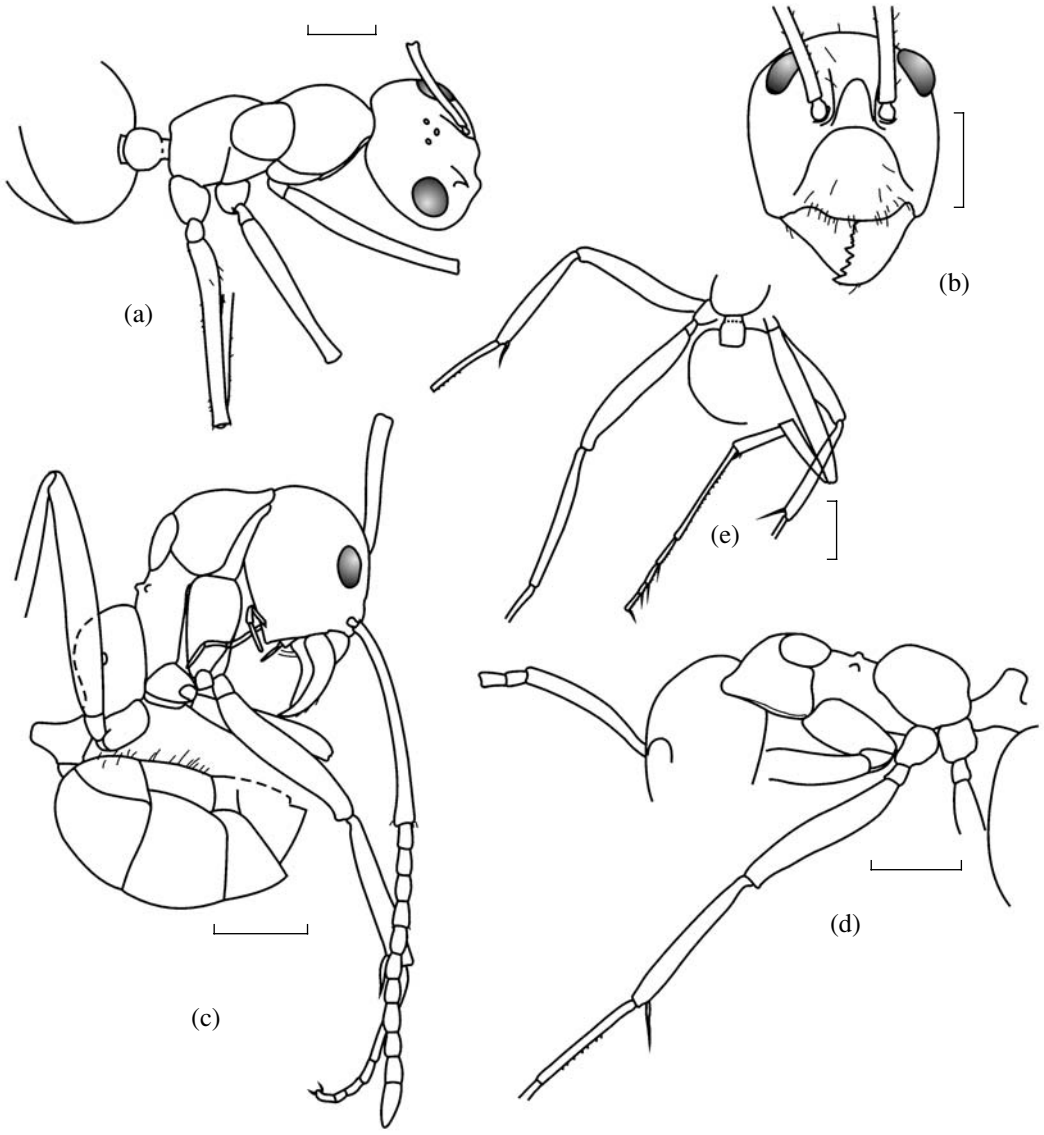

Fig. 1. Species of the genus *Cataglyphoides* gen. nov.: (a, b) *C. constrictus* (Mayr): (a) specimen GZG.BST, no. 04173; (b) specimen GZG.BST, no. 04170, head; (c-e) *C. intermedius* sp. nov. (c) holotype CGC, no. 4385a, (d) paratype no. 4385b; (e) paratype no. 4385c. Scale bars in Figs. 1–3 correspond to 1 mm.

R e m a r k s. Mayr (1868) described this species in the genus *Camponotus* Mayr. Later Wheeler (1915) noted that in this species antennae are inserted at the posterior margin of clypeus, not at some distance from it, as in *Camponotus*, and transferred it to the genus *Formica.* Earlier, based on the figure by Wheeler, I suggested that it may belong to the genus *Cataglyphis* (Dlussky, 1967); however, after reexamining the types it became clear that it cannot be included in the latter genus. The species lacks such important characters of *Cataglyphis* as the presence of a psammophore and narrow propodeal spiracles acquired by these ants as adaptations to arid environments (Dlussky, 1981). It also cannot be assigned to the genus *Formica*, since the structure of petiole and maxillary palps are not characteristic of this genus.

M a t e r i a l. GZG.BST., nos. 05037 (3719.IV.67) (paralectotype), 04167 (G4720), 04168 (G4718), 04169 (B5435), 04170 (B5195), 04172 (G4721), 04173 (G4719), 04174 (B5520), 04175 (B5348), 04209 (N18831) (specimens identified by Wheeler) (Baltic amber).

Cataglyphoides intermedius Dlussky, sp. nov.

E t y m o l o g y. From the Latin *intermedius* (intermediate).

H o l o t y p e. CGC (GPIH, no. 4511), no. 4385a, worker; Baltic amber; Late Eocene.

Description (Figs. 1c–1e). Worker. Head length somewhat greater than width. Occipital margin slightly convex. Clypeus with anterior margin rounded. Eyes oval, situated about the middle of head sides; gena length somewhat greater than maximal eye diameter. Frontal carinae diverging, reaching the middle of eyes. Scape projecting beyond occipital margin of head for more than one-third but less than one-half of its length. Funicle segments elongate, 1st–5th twice as long as wide, distal ones (except for terminal one) about 1.5 times as long as wide. Maxillary palps reaching occipital foramen, fourth segment twice as long as fifth. Mesonotum posteriorly markedly narrowed, forming "'waist." In profile, pronotum and mesonotum evenly convex, mesopropodeal depression virtually absent, propodeum high and evenly rounded. Petiole with high, thick and narrow scale, anterior and posterior sides of scale in profile concave, dorsally subparallel, apex rounded, not ridged; petiole length subequal to height, petiole 1.5 times as long as wide. Entire body finely, superficially shagreened. Decumbent pubescence dense, consisting of very fine hairs which are (at least on mesosoma, petiole, and limbs) much longer than spaces between them. Head with erect hairs on clypeus and frons (1 or 2 pairs). Mesosoma and first two gastral tergites without erect hairs; petiole with one pair of hairs at sides (holotype) or without erect hairs (paratypes). Erect hairs along hind margin of third gastral tergite and over all surface of gastral sternites and last tergites. Scape and legs without erect or semierect hairs.

Measurements (mm): holotype: mesosoma length, 3.0; head length, 2.35; scape length, 2.15; maximal eye diameter, 0.48; hind femur length, 2.5; petiole length, 0.58; petiole height, 0.53; paratype CGC, no. 4385b: mesosoma length, 3.0; paratype CGC, no. 4385c: hind femur length, 2.4; petiole length, 0.75; petiole width, 0.45.

Comparison. Distinct from *C. constrictus* in the petiole shape, shorter scape and absence of erect hairs on scape and legs.

Remarks. Holotype and paratype no. 4385b are visible only in profile, another paratype in dorsal aspect, but in the latter the head is missing. Therefore some important characters (frontal area, presence of carina on clypeus, number of teeth on mandibles) are impossible to see.

Material. Holotype and paratypes CGC, nos. 4385b and 4385c (workers) in the same piece of amber.

Genus *Conoformica* Dlussky, gen. nov.

Etymology. From the Latinized Greek *conus* (cone) and the genus *Formica*.

Type species. *C. bitterfeldiana* sp. nov.

Diagnosis. Workers. Head widened forwards, without distinct occipital angles, with occipital margin convex and lower surface of head slightly concave in profile. Vertex with arched chitinous ridge. Ocelli absent. Funicle segments elongate. Maxillary palps long, 6-segmented, with fourth and fifth segments subequal in length. Psammophore absent. Propodeal spiracles small, rounded. Petiole high, conical, pointed at apex.

Species composition. Type species.

Comparison. Distinct from all known fossil and extant members of the subfamily Formicinae in the presence of chitinous ridge on the vertex and cone-shaped petiole.

Remarks. The presence of acidopore with coronula doubtless indicates that the new genus belongs in the subfamily Formicinae. In habitus the new species resembles workers of several *Camponotus* species, but the character of the antennal insertion and the presence of metapleural glands preclude its assignment to the tribe Camponotini. A similar petiole structure was previously only known in some Dolichoderinae (*Dorymyrmex* Mayr, *Dolichoderus* Lund) and Ponerinae (*Acanthoponera* Mayr, *Odontomachus* Latreille). However, the new genus should be placed in the tribe Formicini, as indicated by the following character set: 12-segmented antennae, character of antennal insertion, position of propodeal spiracles, approximated hind coxae, presence of metapleural glands. Unfortunately, in the only specimen it is impossible to trace the mandible shape and presence of transverse ridge at the base of first gastral sternite, leaving some doubt as to the tribal assignment.

Conoformica bitterfeldiana Dlussky, sp. nov.

Etymology. From the locality (Bitterfeld amber).

Holotype. HM, no. 12/215, worker; Bitterfeld amber; Late Eocene.

Description (Fig. 2). Worker. Body slender with elongate limbs. Eyes oval, markedly convex, displaced backwards. Scape extended far beyond occipital margin, longer than head. Funicle segments (except for basal and terminal one) about twice as long as wide. Sutures separating pronotum, mesonotum and propodeum clearly visible, mesopleural suture untraceable. Anterior margin of mesonotum in profile raised above pronotum. Propodeum laterally compressed, its dorsal and posterior surfaces in profile subequal, forming rounded obtuse angle. Orifice of metapleural gland without hairs. Pulvilli weakly developed, half as long as claws. Body shining, very finely and superficially sculptured. Long erect hairs on head, fore coxae, and gastral tergites and sternites. Mesosome, scape, and femora without erect or semierect hairs. On lower surface of tarsi and inner surface of tibiae rows of thick, acute oblique spinules. Decumbent pubescence absent.

Measurements (mm): mesosoma length, 1.7; head length, 1.0; scape length, 1.3.

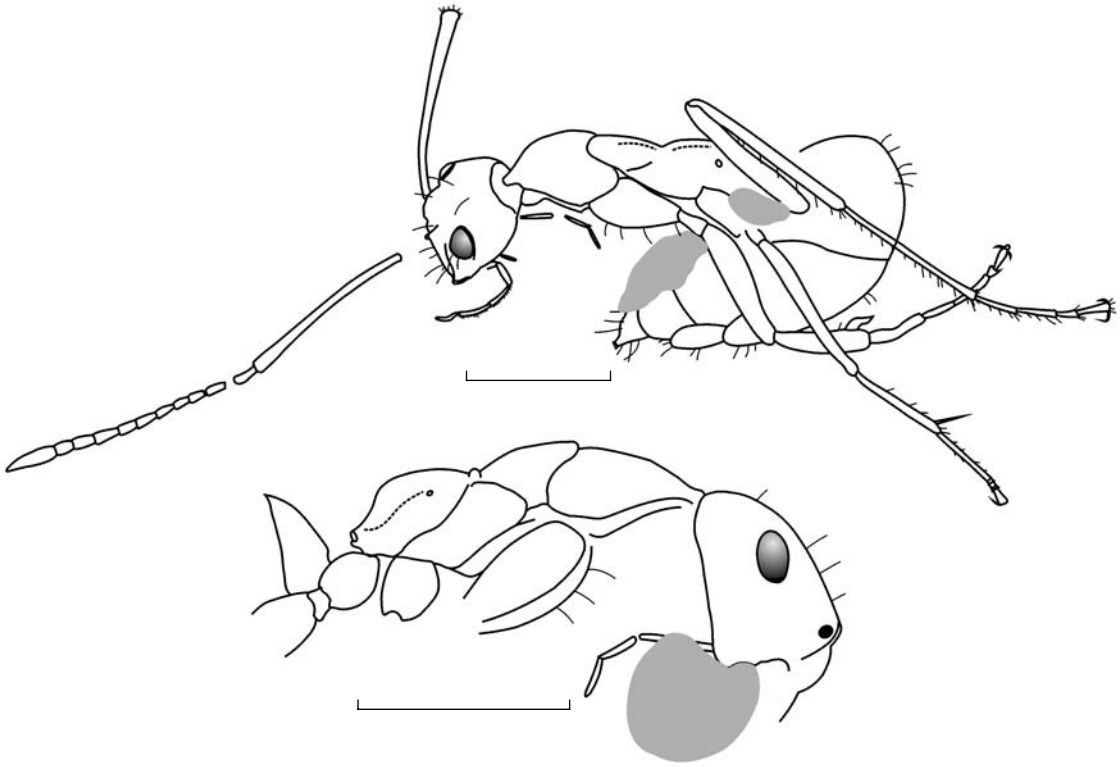

Fig. 2. *Conoformica bitterfeldiana* gen. et sp. nov., holotype HM, no. 12/215 in different views.

R e m a r k s. The convex eye situated in the posterior part of the head and elongate limbs indicate that this ant foraged not in the leaf litter, but in open places, actively using vision. The weak development of pulvilli and numerous oblique stiff setae on the lower surface of tarsi imply that it ran chiefly over the ground as opposed to along tree trunks. Therefore, it can be assumed that this ant was an active herpetobiont.

M a t e r i a l. Holotype.

Genus *Formica* Linnaeus, 1758

T y p e s p e c i e s. *Formica rufa* Linnaeus, 1761.

D i a g n o s i s. Workers. Head slightly narrowed forwards, with rounded occipital angles. Eyes situated above middle of head sides, gena much longer than maximal eye diameter. Ocelli forming obtuse triangle. Apical tooth of mandible usually (in all modern and some fossil species) only slightly longer than preapical one. Maxillary palps either 6-segmented (with fourth segment only slightly longer than, or subequal to, fifth) or shortened, 5-segmented. Psammophore absent. Propodeal spiracles short-oval or rounded. Petiole with scale widened upwards that is wider than petiole length.

S p e c i e s c o m p o s i t i o n. In the Palearctic and Nearctic 334 modern species and subspecies. Also in the genus *Formica* 99 fossil species and subspecies were described, more than half of them (53) by Heer (1849, 1867) from the Miocene localities Oeningen, Germany and Radoboj, Croatia. However, subsequently 31 of them have been transferred to other genera or synonymized, so that this genus now contains 68 valid fossil species (Bolton et al., 2005): 23 from the Late Eocene, 10 from the Oligocene, and 42 from the Miocene.

R e m a r k s. In fact, the number of fossil species is much lower. First, it still includes the Miocene species described by Heer, which are not yet synonymized. It is very unlikely that in one locality so many congeneric species occurred (34 in Radoboj and 18 in Oeningen). Most probably, after revision all these fossils will be ascribed to one or two species. Second, the status of the ten species of *Formica* from Baltic amber described before 1867 remains unclear: *F. gibbosa* Presl, *F. luteola* Presl, *F. macrognatha* Presl, *F. neorufibarbis* Presl, *F. nigra* Presl, *F. parvula* Presl, *F. trigona* Presl (Presl, 1822), *F. cordata* Holl, *F. quadrata* Holl (Holl, 1829), and *F. lucida* Giebel (Giebel, 1856). The types are lost, and the descriptions do not clarify the specific or even the generic position of the inclusions. Mayr (1867), relying on the original figures, assumed that *F. cordata* most probably belongs to the genus *Pheidole*, and *F. lucida* to the family Braconidae, ignoring all other descriptions. Subsequently these species were likewise not mentioned among the species of *Formica* by other authors (Wheeler, 1915; Dlussky, 1967, 1997;

Burnham, 1978). All these species should be treated as Formicidae incertae sedis.

Up to the present the oldest record of *Formica* was from the Late Eocene: Baltic amber and Bagshot Beds, Great Britain, from where *Formica heteroptera* Cockerell, 1920 was described based on a forewing. However, according to our unpublished data, compression fossils belonging to this genus are present in the deposits of Messel and Eckfeld, Germany dated Middle Eocene. Including the species described below, now the fauna of Baltic and other Late Eocene ambers includes nine species.

Formica flori Mayr, 1868

Formica flori: Mayr, 1868, p. 48, pl. II, figs. 35–37 (worker, female, male) (part.); Dalla Torre, 1893, p. 196; André, 1895, p. 82; Wheeler, 1915, pp. 124–125 (part.); Burnham, 1978, p. 115; Ponomarenko and Schultz, 1988, p. 24; Baroni Urbani and Graeser, 1987, p. 1; Bolton, 1995, p. 195; Dlussky and Perkovski, 2002, p. 11; Dlussky, 2002, pp. 2–5, figs. 1–9; Dlussky and Rasnitsyn, 2007, p. 132, fig. 5(9); Perkovski et al., 2007, p. 240.

Formica antiqua Dlussky: Dlussky, 1967, p. 82, figs. 1b, 1c (worker); 1997, p. 59, fig. 3a; Bolton, 1995, p. 191.

Formica baltica Dlussky: Dlussky, 1967, p. 81, fig. 1a (worker); 1997, p. 59; Bolton, 1995, p. 191.

Formica parvula Dlussky: Dlussky, 1967, p. 83, figs. 1d–1f (male); 1997, p. 59; Bolton, 1995, p. 200.

Lectotype (designated: Dlussky, 2002). NHMW, no. 1984/31/210, worker with the label "ST *Formica flori* MAYR, 1868. Eozän, Baltischer Bernstein, Kollektion HANDLIRSCH, Syntypus zu MAYR 1868: 48"; Baltic amber; Late Eocene.

Remarks. So far as this species was recently redescribed in detail (Dlussky, 2002), here I give only a drawing of the lectotype (Fig. 3a). In the same paper synonymy of *F. flori* and *F. gustawi* was established.

F. flori is one of the most abundant species in all Late Eocene ambers. Mayr (1868) described this species from Baltic amber based on 180 specimens. Later André (1895) studied 99 specimens, and Wheeler (1915) studied 1022 specimens, 8.75% of the total of 11678 ant inclusions that he studied. According to our data, this species is also common in Bitterfeld, Rovno, and Scandinavian ambers. All other *Formica* species are rare and are represented in collections by a few specimens.

Material. Baltic amber, 271 specimens (245 workers, 24 males, 2 females), including lectotype and paralectotypes of *F. flori* NHMW, nos. 1847-IX-17, 1865-X-940, 1984/31/196, 1984/31/198 (♂), 1984/31/199 (♂), 1984/31/202, 1984/31/203, 1984/31/205, 1984/31/207 (♂), 1984/31/209, 1984/31/211a and GZG.BST, nos. 04218 (3725.IV.73), 04219 (21.IV.6), 04220 (3772IV120), 05037 (3719.IV.67), holotype of *F. baltica* PIN, no. 364/407, paratype of same species PIN, no.364/366, holotype of *F. antiqua* PIN, no. 364/419, holotype of *F. parvula* PIN, no. 364/414 (♂). Bitterfeld amber, 43 specimens (40 workers, 3 males). Rovno amber, 19 specimens (18 workers, 1 male). Scandinavian amber, 8 specimens (workers).

Formica gustawi Dlussky, 2002

Formica flori: Mayr, 1868, p. 48 (part.); Wheeler, 1915, pp. 124–125 (part.); Dlussky, 1967, p. 80; Ponomarenko and Schultz, 1988, p. 24 (part.).

Formica gustawi: Dlussky, 2002, p. 5, figs. 10–17 (worker, male); Dlussky and Perkovski, 2002, p. 12; Dlussky and Rasnitsyn, 2007, p. 132.

Holotype. NHMW, no.1984/31/204, worker (syntype of *F. flori*); Baltic amber; Late Eocene.

Remarks. So far as this species was recently described in detail (Dlussky, 2002), here I give only a drawing of the holotype (Fig. 3b). In the original description it was erroneously stated that this species possesses 5-segmented maxillary palps.

Mayr (1868) and Wheeler (1915) did not discriminate this species from *F. flori.* Of 24 syntypes of *F. flori* examined by myself, 15 certainly belong to this species and three to *F. gustawi* (one belongs to *Pseudolasius boreus* Wheeler, and the remaining ones are too poorly preserved to identify the species). Of 84 specimens in the collection of GZG.BST identified by Wheeler as *F. flori*, 81 specimens belong to this species and three belong to *F. gustawi.*

Material. Baltic amber: holotype, paratypes: NHMW, nos. 1984/31/197 (♂), 1984/31/208 (worker) (syntypes of *F. flori*), PIN, nos. 364/739 (3 workers), 964/430 (worker); specimen PIN, no. 964/503 (3 ♂); specimen BMNH, In. 18837 (worker, Klebs coll.); specimens ZMUC, nos. 171 (♂, Danzig, D. Jacobsen, 24.03.1916), 177 (♂, Danzig and D. Jacobsen, 24.03.1916); specimens GZG.BST, nos. 03828 (K1095), 03910 (K774), 03943 (?78), 04015 (K5099), 04229 (G1825), 04437 (?242) (workers), 04443 (K5171), 04452 (K923), 04454 (B18945) (♂♂). Bitterfeld amber: specimens MKC, nos. F-68, F-75 (workers); HM, no. 10/214 (worker). Rovno amber: specimens IZANU, nos. K-695, K-2638, K-3504, UA-1255 (workers). Scandinavian amber: specimen ZMUC, 162 (worker, Min. Mus., Rubjerg Knude and F. Hansen, 1912-253).

Formica horrida Wheeler, 1915

Formica horrida: Wheeler, 1915, pp. 125–126, fig. 59; Dlussky, 1967, p. 80; 1997, p. 59; Burnham, 1978, p. 115; Bolton, 1995, p. 196.

The species was described from Baltic amber based on two specimens preserved in one piece of amber and kept in the collection of Geologische Institut, Königsberg. This species is not found in the collections studied.

Formica kutscheri Dlussky, sp. nov.

Etymology. In honor of the paleoentomologist M. Kutscher, in whose collection the species was found.

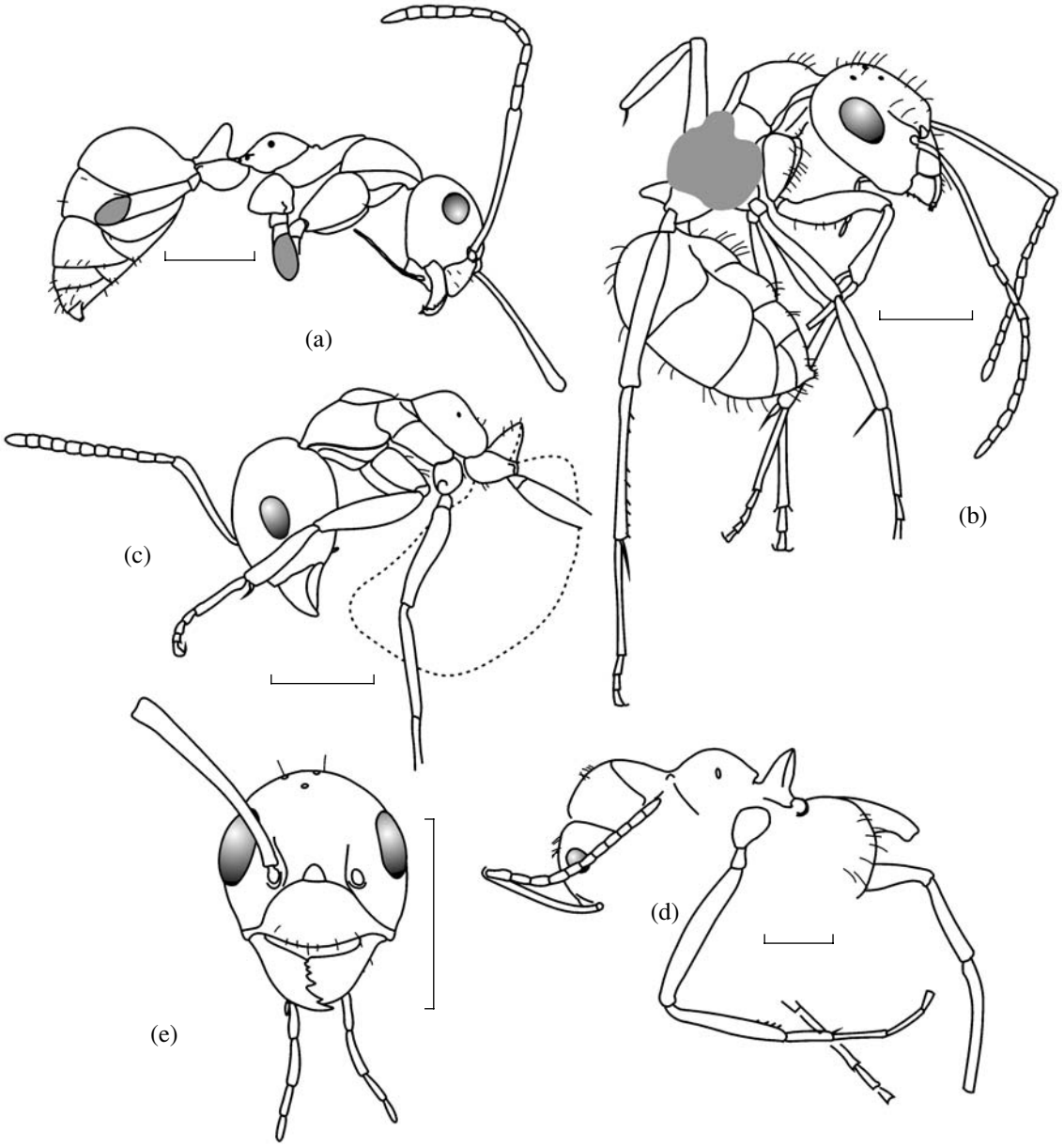

Fig. 3. Species of the genera *Formica* L. and *Protoformica* Dlussky: (a) *Formica flori* Mayr, specimen HM, no. 7/258, Bitterfeld amber; (b) *F. gustawi* Dlussky, holotype NHMW, no. 1984/31/204, Baltic amber; (c) *F. phaethusa* Wheeler, neotype PIN, no. 964/412, Baltic amber; (d) *F. strangulata* Wheeler, holotype GZG.BST, no. 04162, Baltic amber; (e) *Protoformica proformicoides* Dlussky, specimen ZMUC, no. 167, Scandinavian amber.

Holotype. MKC, no. F-67, worker; Bitterfeld amber; Late Eocene.

Description (Figs. 4a, 4b). Worker. Body slender. Head length greater than width. Occipital margin slightly convex. Clypeus with median carina and rounded anterior margin. Eyes large. Frontal carinae diverging, reaching lower margin of eyes. Scape projecting beyond occipital margin of head. Funicle segments elongate, at least twice as long as wide. Mandible with five large teeth, apical one only slightly longer than preapical. Maxillary palps long, apparently 6-segmented. Mesosoma slender, narrowed in middle part. Shape of propodeum not visible. Legs comparatively long. Scale comparatively small, narrow, with upper margin rounded. Body shining, very delicately, superficially shagreened. Frontal area of same structure as surrounding parts of head. Entire body (including scape and legs) in numerous long and short (semi)erect hairs. Eyes bare.

Measurements (mm): holotype: mesosoma length, 1.4; head length, 0.9; head width, 0.75; scape length, 0.9; maximal eye diameter, 0.26; paratype:

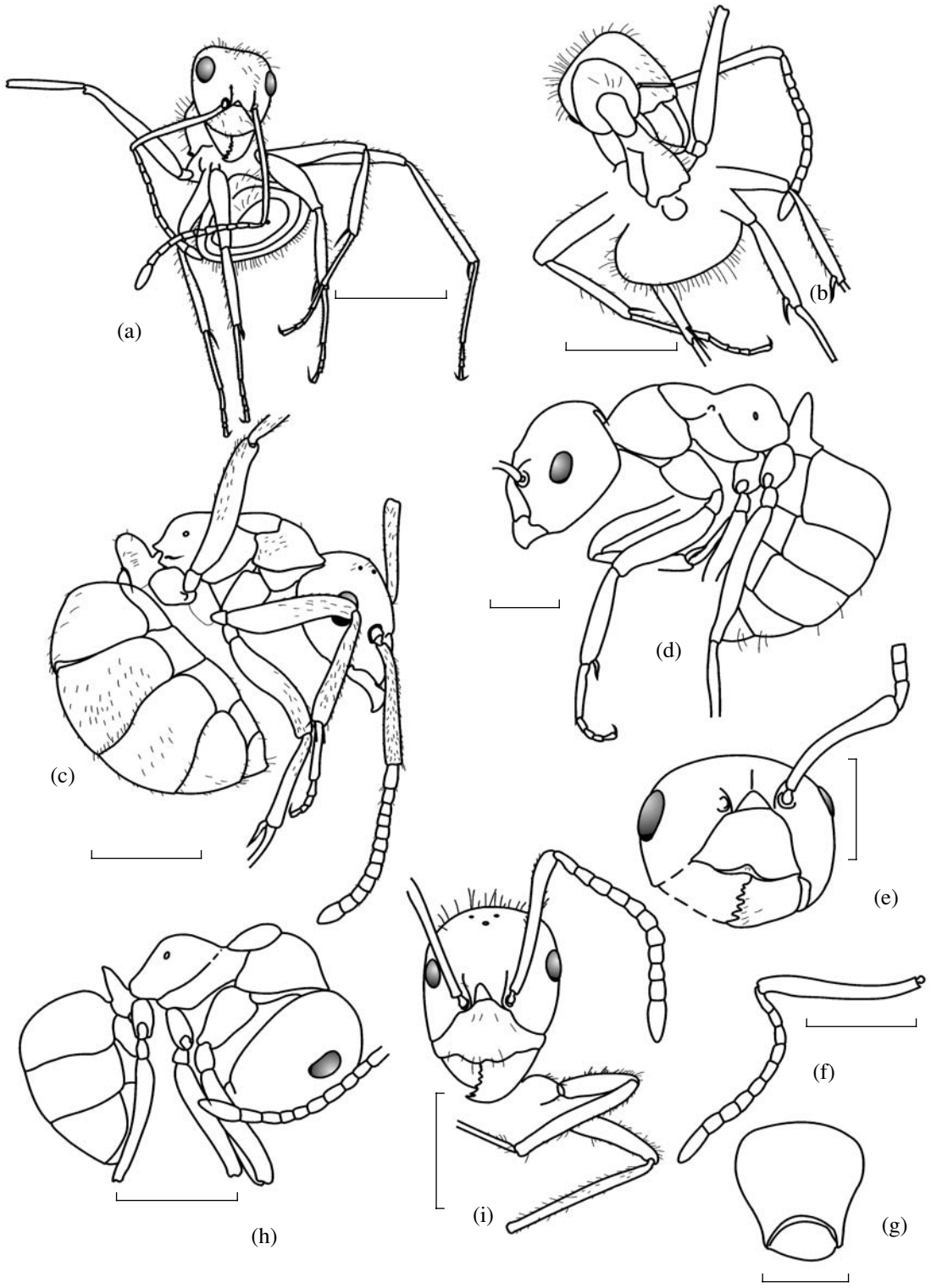

Fig. 4. New species of the genus *Formica* L.: (a, b) *F. kutscheri* sp. nov., holotype MKC, no. F-067 in different views, Bitterfeld amber; (c) *F. palaeopolonica* sp. nov., holotype MZ, no. 15690, Baltic amber; (d–g) *F. radchenkoi* sp. nov., holotype IZANU, no. K-3114, Rovno amber: (d) body in profile, (e) head in anterior view, (f) antenna, (g) scale in posterior view; (h, i) *F. zherikhini* sp. nov., holotype PIN, no. 964/415 in different views (in Fig. 5h chaetotaxy not shown), Baltic amber. Scale bar in Fig. 4g corresponds to 0.5 mm, on the others, to 1 mm.

mesosoma length, 1.7; head width, 0.8; scape length, 1.2.

Comparison. Similar to *F. horrida*, differing in the following characters: thorax comparatively narrower, head larger and limbs longer; anterior margin of clypeus rounded (angulate in *F. horrida*); scape of structure usual for *Formica*, curved at base (straight even at the base in *F. horrida*); erect hairs arranged chaotically, some of them long and curved, some short and straight (according to Wheeler's figure, in *F. horrida* the hairs are straight, of equal length, and evenly spaced).

Material. Holotype and paratype HM, no. 10/210 (Bitterfeld amber).

Formica phaethusa Wheeler, 1915

Formica phaethusa: Wheeler, 1915, pp. 126–127, fig. 60, worker; Dlussky, 1967, p. 80; 1997, p. 59; Burnham, 1978, p. 115; Bolton, 1995, p. 201.

Formica clymene: Wheeler, 1915, pp. 127–128 (worker); Dlussky, 1967, p. 80; 1997, p. 59; Burnham, 1978, p. 115; Bolton, 1995, p. 193. Syn. nov.

Neotype (designated here for stability of nomenclature). PIN, no. 964/412, worker fully corresponding to description and figure by Wheeler and differing only in somewhat smaller size; Baltic amber; Late Eocene.

Description (Fig. 3c). Worker. Body compact. Head length somewhat greater than width. Occipital margin straight or slightly concave. Clypeus with median carina and rounded anterior margin. Eyes of moderate size, oval, slightly convex. Scape somewhat projecting beyond occipital margin of head. 1st–3rd funicle segments about twice, 4th–6th 1.5 times as long as wide. Apical tooth of mandible much longer than preapical. Maxillary palps 5-segmented, short, not or hardly reaching the point midway between mouth and occipital foramen. Pronotum and mesonotum in profile convex, with distinct depression between them. Dorsal and posterior surfaces of propodeum in profile forming strongly rounded obtuse angle, dorsal surface convex, posterior straight or slightly concave. Propodeal spiracles short-oval. Scale wide, its anterior surface convex, posterior flat, upper margin ridged with slight depression in the middle. Entire body rather coarsely, superficially shagreened, was apparently dull in life. Frontal area of same structure as surrounding parts of head. Head with several pairs of erect hairs on clypeus, one to three pairs on frons, and one or two on vertex near ocelli. Mesosoma and scale usually with a few erect hairs. Scape and tibiae without erect hairs. Eyes without erect hairs.

Measurements (mm): neotype: body length, about 6; mesosoma length, 1.75; head length, 1.55; scape length, 1.07; maximal eye diameter, 0.37; specimen HM, no. 7/223: mesosoma length, 2.5; head length, about 1.75; head width, 1.65.

Remarks. Wheeler (1915) described *F. phaethusa* based on two, and *F. clymene*, on one worker from Baltic amber. All these specimens are lost. According to descriptions by Wheeler, these species differ in minor quantitative characters, which fit within the range of intraspecific variation of modern *Formica.* One cannot exclude the possibility that there were other differences, but so far as the types of both species are lost, it is impossible to prove this. Therefore I propose to consider *F. clymene* a junior synonym of *F. phaethusa.*

Material. Baltic amber: PIN, no. 964/412 (three workers, including neotype). Bitterfeld amber: specimens HM, nos. 7/223a, 7/223b, 7/254, 12/210.

Formica palaeopolonica Dlussky, sp. nov.

Etymology. From the Latinized Greek *palaios* (ancient) and Poland.

Holotype. MZ, no. 15690, worker; Baltic amber; Late Eocene.

Description (Fig. 4c). Worker. Body compact. Head length somewhat greater than width. Occipital margin feebly concave. Clypeus with rounded anterior margin. Eyes rather small, oval, feebly convex. Scape somewhat projecting beyond occipital margin of head, about as long as head. Funicle segments comparatively short, first about twice as long as, others, except terminal one, only slightly longer than wide. Mandible with five large teeth, apical tooth much longer than preapical. Maxillary palps 5-segmented, short, not or hardly reaching the point midway between mouth and occipital foramen. Pronotum convex in profile. Mesonotum with flat dorsal surface, smoothly rounded anteriorly, separated from pronotum by distinct promesonotal depression. Mesopleural suture absent. Propodeum in profile angulate, with strongly rounded angle, slightly convex dorsal surface shorter than nearly flat posterior one; mesopropodeal depression shallow and wide. Propodeal spiracles rounded. Scale thick, in profile its anterior surface convex, posterior nearly flat, upper margin not ridged, smoothly rounded. Entire body coarsely shagreened, was apparently dull in life. Long, stiff curved hairs only at anterior margin of clypeus. Additionally, there are very short, thin, semierect or erect hairs nearly indistinguishable from hairs of decumbent pubescence: on frons (one pair in holotype) and near ocelli, few on mesosoma (usually one or two pairs on pronotum), usually several pairs on petiole, quite numerous over entire surface of gastral tergites. Scape and tibiae with numerous semierect hairs. Apart from semierect hairs, there is decumbent pubescence of shorter hairs tightly adpressed to the body; on pronotum these hairs are several times longer, on gaster at most twice as long as spaces between them.

Measurements (mm): holotype: mesosoma length, 1.6; head length, 1.05; scape length, 1.05; hind femur length, 1.45; paratype MZ, no. 16478: mesosoma length, 1.45; head length, 1.0; maximal eye diameter, 0.25; scape length, 1.0; hind femur length, 1.1; paratype MZ, no. 19392a: mesosoma length, 1.55;

paratype MZ, no. 19392b: mesosoma length, 1.4; head length, 1.0; maximal eye diameter, 0.30; hind femur length, 1.3; paratype MZ, no. 20238: mesosoma length, 1.3, head length, 1.1.

Comparison. From *F. phaethusa* that also possesses shortened 5-segmented maxillary palps distinct in the presence of semierect hairs on the scape and legs and in the flattened dorsal surface of propodeum.

Remarks. In habitus, especially in profile, this species is similar to the modern *Alloformica.* The presence of a long apical tooth in the mandible and comparatively short funicle segments in the antenna are characteristic of this genus and *Proformica*, but not of *Formica.* However, because of the head shape (in *Alloformica* head without occipital angles, smoothly rounded behind eyes) and short 5-segmented maxillary palps this species must be placed in the genus *Formica*.

Material. Holotype and paratypes MZ, nos. 16478, 19392a, 19392b, 20238 (Baltic amber).

Formica strangulata Wheeler, 1915

Formica strangulata: Wheeler, 1915, pp. 130–131, fig. 62 (worker); Dlussky, 1967, p. 80; 1997, p. 59; Burnham, 1978, p. 115; Bolton, 1995, p. 204.

Holotype. GZG.BST, no. 04162 (G.5019), worker; Baltic amber; Late Eocene.

Description (Fig. 3d). Worker. Head with slightly convex sides and occipital margin, its length somewhat greater than width. Clypeus with median carina and rounded anterior margin. Eyes large. Frontal carinae diverging, slightly not reaching the middle of eyes. Scape projecting beyond occipital margin of head, longer than head. Funicle segments elongate, first 2.7 times, 2nd and 3rd ones twice as long as wide. Molar edge of mandibles and labial palps not visible. Maxillary palps long, extended beyond occipital foramen, most probably 6-segmented. Pronotum and mesonotum in profile forming a single convex surface. Dorsal surfaces of promesonotum and propodeum in profile forming smooth concave line. Propodeum in profile smoothly rounded, without distinct dorsal and posterior surfaces. Scale comparatively thin, in profile its anterior surface strongly convex, posterior surface slightly convex, upper margin with distinct ridge and slight depression at the middle. Entire body very finely, superficially shagreened. Frontal area of same structure as surrounding parts of head. Erect and semierect hairs comparatively thick and stiff. Head with several pairs of such hairs on clypeus, frons, and vertex near ocelli. On mesosoma, erect hairs only on pronotum. Scale without erect hairs. First gastral tergite with row of hairs along hind margin and about ten hairs in middle part of tergite, its anterior surface without erect hairs. Other tergites with hair rows along hind margin and few hairs in middle part. Scape and legs without erect hairs, only with short thick setae at apices of scape and femora and on inner surface of femora. Decumbent pubescence not visible.

Measurements (mm): mesosoma length, 2.8; hind femur length, 2.4; scape length, 1.8.

Remarks. Wheeler (1915) diagnosed this species on account of the unusual shape of depression between the promesonotum and propodeum. The species is also clearly distinct from others in other characters, including a ridged scale and thick hairs of erect pubescence. Unfortunately, the holotype is considerably concealed by other inclusions, so that some structural details are not visible.

Material. Holotype.

Formica radchenkoi Dlussky, sp. nov.

Etymology. In honor of the myrmecologist A.G. Radchenko, who revealed the species in the collection of IZANU.

Holotype. IZANU, no. K-3114, excellently preserved worker; Rovno amber; Late Eocene.

Description (Figs. 4d–4g). Worker. Body compact. Head length somewhat greater than width. Occipital margin slightly concave. Clypeus with emarginate anterior margin and transverse depression clearly visible in profile. Eyes large. Frontal carinae diverging, reaching the middle of eyes. Frontal groove present. Scape projecting beyond occipital margin of head, slightly shorter than head. First funicle segment about twice, 2nd–4th ones 1.3 times as long as wide. Mandible with five large teeth, apical one only slightly longer than preapical. Maxillary palps reaching occipital foramen, apparently 6-segmented (only three last segments visible); segment length ratio IV:V:VI=0.30:0.18:0.13. Pronotum and mesonotum in profile form a single convex surface with hardly noticeable promesonotal depression. Dorsal and posterior surfaces of propodeum in profile forming strongly rounded right angle. Legs comparatively short and thick. Scale comparatively thick, its anterior surface strongly convex, posterior surface slightly convex, upper margin rounded, not ridged, smoothly rounded in posterior view. Body shining, sparsely punctured, inconspicuously, very finely, superficially sculptured. Frontal area of same structure as surrounding parts of head. Few erect hairs visible only on second and following gastral tergites. Scape and legs without erect hairs. Decumbent pubescence visible only on gaster, consisting of very short hairs, about as long as spaces between them.

Measurements (mm): mesosoma length, 2.7; head length, 2.05; scape length, 1.8; maximal eye diameter, 0.55; petiole width, 0.74.

Comparison. Among fossil species the emarginate anterior margin of clypeus is found only in *F. zherikhini* sp. nov. From the latter *F. radchenkoi* is easily distinguishable in the poorly developed erect pubescence.

Material. Holotype.

***Formica zherikhini* Dlussky, sp. nov.**

Etymology. In memory of the paleontologist V.V. Zherikhin.

Holotype. PIN, no. 964/415, worker; Baltic amber; Late Eocene.

Description (Figs. 4h, 4i). Worker. Head length somewhat greater than width. Occipital margin slightly convex. Clypeus without carina, with anterior margin emarginate medially. Eyes small, oval, slightly convex. Frontal carinae diverging, slightly extended beyond imaginary line connecting lower eye margins. Scape projecting beyond occipital margin of head, about as long as head width. Funicle segments elongate, first 2.5 times, 2nd–5th ones 1.5 times as long as wide. Mandible with six large teeth, apical one only slightly longer than preapical. Maxillary palps 5-segmented, short, not reaching the point midway between mouth and occipital foramen. Anterior margin of mesonotum in profile raised above pronotum, promesonotal depression distinct. In profile, dorsal and posterior surfaces of propodeum forming strongly rounded obtuse angle, dorsal surface slightly convex, posterior straight. Scale high, in profile its anterior and posterior surfaces convex and upper margin narrowly rounded, in posterior view its sides strongly convex and apex angulate. Entire body smooth and shining. Frontal area of same structure as surrounding parts of head. Upper side and occipital margin of head with numerous long erect hairs, sides and lower side of head with shorter semierect hairs. Mesosoma with erect hairs; in profile six to ten hairs visible on each segment. Scape and tibiae with numerous semierect hairs. Gaster with quite abundant erect hairs over entire surface of tergites and sternites. Eyes without erect hairs.

Measurements (mm): mesosoma length, 1.65; head length, 1.33; head width, 1.15; maximal eye diameter, 0.26; scape length, 1.25.

Comparison. This species is at first glance similar to *F. kutscheri*, but easily distinguishable from it in the short maxillary palps, emarginate anterior margin of clypeus, and shape of scale. From *F. radchenkoi* that also possesses emarginate clypeus, distinct in the abundant erect pubescence.

Material. Holotype.

Genus *Protoformica* Dlussky, 1967

Type species. *Formica* (Protoformica) *proformicoides* Dlussky, 1967.

Diagnosis. Workers. Head evenly rounded behind eyes, without distinct occipital angles. Eyes large, situated above middle of head sides, maximal eye diameter equal to gena length or somewhat greater. Ocelli forming obtuse triangle. Funicle segments (except for first and terminal) comparatively short and thick, but slightly longer than wide. Apical and preapical teeth of mandible elongated and partly fused, but apical almost twice as long as preapical one. Maxillary palps 6-segmented, fourth segment about 1.5 times as long as fifth. Psammophore absent. Propodeal spiracles short-oval. Petiole with wide scale widened upwards that is wider than petiole length.

Species composition. Type species.

Comparison. In habitus similar to small specimens of *Formica*, differing from them in the absence of occipital angles of head, peculiar structure of mandibles, and elongate fourth maxillary palpomere.

Remarks. Originally was described as a subgenus of *Formica*, but later raised to the generic status (Dlussky and Fedoseeva, 1988).

***Protoformica proformicoides* Dlussky, 1967**

Formica (Protoformica) proformicodes Dlussky: Dlussky, 1967, p. 85, text–fig. 2 (worker).

Protoformica proformicoides Dlussky: Dlussky, Fedoseeva, 1987, p. 77; Bolton, 1995, p. 369; Dlussky, 1997, p. 60.

Holotype. PIN, no. 364/371, worker; Baltic amber; Late Eocene.

Description (Fig. 3e). Worker. Head length somewhat greater than width. Clypeus with obscured median carina and smoothly rounded anterior margin. Frontal carinae diverging, reaching the middle of eyes. Scape projecting beyond occipital margin of head, 1.2 times as long as head. Funicle segments short and thickened, first 1.5 times as long as second and 2–2.5 times as long as wide, second and third ones of equal length but slightly longer than wide. Mandible with five large teeth. Maxillary palps reaching occipital foramen, fourth segment about 1.5 times as long as fifth, sixth subequal to fifth or slightly shorter. Promesonotal depression hardly traceable. Propodeum in profile smoothly rounded. Scale thick, its upper margin not ridged, rounded in posterior view. Entire body very finely, superficially shagreened. Mandibles with fine longitudinal grooves. Frontal area of same structure as surrounding parts of head. Head with erect hairs on frons (one pair), near ocelli (one or two pairs) and on clypeus. Mesosoma and scale in holotype without erect hairs, in specimen ZMUC, no. 167 two pairs of hairs on pronotum and one on upper margin of scale. Scape and legs without erect hairs. First and second gastral tergites with rows of hairs along hind margin and few hairs on remaining surface; anterior surface of first tergite without erect hairs. Last tergites and all sternites with quite numerous hairs over entire surface. Genae and sides of propodeum with very delicate decumbent pubescence, visible only at high magnification and appropriate light. On gaster decumbent hairs not visible.

Measurements (mm): holotype: mesosoma length, 1.5, head length, 1.05; head width, 0.96; specimen ZMUC, no. 167: mesosoma length, 1.375; head length, 0.875; head width, 0.8; scape length, 1.05; maximal eye diameter, 0.35.

Material. Holotype and specimen ZMUC, no. 167 from Scandinavian amber with the label "Borge Mortensen, 11.07.1960."

Key to identification of Formicini species from Late Eocene ambers of Europe based on workers

1. Petiole with scale that is wider than petiole length. Scape projecting no more than one-third beyond occipital margin of head 2

—Petiole differently shaped. Scape projecting more than one-third beyond occipital head margin 11

2. Head beyond eyes evenly rounded, without distinct occipital angles. Fourth maxillary palpomere 1.5 times as great as fifth. Body length about 4 mm . ……*Protoformica proformicoides* Dlussky

—Head with distinct occipital angles. Fourth maxillary palpomere less than 1.5 times as great as fifth ... 3

3. Scape and tibiae with erect and/or semierect hairs..... 4

—Scape and tibiae without erect and/or semierect hairs..... 7

4. Scape straight, not curved even at base. Anterior margin of clypeus angulate. Body length 3.5–4.5 mm ..... *Formica horrida* Wheeler

—Scape curved at base..... 5

5. Anterior margin of clypeus emarginate. Maxillary palps short, 5-segmented, not reaching the point midway between mouth and occipital foramen. Body length 5 mm .....*F. zherikhini* sp. nov.

—Anterior margin of clypeus rounded..... 6

6. Maxillary palps 5-segmented, not reaching the point midway between mouth and occipital foramen. Body compact. Occipital margin of head slightly concave. Apical tooth of mandible much longer than others. Body length 4.5–7 mm .....*F. palaeopolonica* sp. nov.

—Maxillary palps 6-segmented, reaching occipital foramen. Body slender. Occipital margin of head slightly convex. Apical tooth of mandible only slightly longer than others. Body length 3.5–4 mm .....*F. kutscheri* sp. nov.

7. Anterior margin of clypeus emarginate. Occipital margin of head slightly concave. Maxillary palps 6-segmented, reaching occipital foramen. Scale without ridge along upper margin. Body length 8 mm .....*F. radchenkoi* sp. nov.

—Anterior margin of clypeus not emarginate, rounded or angulate 8

8. Body compact; superficially similar to extant species of *F. rufa* group. Scape shorter than head length. Apical tooth of mandible much longer than others. Maxillary palps 5-segmented, reaching only the point midway between mouth and occipital foramen. Occipital margin of head slightly concave or straight. Anterior margin of clypeus rounded. Scale with ridge along upper margin. Body length 6–10 mm ..... *F. phaethusa* Wheeler

—Body more slender. Scape longer than head. Apical tooth of mandible only slightly longer than preapical one. Maxillary palps 6-segmented, reaching occipital foramen. Occipital margin of head slightly convex 9

9. Scale with ridge along upper margin. Anterior margin of clypeus rounded. Body length 7 mm ..... *F. strangulata* Wheeler

—Scale without ridge, its upper margin rounded in profile. Anterior margin of clypeus usually angulate 10

10. Decumbent pubescence on gaster sparse: decumbent hairs not longer than spaces between them. Anterior surface of first tergite without erect hairs. Body length 5–7 mm..... *F. flori* Mayr

—Decumbent pubescence on gaster dense: decumbent hairs several times as long as spaces between them. In some workers anterior surface of first tergite with erect hairs. Body length 6–8 mm..... *F. gustawi* Dlussky

11. Petiole conical, pointed at apex. Head widened forwards, without distinct occipital angles, with convex occipital margin. Lower surface of head slightly concave in profile. Vertex with arched chitinous ridge. Ocelli absent. Fourth and fifth maxillary palpomeres of subequal length. Body length about 5 mm ..... *Conoformica bitterfeldiana* sp. nov.

—Petiole differently shaped. Head narrowed forwards, with distinct occipital angles. Vertex without arched chitinous ridge. Ocelli present. Fourth maxillary palpomere 1.5–2 times as long as fifth 12

12. Scape and tibiae with numerous erect and semierect hairs. Petiole with nodule and short anterior cylindrical part. Scape half projecting beyond occipital margin of head. Funicle segments 2–3 times as long as wide. Body length 6.5–10 mm ..... *Cataglyphoides constrictus* (Mayr)

—Scape and tibiae without erect or semierect hairs. Petiole with high, thick, and narrow scale. Scape projecting beyond occipital margin of head for less than one-half but more than one-third. Funicle segments 1.5–2 times as long as wide. Body length 7.5–8.5 mm.....*C. intermedius* sp. nov.

DISCUSSION

Wheeler (1915) believed that in Baltic amber the modern structure of the genus *Formica* had been already formed. In particular, he related *F. flori* to the modern species *F. fusca* Linnaeus, *F. horrida* to *F. cinerea* Mayr, and *F. phaethusa* and *F. clymene* to *F. rufa* Linnaeus. In fact, as probable ancestors of the modern *Formica* only *F. flori* and *F. gustawi* may be considered similar to the modern species of the *F. fusca* group, and *F. radchenkoi* possibly belongs to the *F. sanguinea* group. I have previously suggested (Dlussky,

1967) that *F. flori* is closer to *F. gagates* Latreille than to *F. fusca*,, an opinion which is supported by a recent paper of Baroni Urbani and Graeser (1987). These authors examined the body microsculpture of the *F. flori* inclusion under a scanning electron microscope and revealed that it is distinct from all recent *Formica.* The only species showing somewhat similar microsculpture is *F. gagates.*

F. horrida is similar to *F. cinerea* only in the presence of numerous erect hairs over the entire body surface. At the same time this species shows a peculiar structure of the scape, matched in no one modern congener. *F. phaethusa,* being similar in habitus to modern species of the *F. rufa* group, possesses shortened 5-segmented maxillary palps. Among modern species the palp reduction is only observed in the subgenus *Coptoformica,* to which this species clearly does not belong. Moreover, the most primitive species of this subgenus (*F. suecica* Adlerz, *F. exsecta* Nylander, *F. mesasiatica* Dlussky) show normal 6-segmented palps. In *F. palaeopolonica* and *F. phaethusa* the apical tooth of mandible is long and acute, much longer than preapical one. This feature is characteristic of *Alloformica, Cataglyphis* and *Proformica* (in modern *Formica* the apical tooth is only slightly longer than preapical), but maxillary palps in the members of these genera are never shortened as in *F. palaeopolonica* and *F. phaethusa.* Moreover, in the former species the funicle segments are shortened like in the modern species of *Proformica. F. zherikhini* is very similar to *F. sentschuensis* Ruzsky living in Tibet, but cannot be regarded as ancestral to this latter, because it has reduced maxillary palps. Therefore it becomes clear that *Formica* from Late Eocene ambers constitute quite an archaic group, and most of its species are not similar to living congeners.

Of great interest are the species of *Cataglyphoides. C. constrictus* and *C. intermedius* are not only similar in habitus to the modern *Cataglyphis,* but also possess the structure of mandibles and maxillary palps characteristic of the latter genus. However, they lack the characters of *Cataglyphis* that had arisen as adaptations to arid environments (macrosetae at anterior margin of clypeus and mentum forming psammophore, elongate propodeal spiracles, etc.). This genus is likely to be ancestral to *Cataglyphis.* The genus *Protoformica* in several characters is intermediate between the modern *Alloformica, Formica,* and *Proformica* and *Cataglyphis.* Their head structure is similar to *Alloformica,* maxillary palps, to primitive *Cataglyphis,* funicle, to *Proformica,* and mesosoma, to *Formica.* Their mandible structure is intermediate between *Formica,* usually having apical and preapical teeth only slightly enlarged, and other genera, that have the apical tooth much longer than others. The genus *Conoformica* has no analogues in the modern fauna.

Therefore, only a few members of the Late Eocene fauna of Formicini may be considered as ancestors of modern species. At the same time, they already possessed in different combinations those features which subsequently became the key characters of the extant genera of this tribe, except for adaptations to arid environments or social parasitism.

ACKNOWLEDGMENTS

The author is grateful to A.P. Rasnitsyn (PIN), E.E. Perkovski (IZANU), R. Kulicka (MZ), A. Ross (NHML), O. Schultz (NHMW), M. Reich (GZG), C. Gröhn (Glinde, Germany) and M. Kutscher (Sassnitz, Rügen, Germany) for opportunity to study and describe collections of ants from various ambers.

The study was supported by the Russian Foundation for Basic Research (project no. 05-04-49419).

REFERENCES

1. E. André, "Notice sur les fourmis fossiles de l'ambre de la Baltique et description de deux espèces nouvelles," Bull. Soc. Zool. Fr. **20**, 80–84 (1895).
2. C. Baroni Urbani and S. Graeser, "1987 REM-Analysen an einer pyritisierten Ameise aus baltischem Bernstein," Stuttg. Beitr. Naturk., Ser. B, No. 133, 1–16 (1987).
3. B. Bolton, *A New General Catalogue of the Ants of the World* (Harvard Univ. Press, London, 1995).
4. B. Bolton, "Synopsis and Classification of Formicidae," Mem. Am. Entomol. Inst. **71**, 1–370 (2003).
5. B. Bolton, G. Alpert, P. S. Ward, and P. Naskrecki, *Bolton's Catalogue of Ants of the World 1758–2005: CD Version* (Harward Univ. Press, London, 2005).
6. L. Burnham, "Survey of Social Insects in the Fossil Records," Psyche **89**, 85–133 (1978).
7. Dalla Torre C. G., *Catalogus Hymenopterorum, hucusque descriptorum systematicus et synonymicus. V. 7* (W. Engelmann, Leipzig, 1893).
8. G. M. Dlussky, "Ants of the Genus *Formica* from the Baltic Amber," Paleontol. Zh., No. 2, 80–89 (1967).
9. G. M. Dlussky, *Ants of Deserts* (Nauka, Moscow, 1981) [in Russian].
10. G. M. Dlussky, "Genera of Ants (Hymenoptera: Formicidae) from Baltic Amber," Paleontol. Zh., No. 6, 50–62 (1997) [Paleontol. J. **31** (6), 616–627 (1997)].
11. G. M. Dlussky, "Syntypes of the Baltic Amber Ants *Formica flori* Mayr and *Ponera atavia* Mayr (Hymenoptera: Formicidae)," Russ. Entomol. J. **11** (3), 291–298 (2002).
12. G. M. Dlussky and E. B. Fedoseeva, "The Origin and Early Stages in the Evolution of Ants (Hymenoptera, Formicidae)," in *The Cretaceous Biocenotic Crisis and Evolution of Insects* (Nauka, Moscow, 1988), pp. 70–144 [in Russian].
13. G. M. Dlussky and E. E. Perkovski, "Ants (Hymenoptera, Formicidae) from the Rovno Amber," Vestn. Zool. **36** (5), 3–20 (2002).
14. G. M. Dlussky and A. P. Rasnitsyn, "The Paleontological Record and Stages in the Evolution of Ants," Usp. Sovrem. Biol. **127** (2), 118–134 (2007).
15. C. G. Giebel, *Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere. Monographisch Dargestellt.*

Zweiter Band. Gliederthiere. Erste Abtheilung. Insecten und Spinnen (Brockhaus, Leipzig, 1856).

16. A. Handlirsch, *Die fossilen Insekten und Phylogenie der rezenten Formen* (W. Engelmann, Leipzig, 1906–1908).
17. O. Heer, *Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Zweiter Theil: Heuschrecken, Florfliegen, Aderflüger, Schmetterlinge und Fliegen* (W. Engelmann, Leipzig, 1849).
18. O. Heer, "Fossile Hymenopteren aus Oeningen und Radoboj," Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. **22**, 1–42 (1867).
19. F. Holl, *Handbuch der Petrefactenkunde. Bd. 2* (P. O. Hilschersche Buchhandlung, Dresden, 1829), pp. 117–232.
20. G. L. Mayr, "Vorläufige Studien über die Radoboj-Formiciden, in der Sammlung der geologischen Reichsanstalt," Jb. geol. Reichsan. Wien **17**, 47–62 (1867).
21. G. L. Mayr, "Die Ameisen des Baltischen Bernstein," Beitr. Naturk. Preuss. Königsberg **1**, 1–102 (1868).
22. E. E. Perkovski, A. P. Rasnitsyn, A. P. Vlaskin, and M. V. Taraschuk, "A Comparative Analysis of the Baltic and Rovno Amber Arthropod Faunas: Representative Samples," Afr. Invertebr. **48** (1), 229–245 (2007).
23. A. G. Ponomarenko and O. Schultz, "Typen der geologisch-paläontologischen Abteilung: Fossile Insekten," Kataloge wiss. Sammlung Naturhist. Museums in Wien, Paläozoologie **6** (1), 1–30 (1988).
24. J. S. Presl, "Additamenta ad faunam protogaem, sistens descriptiones aliquat animalium in succino inclusorum," in *Deliciae Pragenses, historiam naturalem spectantes, V. 1,* Ed. by J.S. Presl and K.B. Presl (Calvae, Pragae, 1822), pp. 191–210.
25. W. M. Wheeler, "The Ants of the Baltic Amber," Schrift. phys.-ökon. Ges. Königsberg **55**, 1–142 (1915).