

The Ant *Aphaenogaster dluskyana* sp. nov. (Hymenoptera, Formicidae) from the Sakhalin Amber—the Earliest Described Species of an Extant Genus of Myrmicinae

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Abstract—The earliest member of an extant ant genus of the subfamily Myrmicinae, *Aphaenogaster dluskyana* sp. nov., from the Sakhalin amber (Russia, Middle Eocene, 43–47 Ma) is described. Fossil representatives of the genus *Aphaenogaster* are critically analyzed and it is proposed to transfer many of these to the fossil morphotaxon *Paraphaenogaster*. The morphology, distribution, and possible evolutionary trends of the genus *Aphaenogaster* are reviewed and it is suggested that this genus appeared in the territory currently occupied by the Palearctic not later than the Early Eocene (over 50 Ma). *Aphaenogaster dluskyana* can be considered the oldest described representative of an extant genus of the subfamily Myrmicinae, although earlier, as yet undescribed, records of extant genera of Myrmicinae belong to the Early Eocene.

Keywords: Myrmicinae, *Aphaenogaster*, *Paraphaenogaster*, ants, paleontology, taxonomy, evolution, Middle Eocene, Sakhalin amber

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INTRODUCTION

In 1972 a team from the Paleontological Institute of the USSR Academy of Sciences collected large material from amber deposits in the vicinity of the village of Starodubskoe on the eastern coast of southern Sakhalin Island, which included 838 insect specimens (Zherikhin, 1978). These included ten ants (1.2% of the total number of insects), based on which Dlussky (1988) described five extinct genera and seven species, assigned to the extant subfamilies Ponerinae (*Protopone* Dlussky), Aneuretinae (*Aneuretellus* Dlussky), Dolichoderinae (*Eotapinoma* Dlussky, *Zherichinius* Dlussky), and Formicinae (*Chimaeromyrma* Dlussky). It is interesting that representatives of the two genera of Dolichoderinae described from the Sakhalin amber were later found in the much older deposits of Alberta (Canada, Upper Cretaceous, Campanian, 78–79 Ma) (*Eotapinoma macalpinii* Dlussky) (Dlussky, 1999) and in a younger Late Eocene Bitterfeld (=Saxonian) amber (35–37 Ma) (as yet undescribed species of *Zherichinius*) (Dlussky and Rasnitsyn, 2009; Dubovikoff, 2012), whereas seven new species of the genus *Protopone* were described from the Middle Eocene (Lutetian) shale in Germany (Grube Messel, 47 Ma) (Dlussky and Wedmann, 2012).

The age of the Sakhalin amber was debated for a long time. Zherikhin (1978), based on indirect evidence, dated it over a wide range from Paleocene

(Danian, 56–59 Ma) to Middle Eocene (42–47 Ma). Dlussky (1988) tentatively dated this amber as Paleocene and in all subsequent publications on fossil ants, the Sakhalin amber was dated as Paleocene (Dlussky and Fedoseeva, 1988; Archibald et al., 2006; Dlussky and Rasnitsyn, 2007; Aria et al., 2011; Dubovikoff, 2012; LaPolla et al., 2013; and others). Eskov (2002) also accepted this dating. However, as early as the end of the 20th century, Kodrul (1999), based on geological and paleobotanical data, convincingly substantiated the Middle Eocene age of the Naibuchi Formation, in which the Sakhalin amber was found in situ (see also Baranov et al., 2015).

The age of the deposits of the Ventana Formation in Argentina, from which *Ameghinoia piatnizkyi* Viana et Haedo Rossi was described based on imprints (this species was later placed in the genus *Archymyrmex* Cockerell of the subfamily Myrmeciinae; see Dlussky and Perfilieva, 2003), has been debatable for many decades. Originally, these beds were dated as Late Eocene–Early Oligocene (Viana et al., 1957), but, later, these deposits were dated as Late Eocene (Rossi de Garcia, 1983), or were dated within a wide range from the Late Paleocene to Early Oligocene (Petrulevicius, 1999); Dlussky previously considered this species Paleocene (Dlussky and Fedoseeva, 1988). Finally, in the last decade, the Ventana Formation was dated as Middle Eocene (Early Lutetian, 47–48 Ma) (Wilf et al., 2005; Dlussky, 2012). Previously, the Ølst

Formation (Denmark) was dated Upper Paleocene–Lower Eocene (Dlussky and Rasnitsyn, 2007) with numerous remains of *Ypresiomyrma rebekkae* (Rust et Andersen), but now it is clear that these remains belong to the very beginning of the Ypresian (Lower Eocene, ca. 54 Ma) (Archibald et al., 2006).

Two imprints of ant wings were found in the Tadushi Formation previously assigned to the Paleocene (Sikhote-Alin, Russian Far East). They were previously assigned to unidentifiable taxa from the subfamily Formicinae (Dlussky and Fedoseeva, 1988; Dlussky and Rasnitsyn, 2007), but they were later placed in the morphotaxon *Leucotaphus* Donisthorpe (Dlussky and Perfilieva, 2014). The Tadushi Formation is currently dated as the end of the Early Eocene (about 50 Ma) (Makarkin, 2014); hence occurrences of Paleocene ants are currently limited to two unidentified incomplete imprints from the Pascapoo Formation (Alberta, Canada; Mitchell and Wighton, 1979).

MATERIAL AND METHODS

In 2012 one of us (EP) found in the collections of the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN) a small piece (less than 1 g) of amber collected in Starodubskoe in 1972 and containing an earliest known representative of an extant genus of Myrmicinae from the Sakhalin amber, which is described below as *Aphaenogaster dlusskyana* sp. nov.

Inclusion state. The Sakhalin amber experienced high temperatures and pressure after fossilization, resulting in deformation of the shape and proportions of various body parts of the included insects (Dlussky, 1988). This applies to the specimen of the species described below. In particular, the mesosoma is compressed strongly laterally, especially the mesothorax and propodeum, so the mesopleural cuticle has become fragmented and pulled upward and somewhat forward to form what appear to be small “horns,” which clearly were not present in the intact specimen; the propodeum evidently had been strongly elevated and rimmed laterally and dorsally with sharp keels. As a result of the compression, the anterior part of the pronotum was also elongated to form a long, thin “neck.” The gaster is compressed slightly dorsoventrally, so that it appears relatively flat. The shape of the waist and the propodeal spines were apparently only slightly changed. A photograph of the specimen is given below as well as a drawing based on this photograph and reconstructions of the body and its separate parts, aiming to show the original body shape of this species.

The photographs were taken using a Leica M165 stereomicroscope with a Leica DFC425a camera, while the drawings and reconstructions are based on the photographs and microscopic study of various body parts.

Not all morphological elements could be measured in the specimen studied; hence, measurements are only given for structures that could be measured (with the precision to 0.01 mm), in particular: (HL) head length from the top of the occipital margin to anterior margin of the clypeus; (HW) maximum head width behind the eyes; (SL) scape length in profile; (ML) length of the mesosoma in profile from the anterodorsal margin of the pronotum to the posterior margin of the propodeal lobes; (ED) maximum eye diameter; (MDL) mandible length; (MML) masticatory margin of mandible length; (HTL) hind tibia length; (PL) petiole length; (PH) petiole height; (PPL) postpetiole length; (PPH) postpetiole height; (PSL) propodeal spine length; (GL) gastral length. Ratios calculated based on the measurements are given below.

SYSTEMATIC PALEONTOLOGY

Subfamily Myrmicinae Lepeletier, 1835

Genus *Aphaenogaster* Mayr, 1853

Type species. *Aphaenogaster sardoa* Mayr, 1853.

Species composition. Altogether over 180 described species and about 45 infraspecific forms of *Aphaenogaster* (Bolton, 2014; Borowiec and Salata, 2014). The geographical range of this genus is interesting. The overwhelming majority of species (around 100) inhabit the western Palearctic, over 80 of these occur in the Mediterranean; four species with three subspecies are known from Madagascar; around ten species are found in Australia, six are in New Guinea, around 40 are in Central Asia, south of the eastern Palearctic, and in the Oriental Zoogeographic Realm, and fewer than 30 occur in America, from southern Canada to northern Columbia. *Aphaenogaster* is absent in sub-Saharan Africa (Fig. 1).

At present, about 20 fossil *Aphaenogaster* species are known, but some of these cannot be reliably assigned to this genus (see below).

Diagnosis. Worker monomorphic; body 4.5–7 mm long, from yellow to black, but bicolored species very rare. Head variously shaped, always longer than wide, rectangular, oval, in some species strongly elongated, without occipital corners, tapering posteriorly forming “collar”. Eyes well-developed, but not large, approximately at midpoint of lateral head margin, ocelli absent. Mandibles elongated triangular, not widened, masticatory margin with sharp (up to 10) teeth. Palp formula 5, 3. Antennae 12-segmented; scape gently bent at base, without angle, long or very long, always projecting beyond occipital margin, funiculus terminating in 4–5-segmented club, sometimes club absent. Frontal lobes partly covering antennal sockets. Frontal carinae straight or slightly curved. Anterior margin of clypeus convex, often notched in middle.

Mesosoma slender, often elongated; promesonotum convex; propodeum dorsally slightly flattened,



Fig. 1. Map of current distribution (gray shaded) of the genus *Aphaenogaster*, its fossil representatives (black dots), and the morphotaxon *Paraphaenogaster* (black squares).

lying clearly below promesonotum, with acute teeth or long spines, less commonly, angular. Petiole with well-developed, commonly long cylindrical part and rounded or conical node; postpetiole subspherical, without ventral tooth. Mesotibiae and metatibiae with relatively large simple spur. Body sculpture varying from almost completely absent (body smooth and shiny) to relatively coarsely rugose and punctate; gaster either smooth or densely sculptured. Standing hairs not abundant, decumbent pubescence sparse or absent.

Gynes (queens) larger than workers, body 7–9 mm long. Generally similar to workers (except for presence of ocelli and wings and mesosomal morphology). Scutum strongly convex, completely or almost completely covering prothorax.

Males essentially smaller than gynes, body 4.5–6 mm long, brown or black. Head relatively small, in many species compressed strongly dorsoventrally; eyes and ocelli large. Mandibles triangular, with well-developed masticatory margin and sharp teeth. Antennae 13-segmented (very rarely 12-segmented); scape short, antennal funiculus filamentous, without well-outlined club or with unclear 4–5-segmented club. Palp formula as in workers or gynes. Scutum without Mayrian furrows, convex, in many species very

strongly convex, domed; propodeum lying far below scutum level, usually with blunt tubercles. Forewings with closed cells *1r+2r*, *rm*, and *mcu*; sometimes, cell *3r* also closed, but in some species *rm* cell absent (see below). Legs long and slender, spurs as in workers.

Aphaenogaster dluskyana Radchenko et Perkovsky sp. nov.

E t y m o l o g y. In memory of the outstanding Russian myrmecologist Professor Gennady Mikhailovich Dlusky (1937–2014).

H o l o t y p e. PIN, no. 3387/172, worker; Sakhalin amber, Middle Eocene.

D e s c r i p t i o n (Figs. 2–5). Worker. The body is about 4.0 mm long. The head is elongated-rectangular, with very feebly convex sides, 1.3 times longer than wide; the occipital corners are distinct, narrowly rounded; the occipital margin is weakly convex. The frontal lobes are well developed, slightly raised, partly covering the antennal sockets; frontal carinae are straight. The anterior margin of the clypeus has a wide, but shallow notch. Eyes rather small, positioned approximately in the middle of the sides of the head. The antennae are 12-segmented; the scape is long, longer than the width of the head, projecting beyond the occipital margin approximately to a third of its

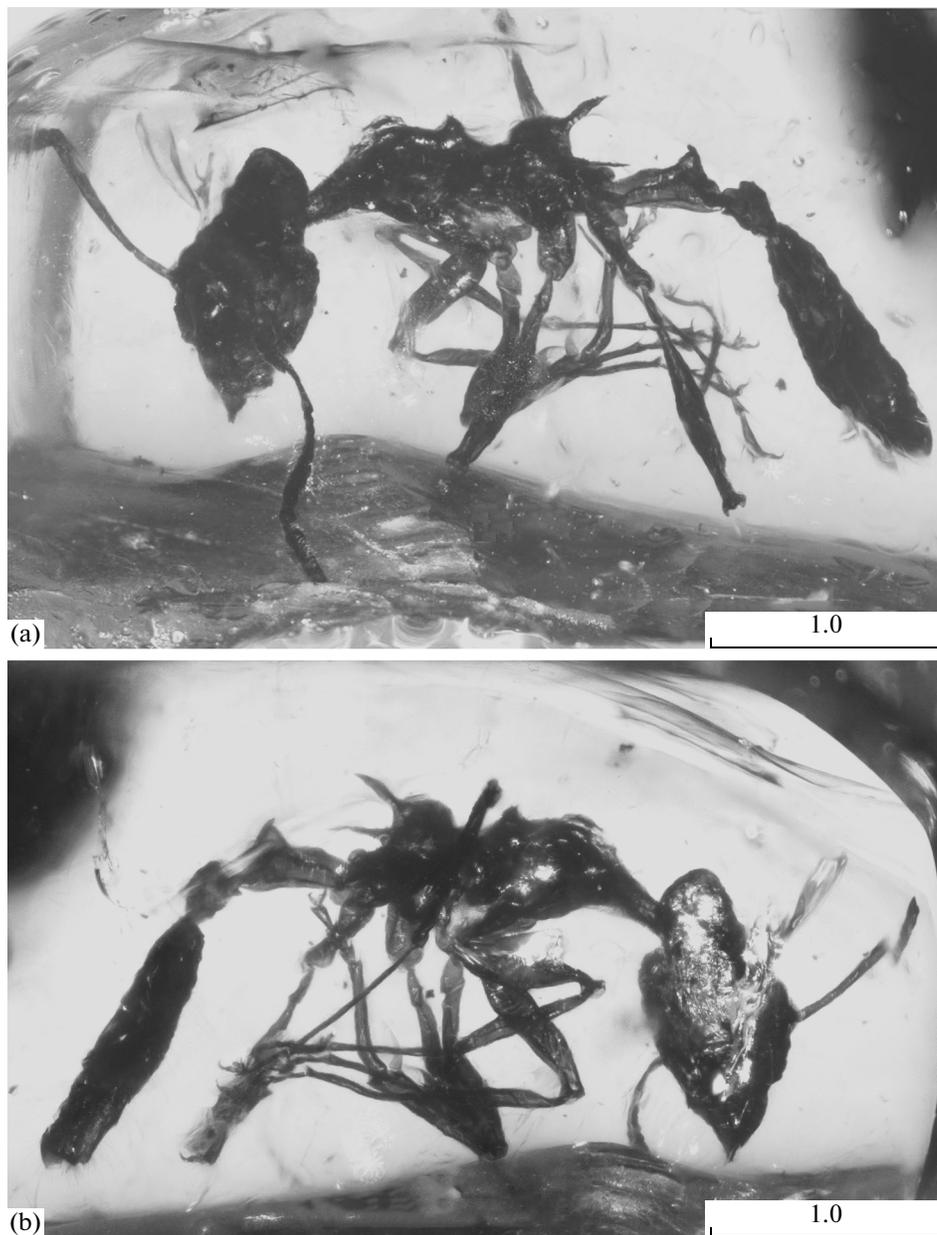


Fig. 2. Photograph of the holotype of *Aphaenogaster dluskyana* sp. nov.: (a) left and (b) right lateral views. Scale bars here and below in mm.

length. Segments of the funiculus are elongated; the club is 4-segmented (a more precise characterization of the length-to-width ratio of the funiculus segments is impossible, since they are deformed to varying extent). The palp formula is 5, 3. The mandibles are elongated triangular, their length equals the head width; the masticatory margin is long, 80% of the mandible length, with six sharp teeth, of which the apical is the largest.

The mesosoma is long and slender; the pronotum is convex; the metanotal groove is wide and deep; the propodeum is convex, with long, thin, straight, slightly divergent, not widened at the base

spines. The petiole is twice as long as high, with a long cylindrical part and a low node widely rounded at the top; the postpetiole is lower than the petiole, subspherical. The legs are long; the pro- and mesotibiae have a short, simple spur (possibly, the spurs in this specimen are poorly visible, but they appear to be shorter than in extant species of *Aphaenogaster*).

The head is smooth (at least the sculpture in the specimen studied is not visible), but the mesosoma has relatively coarse longitudinal rugae. The waist and gaster are smooth.

The occipital margin of the head, frons, and clypeus have numerous long standing hairs. The mesosoma,

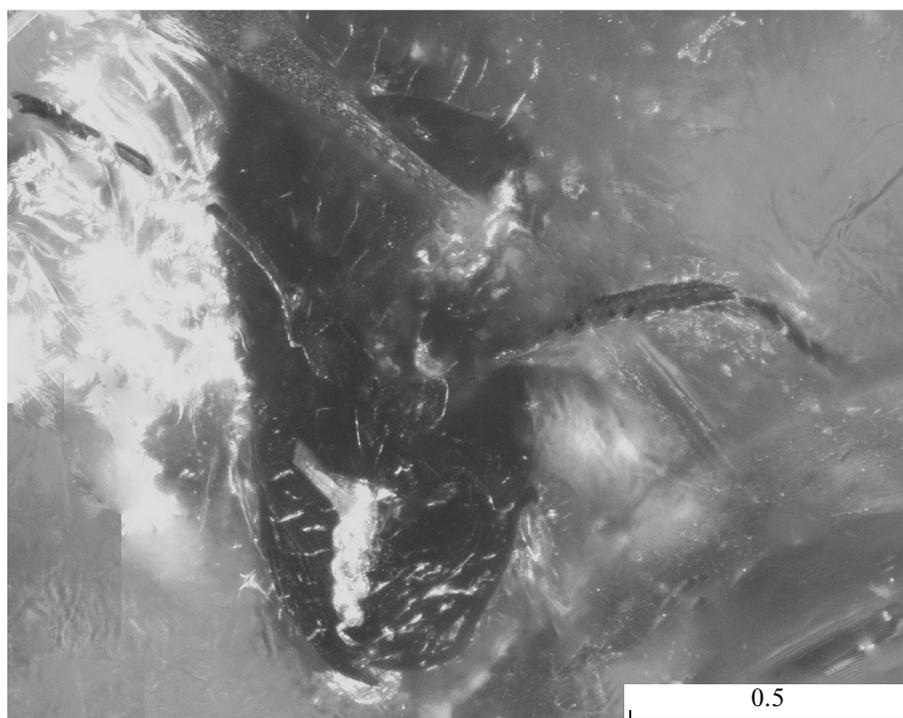


Fig. 3. Photograph of the head of the holotype of *Aphaenogaster dluskyana* sp. nov., dorsal view.

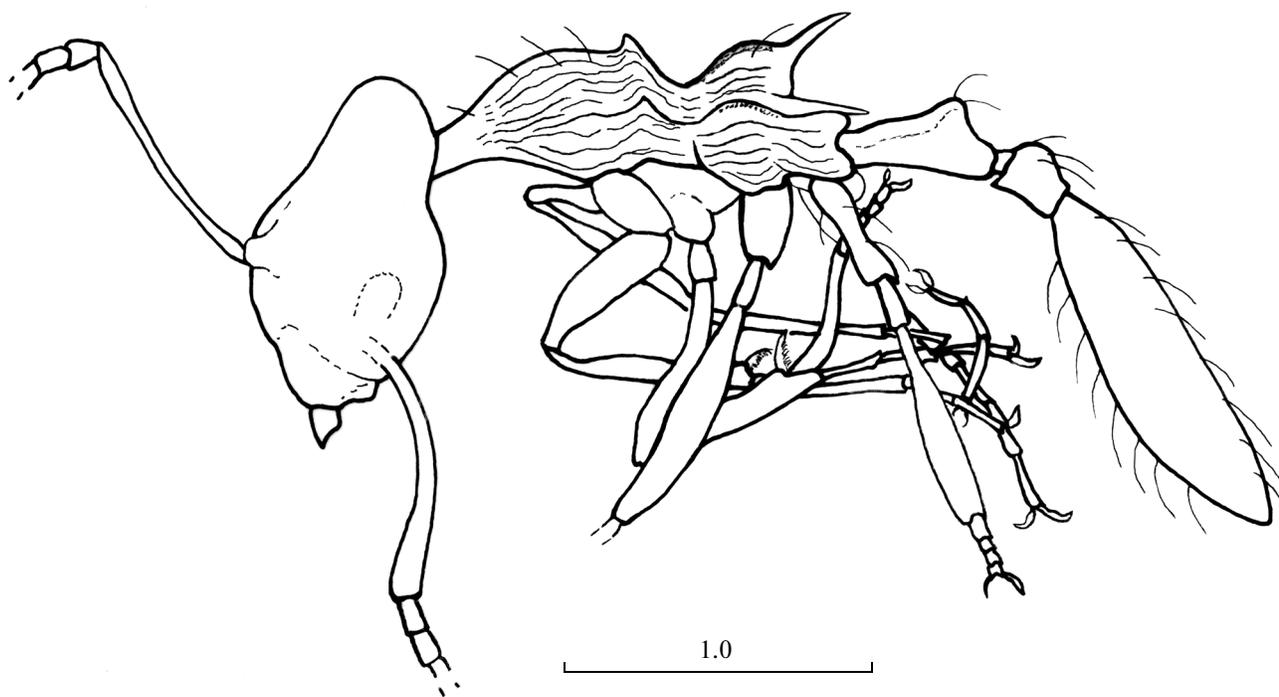


Fig. 4. Line drawing based on a photograph of the presumed original appearance of the holotype of *Aphaenogaster dluskyana* sp. nov., left lateral view.

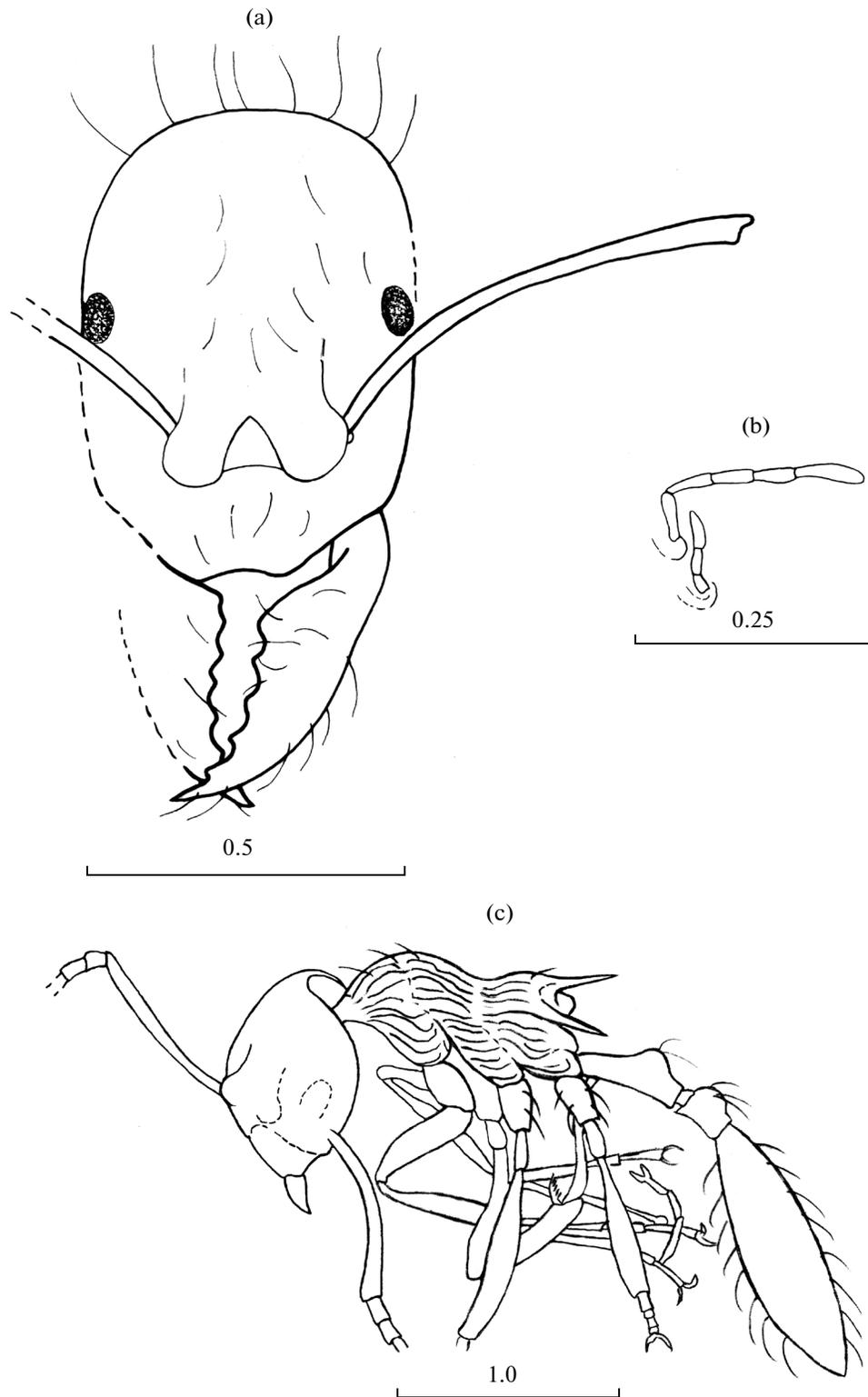


Fig. 5. Line drawings based on photographs of the head of the holotype *Aphaenogaster dluskyana* sp. nov.: (a) dorsal view, (b) of the maxillary and labial palps, (c) reconstruction of its body appearance, left lateral view.

waist, coxae, and gaster also have such hairs, which are especially numerous, long, and standing on the gastral sternites; tarsi have dense, short subdecumbent pilosity. The claws are simple.

M e a s u r e m e n t s in mm: HL = 0.77, HW = 0.59, SL = 0.64, ML = 1.24, ED = 0.17, MDL = 0.59, MML = 0.47, HTL = 0.78, PL = 0.48, PH = 0.23, PPL = 0.21, PPH = 0.20, PSL = 0.31, GL = 1.24. Indices: HL/HW = 1.31, SL/HL = 0.83, SL/HW = 1.09, ED/HL = 0.22, ED/HW = 0.29, PL/PH = 2.06, PL/PW = 0.82, PPL/PPH = 1.07, ML/HL = 0.76, ML/HW = 1.00, MML/MDL = 0.80, PSL/HL = 0.41, HTL/HL = 1.02, HTL/HW = 1.33.

C o m p a r i s o n. This species differs from all known species of *Aphaenogaster* from the Late Eocene amber of Europe and the Upper Eocene deposits of the United States in the long spines of the propodeum, and from *A. amphioceanica* Andrade, 1995 from the Dominican amber (Middle Miocene) – in the shape of the head (in the latter species it is strongly elongated, without occipital corners, and forms a “collar” posteriorly). This species is distinguished from *A. praerelicta* Andrade, 1995 from the Mexican amber (Middle Miocene) by the propodeal spines not widening at the base, narrowly rounded occipital corners, widely rounded node of the petiole, and also by the smaller size (body length of *A. dluskyana* is about 4 mm, and over 6 mm in *A. praerelicta*); furthermore, *A. praerelicta* has teeth on the pronotum.

R e m a r k s. Based on all visible characters, the specimen of the new species is assigned to the genus *Aphaenogaster*; particular characters include the habitus, the morphology of the head, mesosoma, petiole, antennae, legs, and even the palp formula. We were not able to find any structures that would allow the assignment of this species to any other extant or fossil genera of Myrmicinae; nor could we justify the recognition of a new extinct genus.

M a t e r i a l. Holotype.

DISCUSSION

Members of some extant ant subfamilies are known from the Upper Cretaceous, beginning from the end of the Turonian (92 Ma) (see reviews in Dlussky and Rasnitsyn, 2007; LaPolla et al., 2013, and literature cited therein), but the earliest records of extant genera are considerably younger and dated Early Eocene (53 Ma).

These are *Platythyrea* Roger (Ponerinae), *Gesomyrmex* Mayr (Formicinae), *Tetraponera* F. Smith (Pseudomyrmecinae), and another four extant genera including as yet undescribed new species from the Oise amber (France); altogether 40 “morphotypes” (species?) are tentatively accounted for, from the above subfamilies and also Dolichoderinae, Myrmecinae, and Myrmicinae (Aria et al., 2011; LaPolla et al., 2013).

Extant ant genera from the Early Eocene amber (50–52 Ma) of Cambay (India) belong to the subfamilies Dolichoderinae, Formicinae, Ponerinae, Pseudomyrmecinae, and Myrmicinae (Rust et al., 2010, material not yet completely examined). The above authors published a photograph of a myrmicine ant from amber (*loc. cit.*, Fig. 2b), which they consider similar to *Lordomyrma* Emery, although, judging from the characters visible in the photograph (9-segmented antenna and presence of antennal scrobes, shape and position of the eyes, characteristic shape of mesosoma and waist, long standing hairs on the body, etc.) we assume that this is more likely a representative of *Meranoplus* F. Smith.

A rich and diverse ant fauna is described from the Early Eocene Fushun amber (Liaoning, China) and these are all assigned to extinct genera of extant subfamilies (Hong, 2002). However, this material needs a serious revision, as it cannot be excluded that at least some of the species belong to extant genera. For instance, nine genera were assigned by Hong (2002) to the subfamily Myrmicinae, but, judging from the photographs and figures, six of these belong to the subfamilies Aneuretinae and Ponerinae, and only *Brachytarsites* Hong, *Orbigastrula* Hong, and *Sinomyrmex* Hong are indeed Myrmicinae. The last genus is similar to the extant genus *Pheidole* Westwood, so these names may turn out to be synonyms.

Finally, the Hat Creek amber from British Columbia (Canada) dated Early Eocene (see Archibald and Makarkin, 2004 for a discussion of the age of this amber), contained three extant ant genera: *Technomyrmex* Mayr (this species was later reidentified as a species of *Tapinoma* Foerster, see Moreau et al., 2006), *Dolichoderus* Lund (Dolichoderinae), and *Leptothorax* Mayr (Myrmicinae) (Poinar et al. 1999). It should be noted that this information, for reasons unknown, remained unnoticed by many authors, and is not mentioned in reviews on fossil ants (e.g., Dlussky and Rasnitsyn, 2007; LaPolla et al., 2013). Judging from the photograph of “*Leptothorax*” in the above paper, this species may belong to the genus *Temnothorax* Mayr, and possibly to *Tetramorium* Mayr; at least to one of the extant Myrmicinae genera.

Members of the extant subfamilies Aneuretinae, Dolichoderinae, Myrmecinae, Myrmicinae, Ponerinae, and of the extinct subfamily Formicinae, including the genera *Dolichoderus* and *Pachycondyla* F. Smith from the Lower and Middle Eocene of the western United States (Green River, Klondike, Kishenehn), and Canada (Horse River, Falkland, McAbee) (Dlussky and Rasnitsyn, 2003; Archibald et al., 2006, 2011). It should be noted that the assignment of the imprint to the last genus is doubtful, because it does not have a petiole and gaster. Furthermore, *Pachycondyla* is certainly a collective genus, and many generic names have been revived from synonymy with *Pachycondyla* (Schmidt and Shattuck, 2014), the view supported here. Two morphotaxa from Green River,

Myrmecites Dlussky et Rasnitsyn and *Solenopsites* Dlussky et Rasnitsyn (Dlussky and Rasnitsyn, 2003), are assigned to Myrmicinae. It should be noted that, previously, the age of the above beds was considered as Middle Eocene (Dlussky and Rasnitsyn, 2003), but at present they are dated as Early Eocene (Archibald et al., 2011; LaPolla et al., 2013).

The amber of Arkansas (United States) containing a fossil species of *Iridomyrmex* Mayr (Dolichoderinae) is dated Middle Eocene (45 Ma), although the taxonomic assignment of this insect is not clear (D.A. Dubovikov, pers. comm., 2014), and also extinct genera of Formicinae and Myrmicinae (Wilson, 1985). It is noteworthy that, for a long time, *Iridomyrmex* (Dolichoderinae) was thought to be the earliest occurrence of an extant genus, while *Eocenidris* Wilson was thought to be the earliest member of the subfamily Myrmicinae.

The extant genera *Gesomyrmex* Mayr, *Oecophylla* F. Smith (Formicinae), and *Pachycondyla* (Ponerinae) as well as a number of extinct genera from the extant subfamilies Dolichoderinae, Amblyoponinae, Ectatomminae, Ponerinae, Myrmeciinae, Pseudomyrmecinae, Cerapachyinae, and Myrmicinae, and the extinct subfamily Formiciinae were found in the Middle Eocene beds of Germany (Messel, 47 Ma; Eckfeld, 44 Ma) (Lutz, 1986; Dlussky et al., 2008, 2009; Dlussky, 2012; Dlussky and Wedmann, 2012; LaPolla et al., 2013). It should be stressed that material from these Lagerstätten is only partly studied and no generic level identification is referred to the subfamilies Dolichoderinae, Pseudomyrmecinae, Cerapachyinae, and Myrmicinae from these localities in available publications.

Thus, *Aphaenogaster dluskyana* can be considered the earliest confirmed and described representative of an extant genus from the subfamily Myrmicinae, although earlier but as yet undescribed records of extant myrmicine genera are known from the Early Eocene. On the whole, judging from the existing data on fossil ants, the occurrence of an extant myrmicine genus in Sakhalin amber might suggest a younger, possibly Middle Eocene age for the amber.

As mentioned above, to date, about 20 fossil species have been placed in, or transferred to, the genus *Aphaenogaster*. However, the analysis conducted in this study casts doubt on the assignment of many of these species to this genus. For instance, in our opinion, only nine of these species certainly belong to *Aphaenogaster*: *A. amphioceanica* (Dominican amber, Middle Miocene), *A. antiqua* Dlussky, 2002 (in Dlussky and Perkovsky, 2002) (Rovno amber, Ukraine, Late Eocene), *A. archaica* (Meunier, 1915) (Rott, Germany, Late Oligocene), *A. donisthorpei* Carpenter, 1930 and *A. mayri* Carpenter, 1930 (Florissant, United States, terminal Eocene), *A. mersa* Wheeler, 1915, *A. oligocenica* Wheeler, 1915, *A. sommerfeldti* Mayr, 1868 (Baltic amber, Late Eocene), and *A. praerelicta* (Mexican amber, Middle Miocene).

Aphaenogaster berendti Mayr from the Baltic amber was justifiably transferred to the genus *Stenammina* Westwood (Wheeler, 1915). Bolton (1995, 2014) without any explanation considered *Aphaenogaster longaeva* Scudder (Quesnel, British Columbia, Canada, Eocene; see Archibald and Makarkin, 2004) within this genus, although even Carpenter (1930) suggested that this species be considered as incertae sedis in the subfamily Myrmicinae, citing it as “(Myrmicinae) *longaeva*.” He noted that he had an imprint of a forewing and some body parts and, although the waist was typically myrmicine, no generic determination could be made. Judging from the description of *A. longaeva* (Scudder, 1877), we share Carpenter’s opinion. Mayr (1867) transferred *Poneropsis livida* Heer (Radoboj Limestone, Croatia, Early Miocene) to the genus *Aphaenogaster*, although (Dlussky and Putyatina, 2014) after having reexamined Heer’s collection, showed that this species belongs to the genus *Liometopum* Mayr from the subfamily Dolichoderinae.

Finally, the remaining fossil species of “*Aphaenogaster*” should apparently be transferred to the genus *Paraphaenogaster* Dlussky, originally described based on males from the Middle Miocene of Stavropol Krai (Russia) (Dlussky, 1981). Until recently, this genus included only a single species *P. microphthalmus* Dlussky, which is similar in mesosome morphology to males of the genus *Aphaenogaster*, but distinguished from them by the small eyes, absence of the closed cell *rm* on the forewing, and other venation details (Dlussky, 1981). However, now *Paraphaenogaster* is considered as a morphotaxon in the subfamily Myrmicinae (for terminology see Dlussky and Rasnitsyn, 2003; Zherikhin et al., 2008; formally, according to the International Code of Zoological Nomenclature (ICZN, 1999), *Paraphaenogaster* should be considered as a collective group), recognized based on the forewing venation morphology (Dlussky and Perfilieva, 2014; Dlussky and Putyatina, 2014). It should be said that various previously used nomenclatures of the forewing veins and cells of *Paraphaenogaster* have very recently been changed, even compared to the above cited papers by Dlussky, Perfilieva, and Putyatina (*loc. cit.*), and the venation under consideration can be characterized in the following way (see Perfilieva, 2010, and her personal communication, November, 2014).

The cells *1+2r* and *mcu* are closed, the cell *rm* is completely reduced (due to the disappearance of the transverse vein *rs-m*), the cell *3r* in most cases is open at the top; sections *2RS+M* and *3RS* are distinct, resulting in that the free branches of the veins *RS* and *M* extend from the cell *1+2r* separately, in particular, the vein *M* branches off far more proximally than the transverse vein *2r-rs*. A similar venation is characteristic of other members of the tribe Pheidolini (*Lophomyrmex* Emery, some *Pheidole*, and *Aphaenogaster*) and the tribes Solenopsidini (e.g., *Solenopsis* Westwood and *Carebara* Westwood).

At present, the morphotaxon *Paraphaenogaster* includes *Myrmica bicolor* Heer, *M. concinna* Heer, *M. jurinei* Heer, *M. tertiaria* Heer, and *M. tertiaria radobojana* Heer from the Early Miocene of Radoboj (Dlussky and Putyatina, 2014; also see Radchenko and Elmes, 2010), and a recently described species *P. hooleyana* based on imprints from the Upper Eocene of the Isle of Wight (England) (Dlussky and Perfilieva, 2014). In addition, Dlussky and Putyatina (2014) considered that several other species of “*Myrmica*” described by Heer (1849) from the Lower–Middle Miocene of Parschlug (Austria) (Kovar-Eder et al., 2004) and Middle Miocene of *Oeningen* (Germany), and *Carebara bohémica* (Novák, 1877) from the Upper Oligocene shale of the Czechia should also be assigned to *Paraphaenogaster*. We examined a photograph from Dlussky’s archive of a wing of the holotype of *Aphaenogaster pannonica* Bachmayer (Austria, Upper Miocene, described based on a forewing), and suggest that this species should be placed in *Paraphaenogaster*; this agrees with the original description and the drawing of the wing (Bachmayer, 1960).

We also agree with the suggestion of Dlussky and Putyatina (*loc. cit.*) that the latter genus should include the Middle Miocene species from Shanwang (China): *A. shanwangensis* (Hong, 1984) (originally described in the genus *Paraphaenogaster*, but later transferred to the new subgenus *Sinaphaenogaster* Zhang of the genus *Aphaenogaster*) and also *A. (Sinaphaenogaster) lapidescens* Zhang and *A. (Deromyrma) paludosa* Zhang (Zhang, 1989).

As mentioned above, in some *Aphaenogaster*, the forewing venation is similar to that of *Paraphaenogaster*, which includes species from the “subgenera” (at present, *Aphaenogaster* is formally not subdivided into subgenera) *Deromyrma* Forel, *Nystalomyrma* Wheeler, and *Planimyrmica* Viehmeyer (Emery, 1921). Evidently, because of this, *A. avita* Fujiyama (Japan, Miocene; Fujiyama, 1970), *A. dumetorum* (Lin) (China, Miocene; see Zhang et al., 1994) were assigned to the subgenus *Deromyrma*, but we are inclined to assign these species to *Paraphaenogaster*. Two species from the terminal Eocene and Oligocene deposits of France, *A. maculipes* Théobald and *A. maculata* Théobald (Théobald, 1937), certainly belong to *Paraphaenogaster* based on the forewing venation. Finally, forewings with the venation characteristic of this morphotaxon have been found in different deposits dated from the Early Oligocene to Pliocene in Germany and Russian Far East, but this material is not yet described (Dlussky and Putyatina, 2014).

It should be noted that all amber species of *Aphaenogaster* are only described based on workers, and it is possible that their so far unknown sexual individuals could have wing venation characteristic of the morphotaxon *Paraphaenogaster*. A single species, *A. mayri*, was described from all three castes and, although these were not amber specimens but imprints, the male cer-

tainly belongs to the genus *Aphaenogaster* based on the wing venation.

Most representatives of *Aphaenogaster* can be considered as mesoxerophiles and mesothermophiles and inhabit mostly xerophytic forests of the Mediterranean type and their derivatives, but are absent in real deserts and steppes as well as in the taiga. They make nests mainly in the soil or in the crevices in the rocks and forage mainly on the surface of the soil or on the forest floor. There are also mesophile species inhabiting more humid, but sufficiently warm deciduous and partly mixed forests, where they make nests in dry branches or in wood remains. At the same time, most inhabitants of tropical regions are dendrobionts, making nests and foraging in the tree canopies. Colonies in the *Aphaenogaster* species are relatively small, usually monogyne, and contain from several hundred to two or three thousand workers. All of them are primarily zoonecrophages, but their forage may also contain a large proportion of seeds of grassy plants.

Species of *Aphaenogaster* with a relatively short mesosoma, antennae, and legs, subrectangular head with weakly convex lateral sides and distinct, narrowly rounded occipital corners and short propodeal teeth can be considered as the least specialized. Morphological evolution in the genus apparently followed the trend of the general elongation of the body, antennae, legs, and head, which can completely lack occipital corners and is narrowed sharply posteriorly. Interestingly, all fossil species of *Aphaenogaster* from European ambers (Late Eocene) and Florissant shale (terminal Eocene) are morphologically unspecialized and similar to the modern representatives of the “subgenus” *Attomyrma* Emery, but Middle Miocene *A. amphioceanica* from the Dominican amber is highly specialized, with an elongated, narrowing posteriorly head without occipital corners and with a “collar,” whereas *A. praerelicta* from the Mexican amber of the same age is weakly specialized morphologically, but with long propodeal spines, as in many North and Central American species and even with teeth on the pronotum, which is only characteristic of some species from New Guinea (Andrade, 1995).

It is difficult to speculate on the time and place of origin of *Aphaenogaster*, but it can be suggested that this genus appeared in the territory of the modern Palearctic not later than the Early Eocene. This is suggested by the modern geographical range of the genus, with the centers of species diversification in the southern regions of the Palearctic, the distribution of the most primitive species in nontropical regions and also the ecology of its representatives. Most of the modern records are located in the areas with warm temperate or subtropical climates (see Fig. 1).

It is possible that species of *Aphaenogaster* developed in the Early Cenozoic forests and, in the Eocene, they were still few and, like members of the tribe Myrmicini, experienced heavy competition pressure from the then dominant Ponerinae and Dolichoderinae.

Later, as a result of a climatic change toward cooling and aridification, they could have acquired certain competitive advantages and occupied ecological niches in the forest floor and partly in the tree tier as well as moving to open landscapes.

Thus, paleontological data do not suggest that earlier members of *Aphaenogaster* were evolutionarily more primitive than the younger species or even than many modern species and the age of this genus should be pushed back to at least the Early Eocene, more than 50 Ma.

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