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Miocene Ants (Hymenoptera, Formicidae) from Crimea

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Abstract—Ant imprints, new and previously known, from Middle Miocene deposits near Kerch (Crimean Peninsula, Russia) are described or redescribed. A new Myrmicinae species, *Solenopsis atavinus* sp. nov., is described based on a wingless female. A winged female similar to the earlier described *Dolichoderus tauricus* Dlussky, 1981 is found: due to the excellent preservation of this specimen, the new specimen and the holotype of *D. tauricus* are redescribed and can be reclassified as *Ponerites tauricus* (Dlussky, 1981), comb. nov. *Oecophylla taurica* sp. nov. is described based on a partly preserved imprint of a female thorax with a forewing, the venation of which allows it to be positively identified as a weaver ant. Two other species are transferred from the formal genus *Camponotites* to *Oecophylla* based on forewing venation: *O. kraussei* (Dlussky et Rasnitsyn, 1999), comb. nov. (Early Eocene, United States) and *O. macroptera* (Dlussky, 1981), comb. nov. (Middle Miocene, Stavropol, Russia). One of the studied forewing imprints is similar in venation to *Paraphaenogaster microphthalmus* Dlussky, 1981, described from the Middle Miocene of Vishnevaya Balka (Stavropol province, Russia) and so is attributed to this species. *Dolichoderus tavridus* sp. nov. is described based on a forewing.

Keywords: Middle Miocene, fossils ants, Formicidae, *Oecophylla*, *Solenopsis*, Crimea
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INTRODUCTION

In this paper we describe imprints of ants (Hymenoptera, Formicidae) from the collection of the Arthropod Laboratory of the A.A. Borissiak Paleontological Institute, Russian Academy of Sciences (PIN). The studied material is represented by imprints from marine deposits of the Eastern Paratethys along the northern coast of the Kerch Peninsula (Crimean Peninsula) from Cape Tarkhan to Yurkino Village. The Malyi Kamyshlak locality (hypostratotype of the Tarkhan Regional Stage) is 3 km from Yurkino Village; these deposits date to the Middle Miocene (Tarkhan Regional Stage, Argun Beds; Gontsharova, 1989); the material was collected in expeditions in 1972 (coll. no. 287) and 1985 (coll. no. 4204). Ant imprints from collection no. 4703 are from Khronya Cape (south-east of Yurkino Village); the deposits are dated Late Miocene (Sarmatian; Nevesskaya et al., 1986).

In her monograph on bivalves (Gontsharova, 1989, p. 9), she says that insects from these collections were identified by the following authors: V.V. Zherikhin, M. Klimashevsky, V.G. Kovalev, A.G. Ponomarenko, Yu.A. Popov, L.N. Pritykina, A.P. Rasnitsyn, I.D. Sukatsheva, and D.E. Shcherbakov. She also referred to a number of provisionally identified insects (altogether 135): 1 dragonfly, 2 cockroaches, 5 orthopterans, 3 termites, 16 homopterans, 10 heteropterans, 70 beetles (including a scarab and a weevil), 4 dipterans, and several imprints provisionally identified as hymenopterans—families Ichneumonidae, Formicidae (Ponerinae, Formicinae, Dolichoderinae—*Dolichoderus tauricus* Dlussky, 1981). At present only *Dolichoderus tauricus* Dlussky, 1981 from coll. no. 287 has been described from this material (Dlussky, 1981). The fossil insect collections included imprints of seven ant specimens in various states of preservation, including *D. tauricus*, a description of which is given in this paper.

MATERIAL AND METHODS

The ant forewing venation nomenclature used in this paper follows our previous papers (Perfilieva, 2010; Dlussky et al., 2015) and is given in Fig. 1; it is consistent with the accepted terminology for Hymenoptera (Rasnitsyn, 1980). Descriptions follow standard methods using various indices (Dlussky, 1981; Antropov et al., 2014). Abbreviations of measurements used and explanation of abbreviations are as follows: (BL) total body length; (FWL) forewing length; (FWPt) distance between the base of a forewing and

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[†] Deceased.

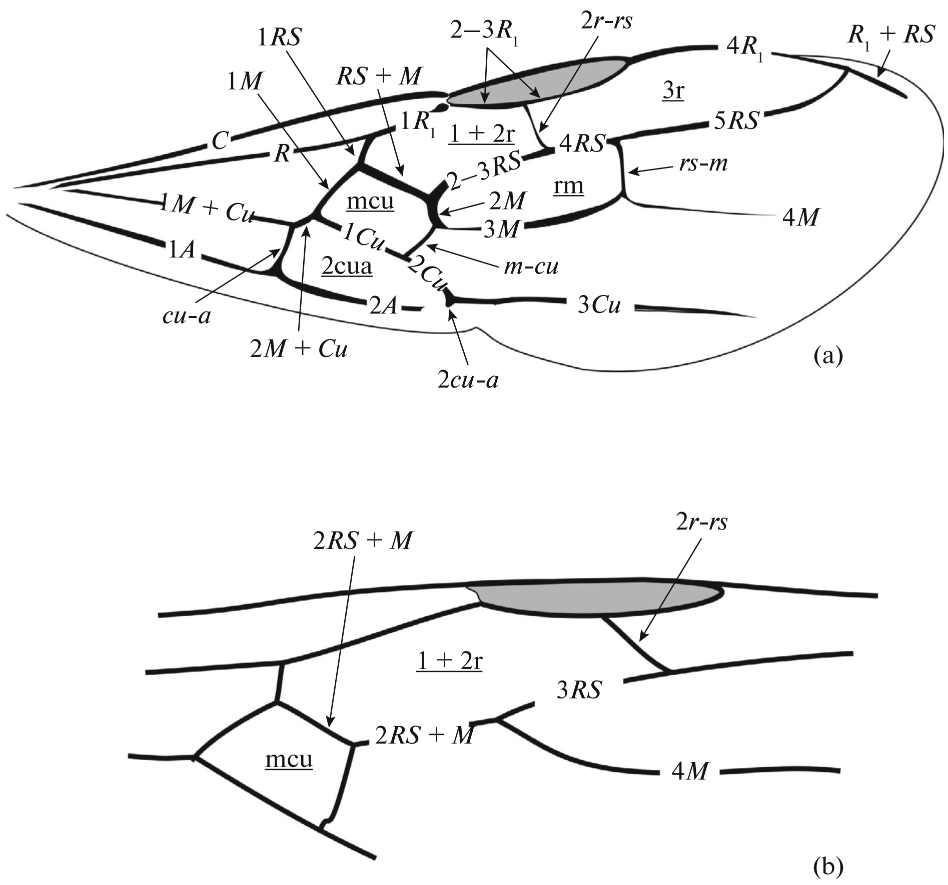


Fig. 1. Venation nomenclature of the ant forewing: (a) venation nomenclature for the complete venation scheme; (b) nomenclature for reduced venation characteristic of the forewings of *Paraphaenogaster* sp.

that of pterostigma; $\mathrm{Icu} = [1Cu + (2M + Cu)]/1Cu$ shows the position of the *cu-a* crossvein relative to the mediocubital (mcu) cell; $\mathrm{Icua} = [(1M + Cu) + (2M + Cu)]/(1M + Cu)$ reflects the position of the *cu-a* crossvein relative to the wing base.

SYSTEMATIC PALEONTOLOGY

Family Formicidae Latreille, 1809

Subfamily Ponerinae Lepeletier de Saint-Fargeau, 1835

Genus (formal) *Ponerites* Dlussky et Rasnitsyn, 2003

Type species. *Ponerites eocenicus* Dlussky et Rasnitsyn, 2003.

Diagnosis (for imprints). Fossil ants, preservation of which precludes their assignment to particular orthotaxa, with following set of characters: small or medium-sized ants; head nearly rectangular with rounded occipital angles; eyes relatively small, shifted to anterior margin of head (sometimes this character is not treated as diagnostic: Dlussky and Rasnitsyn, 2003; Dlussky and Putyatina, 2014); mandibles triangular with denticulate masticatory margin; workers with promesonotal and mesopropodeal sutures; head, alitrunk and waist lack prominent sculpture, denticles or spines; petioles with thick scale; gaster with constriction between first and second segments of gaster (III and IV abdominal segments); tergite and sternite of second gaster segment (IV abdominal) of almost equal size, abdominal apex not directed downwards, sting well-developed. Forewings with closed 1 + 2r, 3r, rm and mcu cells, shape of rm and mcu cells varies. $\mathrm{Icu} < 1.5$, $\mathrm{Icua} < 1.2$.

Species composition. 14 species known from the Eocene to the Miocene (Bolton, 2016). Lower Eocene, Green River Formation: *P. coloradensis* Dlussky et Rasnitsyn, 2003; *P. eocenicus* Dlussky et Rasnitsyn, 2003; *P. hypoponeroides* Dlussky et Rasnitsyn, 2003 (Dlussky and Rasnitsyn, 2003). Middle Eocene, Kishenehn Formation: *P. kishenehne* LaPolla et Greenwalt, 2015 (LaPolla and Greenwalt, 2015). Upper Eocene, Bembridge Marls: *P. crawleyi* Donisthorpe, 1920; *P. antropovi* Dlussky et Perfilieva, 2014; *P. hooleyi* Dlussky et Perfilieva, 2014 (Antropov et al., 2014). Lower Miocene, Radoboy (Croatia): *P. atavinus* Heer, 1849; *P. elongatus* Heer, 1867; *P. gracilior* Heer, 1867; *P. nitidus* Heer, 1849; *P. oblongiceps* Dlussky et Putyatina, 2014; *P. tenuis* Heer, 1867 (Heer, 1849, 1867; Dlussky and Putyatina, 2014). Middle Miocene, Northern Caucasus: *P. umbrus* Popov, 1932; Crimea: *P. tauricus* Dlussky, 1981 (Popov, 1932; Dlussky, 1981).

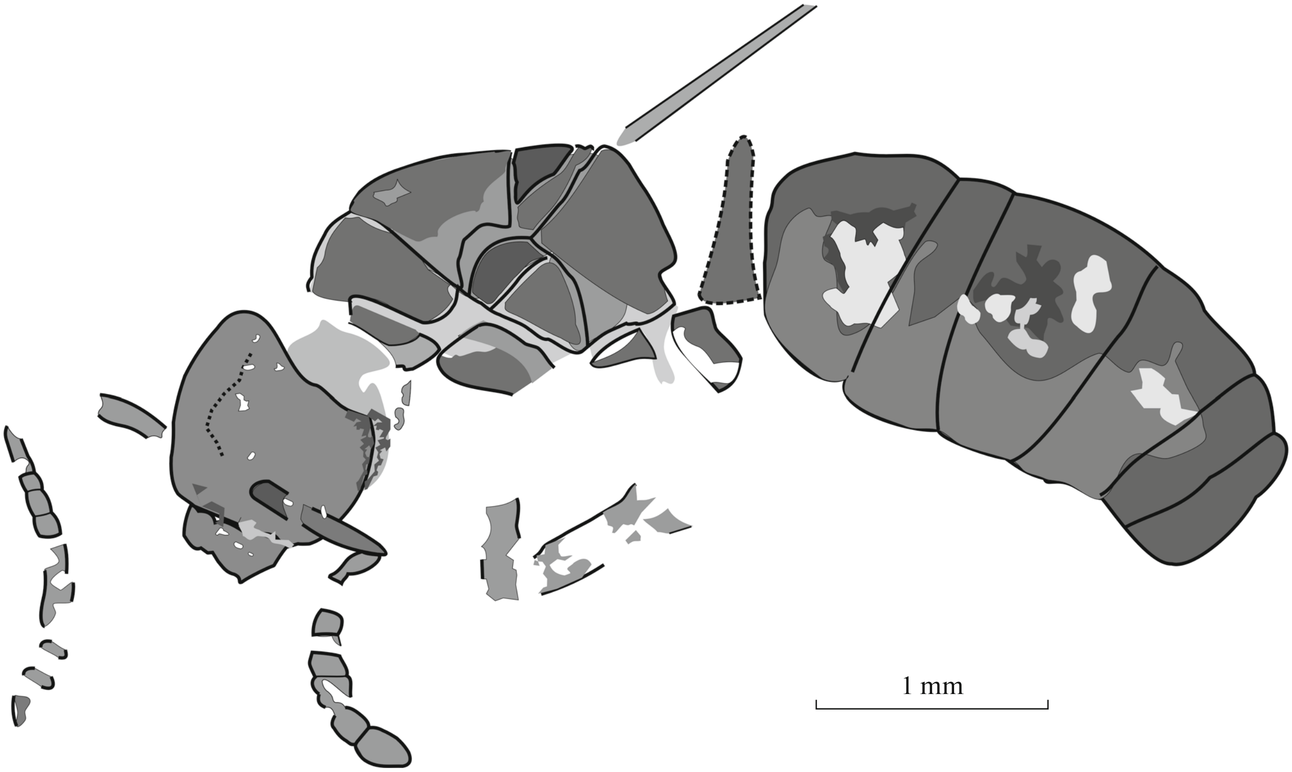


Fig. 2. *Ponerites tauricus* (Dlussky, 1981), comb. nov., holotype PIN, no. 287/343.

Remarks. The diagnosis given for this formal group by Dlussky and Rasnitsyn, 2003 can characterize non-specialized small and medium-sized ants of the subfamily Ponerinae, such as species of *Ponera* Latreille, 1804 and *Hypoponera* Santschi, 1938. A relatively large range of the forewing venation types, including quadrangular and triangular forms of the radiomedial cell, demonstrates that the group is taxonomically combined.

Ponerites tauricus (Dlussky, 1981) comb. nov.

Plate 7, figs. 1, 2

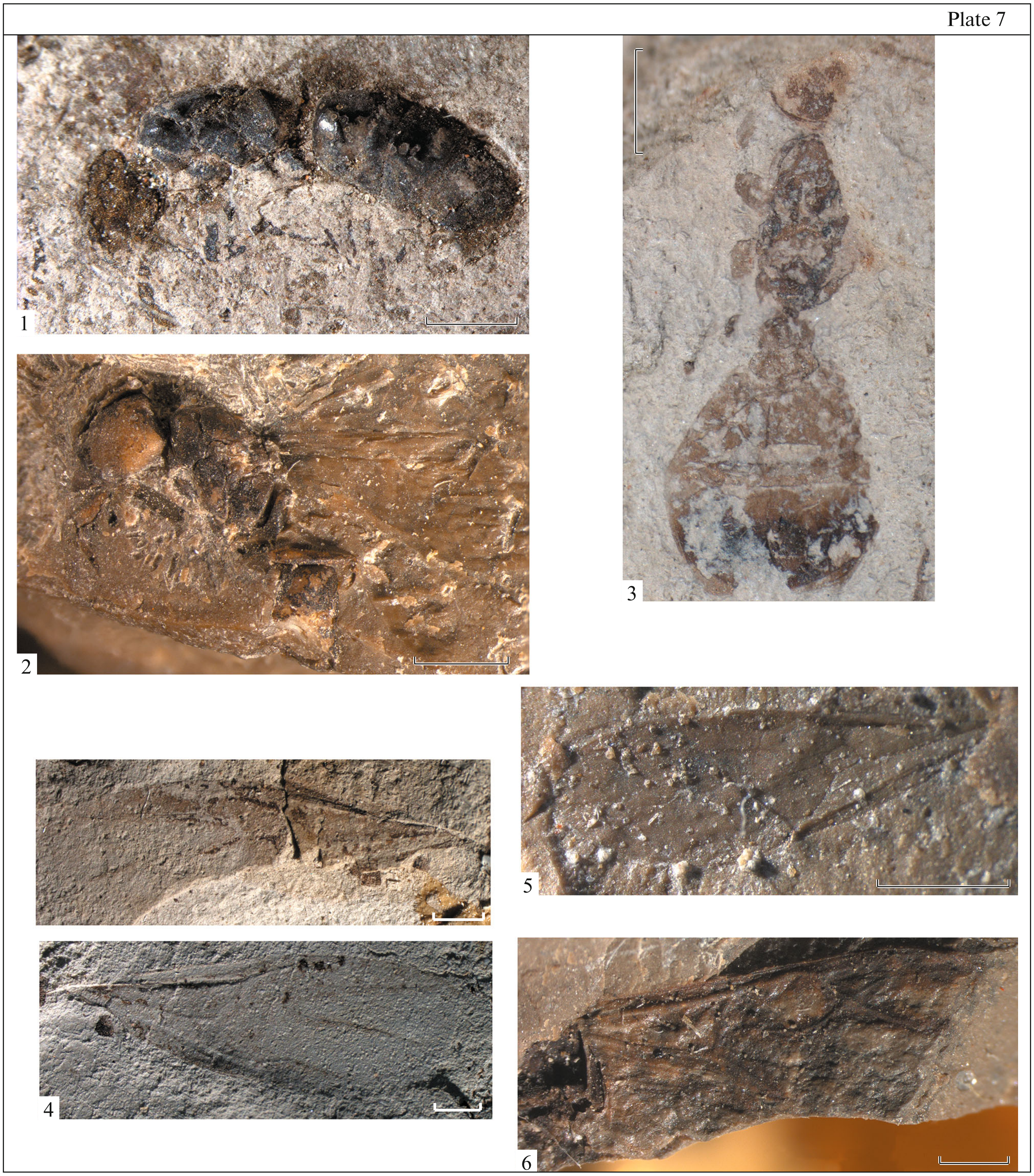
Dolichoderus tauricus: Dlussky, 1981, p. 70, text-figs. 52a, 52b.

Holotype. PIN, no. 287/343, three-dimensional part and counterpart of a female; Crimea, Malyi Kamyshlak locality; Middle Miocene, Upper Tarkhanian.

Description (Figs. 2, 3). Female. The head is rectangular, with slightly convex sides, rounded occipital angles and weakly concave occipital margin. The anterior margin of the clypeus is slightly rounded convex. The eyes are rounded, relatively small, strongly shifted anteriorly, so the gena is almost the same or slightly shorter than the maximum eye diameter. The antennae are12-segmented, with an unclear 3-segmented club. The scape is curved, reaching the occipital margin of the head. Segments 2–5 of the funiculus are slightly longer than wide. The mesosome is comparatively massive; its length is 1.5 times its height. All mesosome sutures are deep and distinct. The pronotum has rounded posterior angles. The scutum does not overhangs the pronotum; it is slightly shorter than wide. The scutellum is transverse. The dorsal surfaces of the scutum and scutellum are weakly convex in profile. The mesopleura has a distinct transverse suture. The dorsal and posterior surfaces of the propodeum form a rounded obtuse angle, and the dorsal surface is several times shorter than the posterior surface. The posterior surface of the propodeum is straight or slightly concave in profile, separated from the lateral surfaces by a relatively sharp shoulder. No petiole was preserved in the holotype, whereas in the paratype, the petiole has a high scale (height 2.9 times its length). The anterior and posterior surfaces of the petiole are almost parallel, the apex has slightly rounded angles. The entire body is covered by very fine granulated sculpture.

The venation of the forewing of the holotype is only partly preserved, but it is possibly to observe that the mcu cell is pentagonal, whereas the rm cell is quadrangular. In specimen PIN, no. 4204/31, the wing apex is not observed (Figs. 3a, 3b). The mcu cell is medium-sized, pentagonal, $RS + M$ is approximately twice the length of the $2M$ vein; the opposite side, formed by $1M$ and *m-cu* crossveins are approximately of the same length and are parallel to each other. The base of the rm cell is well-developed, therefore the cell is either quadrangular or pentagonal—the apex of the rm cell, like 3r, was not preserved. The *m-cu* cross vein situated near the mediocubital cell, so Icu = 1.37 and Icua = 1.12.

Plate 7



Explanation of Plate 7

Figs. 1 and 2. *Ponerites tauricus* (Dlussky, 1981), comb. nov.: (1) holotype PIN, no. 287/343; (2) specimen PIN, no. 4204/31.

Fig. 3. *Solenopsis atavinus* sp. nov., holotype PIN, no. 4703/23a.

Fig. 4. *Paraphaenogaster microphthalmus* Dlussky, 1981, specimen PIN, no. 4703/22, forewing, part and counterpart.

Fig. 5. *Dolichoderus tavridus* sp. nov., holotype PIN, no. 4204/30, forewing.

Fig. 6. *Oecophylla taurica* sp. nov., holotype PIN, no. 4204/32, forewing.

Scale bar 1 mm.

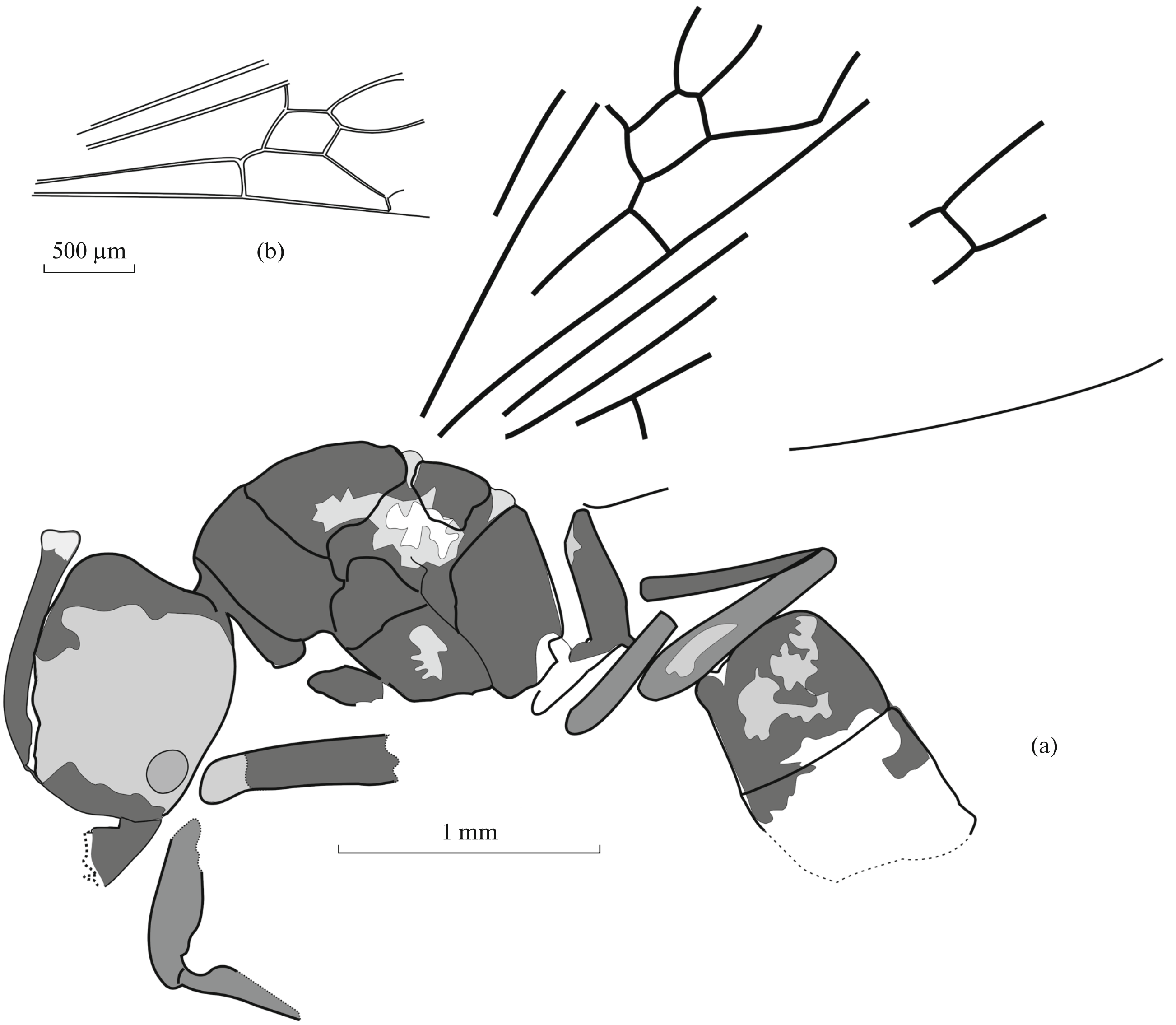


Fig. 3. *Ponerites tauricus* (Dlussky, 1981), comb. nov., specimen PIN, no. 4204/31: (a) general view of the specimen, (b) reconstruction of forewing venation.

The hindwing is almost not observed; the wing is almost indiscernible.

Measurements in mm: Holotype PIN, no. 287/343: mesosome length 1.6, head length 0.96, head width 0.85, petiole length ca. 0.32, petiole height almost 0.7, maximum eye diameter 0.18. Specimen PIN, no. 4204/31: mesosome length 1.7, head length 1.0, head width 0.8, scape length 0.9, maximum eye diameter 0.2, length petiole almost 0.36, petiole height 0.63. Body length 4.5–5.5 mm.

Comparison. In contrast to the Eocene species, *P. tauricus* has a relatively high and narrow petiole in profile view.

This species differs from *P. umbrus* in the smaller size (body length *P. umbrus* 6.25 mm, wing length 4.5 mm), and concave shape of the occipital margin of the head. The wing venation differs in the shape of the rm cell (in *P. umbrus* the rm cell is elongated), in the proportions of the length of $RS + M$ and $2M$ (in *P. umbrus* they are almost the same, while in the new species $2M$ is considerably shorter than $RS + M$).

P. elongatus, P. nitidus, and *P. gracilior* are considerably larger than *P. tauricus*(BL = 16.1 mm, BL = 9.8 mm, BL = 17 mm). *P. oblongiceps* (BL = 6–7 mm) is somewhat larger than *P. tauricus*, and has larger eyes, which are arranged almost in mid-gena, whereas in *P. tauricus* they are at the base of the antennae.

P. tenuis and *P. atavinus* are described from males, hence confident comparison is difficult. However the larger size of *P. tenuis* precludes synonymy with the females of *P. tauricus*. Venation (triangular rm cell and the shape of the mcu cell with an increased length of $1M$) of a male of *P. atavinus* and the position of the

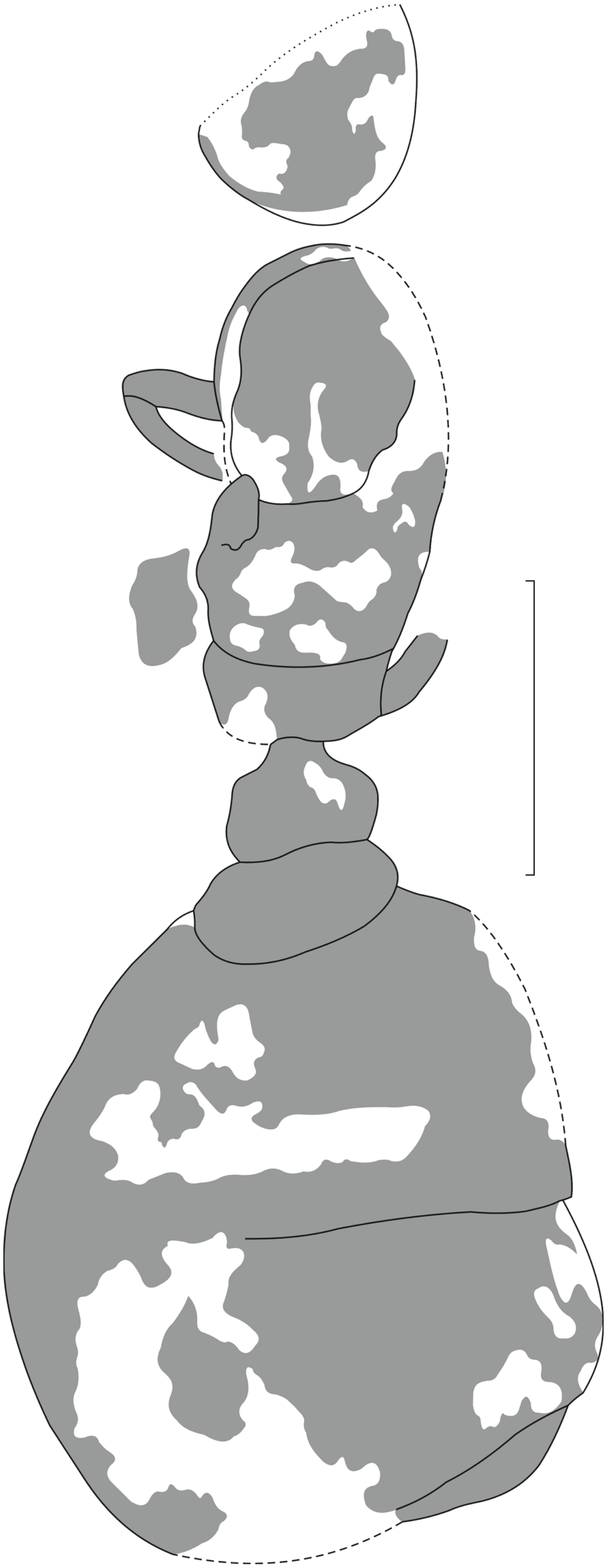


Fig. 4. *Solenopsis atavinus* sp. nov., holotype PIN, no. 4703/23a.

eyes of the posterior head margin also distinguish it from the female of *P. tauricus*.

The wings of Ponerinae found in the Miocene deposits of the Stavropol Region (Vishnevaya Balka), can be distinguished based on a considerably larger wing size in *Taphopone karaganensis* Dlussky, 1981 and *T. stauropolitanus* Dlussky, 1981 (wing length 5.7 mm and 5.2 mm respectively) (both species were reassigned from *Ponerites* to *Taphopone* Dlussky et Perfilieva, 2014: Antropov et al., 2014). The wing of *T. karaganensis* is also distinguished by the shape and relatively large size of the mcu cell.

Remarks. This species was originally erroneously described in the genus *Dolichoderus* Lund, 1831 (Dlussky, 1981). New studies and a well-preserved second specimen discovered later allowed a positive assignment of this species to Ponerinae based on wing venation, Icu < 1.5 and Icua < 1.2 and constriction between the first and second abdominal segments.

Material. Apart from the holotype, three-dimensional part and counterpart imprints of a winged female, specimen PIN, no. 4204/31 from the type locality.

Subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1835

Genus *Solenopsis* Westwood, 1840

Type species. *Solenopsis mandibularis* Westwood, 1840 (junior synonym of *Atta geminata* Fabricius, 1804); by monotypy.

Diagnosis. Head with rounded occipital angles, oval or triangular in shape. Propodeum rounded, lacking denticles or spines. Petiole is not compressed dorso-ventrally and can be similar to postpetiole. Petiolar segments wide. Antennae 10-segmented with club formed by apical and pre-apical segments.

Species composition. In the modern fauna, 220 valid species and subspecies are found in all continents (Bolton, 2016). In addition, eight *Solenopsis* species have been described from the Oligocene of France and Germany (Théobald, 1937), but these data are in need of revision. Most likely all or some of these species should be referred to other genera.

Solenopsis atavinus Perfilieva, Dubovikoff et Dlussky, sp. nov.

Plate 7, fig. 3

Etymology. From the Latin *atavinus* (ancestral).

Holotype. PIN, no. 4703/23a, incompletely preserved imprint of a female; Crimea, south-eastern margin of Yurkino Village, Khronya Cape; Upper Miocene, Sarmatian.

Description (Fig. 4). Female. The body length is 5.5 mm. The occipital head margin is smoothly rounded; the occipital angle is not developed. The mesosome is long and narrow, its 2.2 times as long as wide, whereas the width almost equals the head width.

The scutum does not cover the pronotum; its length is 1.4 times its width. The propodeum lacks spines or teeth. The waist is two-segmented. The petiole has a node and short anterior cylindrical part; its width is 1.4 of its length. The postpetiole is transverse, 1.4 wider than the petiole. The gaster is oval.

Measurements in mm: holotype: body length 5.8–6.0, mesosome length 1.7, mesosome width 0.78, scutum length 0.83, petiole length 0.37, petiole width 0.52, postpetiole width 0.72. Paratype: gaster length 2.5, gaster width 1.85.

Comparison. Of the eight fossil species described, *S. blanda* Förster, 1891 is the most similar in female size (BL = 6 mm). *S. atavinus* is distinguished by the elongated thorax (length 2.2 of its width, whereas in *S. blanda* it is 1.3 of the width).

Material. Apart from the holotype, paratype PIN, no. 4703/23b, abdomen of another specimen in the same sample; type locality.

Genus (formal) *Paraphaenogaster* Dlussky, 1981

Type species. *Paraphaenogaster microphthalmus* Dlussky, 1981, Miocene of Northern Caucasus.

Diagnosis (forewing imprints). Forewings with rm cell reduced. Third radial cell usually not closed: free branch of *RS* long, not reaching R_1, but rarely meeting it, so 3r becoming closed. Crossvein 2*r-rs* directly vertical to pterostigma bottom margin or slightly inclined by bottom end to wing apex and relatively short. Radiomedial cell absent due to complete reduction of transverse *rs-m*. 2*RS* + *M* and 3*RS* well developed, so free *M* branch deviating considerably more proximal of 2*r-rs*. Cell mcu trapezoid and medium-sized. Second cubitoanal cell not formed.

Species composition. Apart from the type species *P. microphthalmus* from the Middle Miocene of the Stavropol Region (Vishnevaya Balka; Dlussky, 1981) and Crimea (see below), three fossil species are known: from the Upper Eocene Bembridge Marls (Great Britain), *P. hooleyana* Dlussky et Perfilieva, 2014 (Antropov et al., 2014) and from the Lower Miocene of Croatia (Radoboy) *P. tertiaria* (Heer, 1849) and *P. jurinei* (Heer, 1849) (Dlussky and Putyatina, 2014). *Aphaenogaster shanwangensis* (Hong, 1984), *A. lapidescens* Zhang, 1989, and *A. paludosa* Zhang, 1989 from the Lower Miocene of China have a similar venation and can be assigned to this formal-genus (Hong, 1984; Zhang, 1989). Also this genus should probably include imprints of isolated wings from the Grubstake Formation, Upper Miocene, Central Alaska), housed as UAF-GS 2, 4, 5, and 19 in the University of Alaska. The authors of the description of this locality suggested that the wings are similar to those of *Solenopsis* or *Carebara* Westwood, 1840 (Grimaldi and Triplehorn, 2008).

Remarks. Previously the nomenclature of venation in *Paraphaenogaster* was variously interpreted (Dlussky, 1981; Antropov et al., 2014; Dlussky and Putyatina, 2014). The study of the evolution of venation in Myrmicinae (Perfilieva, 2008, 2010), showed that the radiomedial cell in the wing of *Paraphaenogaster* was reduced by the disappearance of the *rs-m* vein at the stage of the triangular cell with a long stem, hence the well-developed elements in this region should be referred to as 2*RS* + *M* and 3*RS* (Fig. 1b).

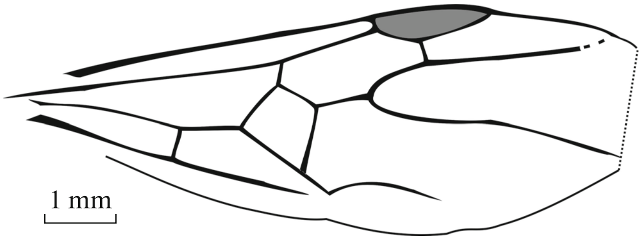


Fig. 5. *Paraphaenogaster microphthalmus* Dlussky, 1981, specimen PIN, no. 4703/22, forewing.

Paraphaenogaster microphthalmus Dlussky, 1981

Plate 7, fig. 4

Paraphaenogaster microphthalmus: Dlussky, 1981, p. 68, text-fig. 51a, 51b (male).

Holotype. PIN, no. 224/213, imprint of a male specimen and of a forewing lying nearby; Stavropol region, Vishnevaya Balka, Outcrop no. 4; Miocene, Karagan Regional Stage.

Description (wing imprints) (Fig. 5). The forewing is without a radiomedial cell. 5*RS* very closely approaches the wing margin, and possibly 3r is closed. The transverse vein *rs-m* is completely reduced, therefore the rm cell is absent. The free branch *M* extends from 2*RS* + *M* is considerably more proximal of the meeting point with 2*r-rs* so 3*RS* and 2*RS* + *M* approximately the same length. The mediocubital cell is medium-sized, relatively high: the height of the trapezoid cell (distance between *RS* + *M* and 1*Cu*) approximately equals the median (midline) of this trapezoid, the ratio of the mcu cell height and its median line is 0.9. Icu = 1.7, Icua = 1.4.

Measurements in mm. FWL = 9.0, FWPt = 4.5, maximum wing width ca. 3.0.

Comparison. The wing size of the Miocene *P. jurinei* and Eocene *P. hooleyana* is smaller than in *P. microphthalmus* (7.5, 4.6 and 9.0 mm, respectively). *P. tertiaria* has a relatively shorter 3r cell than *P. microphthalmus*.

Remarks. In the original species diagnosis, venation is not mentioned. Based on a new imprint and the holotype we were able to include venation features in the species diagnosis.

Material. Apart from the holotype, specimen PIN, no. 4703/22, part and counterpart of a forewing; Crimea, south-eastern margin of Yurkino Village, Khronya Cape; Upper Miocene, Sarmatian.

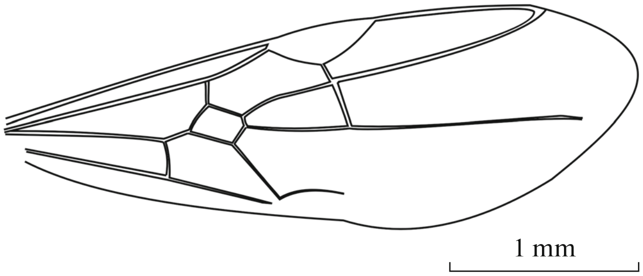


Fig. 6. *Dolichoderus tavridus* sp. nov., holotype PIN, no. 4204/30, forewing.

Subfamily Dolichoderinae Forel, 1878

Genus *Dolichoderus* Lund, 1831

Type species. *Formica attelaboides* Lund, 1831.

Diagnosis (wing imprints). Forewing with closed 1 + 2r, 3r, rm and mcu cells; cua cell not formed (often the angle between 1*Cu* and 2*Cu* is not pronounced, and 2*cu-a* is absent); rm cell is usually triangular, sometimes with a stem, rarely quadrangular, with very short 2*M* section. 1*RS* perpendicular or slightly inclined to *R*. Apex of 3r cell lies on wing margin; section R_1 + *RS* usually, but not always absent. Crossveins 2*r-rs* and *rs-m* usually forming single line, or *rs-m* lying somewhat more distal. Cell mcu medium-sized, rhomboid, rectangular, or trapezoid. Hindwing with reduced free branch *M* and similar in venation to *Liometopum* Mayr. Position of *cu-a* characteristic of dolichoderins, i.e., Icua > 1.15, Icu > 1.45.

Species composition. Modern members (132 species) occur mainly in the Neotropical, Indo-Australian, and the Australian regions. Only nine species are found in the Oriental , four in the Nearctic, two in the Palearctic, and none in the Afrotropical bioregions. At present 49 fossil species are known (Bolton, 2016) (including *D. tauricus*, see above), known beginning from the Early Eocene: *D. kohlsi* Dlussky et Rasnitsyn, 2002 from Green River, United States (Dlussky and Rasnitsyn, 2002). The Middle Eocene is represented by *D. dlusskyi* LaPolla et Greenwalt, 2015 (Kishenen, USA: LaPolla and Greenwalt, 2015). In the Upper Eocene, species of *Dolichoderus* were most diverse: they include *D. vectensis* Donisthorpe, 1920 (Bembridge, Great Britain: Donisthorpe, 1920; Antropov et al., 2014), *D. antiquus* Carpenter, 1930 and *D. rohweri* Carpenter, 1930 (Florissant, USA: Carpenter, 1930), *D. kutschlinicus* Deichmüller, 1881 (Kuchlin, Czech Republic: Deichmüller, 1881), *D. pinguis* Dlussky, Rasnitsyn et Perfilieva, 2015 (Bolshaya Svetlovodnaya, Primorye Region, Russia: Dlussky et al., 2015) and 25 from European Late Eocene ambers: *D. balticus* Mayr, 1868, *D. sculpturatus* Mayr, 1868, *D. tertiaries* Mayr, 1868, *D. cornutus* Mayr, 1868, *D. longipennis* Mayr, 1868 (Baltic amber: Mayr, 1868); *D. brevicornis* Dlussky, 2002*, D. longipilosus* Dlussky, 2002, *D. nanus* Dlussky, 2002, *D. polessus* Dlussky, 2002, *D. polonicus* Dlussky, 2002, *D. robustus* Dlussky, 2002 (Baltic and Rovno ambers: Dlussky, 2002); *D. elegans* Wheeler, 1915, *D. mesosternalis* Wheeler, 1915, *D. passalomma* Wheeler, 1915, *D. vexillarius* Wheeler, 1915 (Baltic amber: Wheeler, 1915); *D. brevipennis* Dlussky, 2008, *D. brevipalpis* Dlussky, 2008, *D. granulinotus* Dlussky, 2008, *D. kutscheri* Dlussky, 2008, *D. lucidus* Dlussky, 2008, *D. perkovskyi* Dlussky, 2008, *D. pilipes* Dlussky, 2008, *D. punctatus* Dlussky, 2008, *D. vlaskini* Dlussky, 2008 (Baltic, Bitterfeld, Saxony, Scandinavia, Rovno ambers: Dlussky, 2008); *D. zherichini* Dlussky et Perkovsky, 2002 (Rovno amber: Dlussky and Perkovsky 2002).

Five ant species are known from the Lower Oligocene and the vicinity of the Eocene–Oligocene boundary of continental Europe: *D. affectus* Théobald, 1937, *D. bruneti* Théobald, 1937, *D. coquandi* Théobald, 1937, *D. oviformis* Théobald, 1937 (Kleinkembs, Aix-en-Provence, Célas, France: Théobald, 1937); *D. explicans* (Förster, 1891) (Brunstatt, France: Förster, 1891).

Twelve species (taking into account the exclusion of *D. tauricus*, reassigned to *Ponerites* in this paper) are described from the Miocene: *D. heeri* Dlussky et Putyatina, 2014 (Croatia, Radoboy: Dlussky, Putyatina, 2014); *D. caribbaeus* Wilson, 1985, *D. primitivus* Wilson, 1985, *D. prolaminatus* Wilson, 1985 and *D. dibolius* Wilson, 1985 (Dominican amber: Wilson, 1985); *D. lacinius* Zhang, 1989, *D. evolans* Zhang, 1989 (China: Zhang, 1989), *D. jiaoyanshanensis* Hong, 1985 (China: Hong, 1985), *D. luridivenosus* Zhang, Sun et Zhang, 1994, *D. transversipetiolaris* Zhang, Sun et Zhang, 1994 (China: Zhang et al., 1994*); D. obliteratus* Scudder, 1877 (Canada: Scudder, 1877); *D. tavridus* **sp. nov.** (Crimea, see below).

Remarks. The section R_1 + *RS* and position of the apex of cell 3r are the best differentiation criteria of the wings of *Dolichoderus* and *Liometopum*: in the wings of *Liometopum* the cell 3r apex is not on the wing margin and the section R_1 + *RS* is considerably elongated. In specimens where the mediocubital cell characters are similar, and the region of the wing with the apex of cell 3r are missing from the imprints, it is not at present possible to distinguish these two genera.

Dolichoderus tavridus Perfilieva, Dubovikoff et Dlussky, sp. nov.

Plate 7, fig. 5

Etymology. From Tavrida, the old Russian name of the Crimean Peninsula, given after it was incorporated by Russian Empire in 1783.

Holotype. PIN, no. 4204/30, forewing; Crimea, Kerch Peninsula, Malyi Kamyshlak; Middle Miocene, Upper Tarkhanian.

Description (Fig. 6). The pterostigma is rounded. The 3r cell is closed, its apex is on the wing margin. The 3r cell is approximately 1.8 the length of the 1 + 2r cell. The radiomedial cell (rm) with no stem.

There is a small contact zone with the mcu cell (segment 2*M* is very short). The mcu cell is relatively small, almost rectangular; 1*M* and *m-cu* are almost the same length and parallel. 1*M* is1.5 longer than 1*RS*. The distal margin of the mediacubital cell does not reach the base of the pterostigma. The veins 2*r-rs* and *rs-m* lie almost in one line. The crossvein *cu-a* is locate more proximal of the mcu cell, at a distance almost equal its length. Icu = 1.6, Icua = 1.2.

Measurements in mm. FWL=3.4, maximum width about 1.1. FWPt = 1.2, cell length 1 + 2r = 1.2 mm, 1R_1 = 0.4.

Remarks. The forewing venation and its size allow the reasonably positive assignment of this specimen to the subfamily Dolichoderinae. The material studied shows that similar venation may be observed in *Tapinoma* Foerster, *Iridomyrmex* Mayr, and *Dolichoderus*. However, taking in to account the size of the wing and the fact that the fossil members of the genus *Iridomyrmex* are not confirmed, we assign this imprint to the genus *Dolichoderus*.

Material. Holotype.

Subfamily Formicinae Latreille, 1809

Genus *Oecophylla* F. Smith, 1860

Type species. *Formica virescens* Fabricius, 1775 (junior synonym of *Oecophylla smaragdina* (Fabricius, 1775)).

Diagnosis. The size is usually large or medium. The head is almost rectangular, with rounded occipital angles. The antennae geniculate in both sexes; the scape base is somewhat at a distance from the clypeus; the mandibles are large, triangular, cutting edge with sharp teeth on the masticatory margin. The petiole is elongated, lacking a scale or node in workers. The node can be conspicuous in females. The gaster is compact. The legs are elongate. The forewings are with closed 3r and 1 + 2r cells, the rm and mcu cells are absent. The 3r cell is almost as long as the 1 + 2r cell, but is considerably narrower than it. The bottom margin delineated by 5*RS* is noticeably concave. The 1 + 2r cell is delimited at the bottom by the convex segment *RS* + *M*; the main (almost all) part of the top border of the cell 1 + 2r is formed by 1R_1. The pterostigma is narrow. Its distal part relative to the crossvein 2*r-rs* is considerably longer than the proximal part (i.e., 2R_1 is clearly shorter than 3R_1). Thus, most of the pterostigma is in the cell 3r. The veins 5*RS* and free branch of the medial vein (*M*) extends from the same nodule. The 1*RS* and 1*M* are of approximately the same length, forming a straight line. The crossvein 2*r-rs* is considerably inclined at the bottom end to the wing apex. The hindwings lack a longitudinal *M*. The crossvein *cu-a* ic located such that 1*M* + *Cu* is not shorter than 2*M* + *Cu*. The crossvein formed by1*M* and *rs-m* is significantly concave. The female wings are considerably larger than the male wings.

Species composition. Two extant species: *O. smaragdina*, in the Oriental Region and Indo-Malay Region, and *O. longinoda* Latreille, 1802, from the Afrotropical Region. Fossils representatives of this genus are known beginning from the Early Eocene (Klondike Mountain Formation, Washington State, United States: Dlussky and Rasnitsyn, 1999): *Camponotites kraussei* Dlussky et Rasnitsyn, 1999 based on distinct characters of forewing venation and the elongated petiole, should be assigned to this genus. Two species are described from the Middle Eocene: *O. longiceps* Dlussky, 2008 (Grube Messel, Germany) and *O. eckfeldiana* Dlussky, 2008 (Eckfeld, Germany: Dlussky et al., 2008), six species from the Upper Eocene: *O. brischkei* Mayr, 1868 and *O. crassinoda* Wheeler, 1922 (=*O. brevinodis* Wheeler, 1915) (Baltic amber: Wheeler, 1915, 1922), *O. praeclara* Förster, 1891 (Brunstadt, Germany), *O. bartoniana* Cockerell, 1920 (Bagshot Beds, Bournemouth, Great Britain: Cockerell, 1920), *O. atavina* Cockerell, 1915, *O. megarche* Cockerell, 1915 (Bembridge, Great Britain: Cockerell, 1915; Antropov et al., 2014).

Two species are described from the Oligocene of Europe *O. superba* Théobald, 1937 (Kleinkembs, France: Théobald, 1937) and *O. sicula* Emery, 1891 (Sicilian amber: Emery, 1891). The following species are known from the Miocene deposits: *O. obesa* Heer, 1849, *O. radobojana* Heer, 1849 (Croatia: Heer, 1849), *O. leakeyi* Wilson et Taylor, 1964 (Kenya: Wilson and Taylor, 1964), *O. xiejiaheensis* Hong, 1984 (Shanwang, China: Hong, 1984) and *O. taurica* sp. nov. Apart from that, *Camponotites macropterus* Dlussky, 1981 from the Vishnevaya Balka locality with a forewing ca. 17 mm long (specimen PIN, no. 254/2880; Middle Miocene, Stavropol Region), is apparently a female of the genus *Oecophylla*.

Thus, to date, 13 fossil species of *Oecophylla* have been described, but, including *O. taurica* sp. nov. and the reassignment to this genus of two species of *Camponotites—O. macroptera* (Dlussky, 1981), comb. nov. and *O. kraussei* (Dlussky and Rasnitsyn, 1999), comb. nov.—the genus *Oecophylla* now includes 16 fossil species.

Remarks. *O. bartoniana* and *O. praeclara* were described based on isolated forewings, hence they may belong to one of the described species.

Oecophylla taurica Perfilieva, Dubovikoff et Dlussky, sp. nov.

Plate 7, fig. 6

Etymology. From the Tauric Peninsula, the ancient Greek name for the Crimean Peninsula.

Holotype. PIN, no. 4204/32, partial imprint of thorax, petiole and forewing of a female (?); Crimea, Kerch Peninsula, Malyi Kamyshlak; Middle Miocene, Upper Tarkhanian.

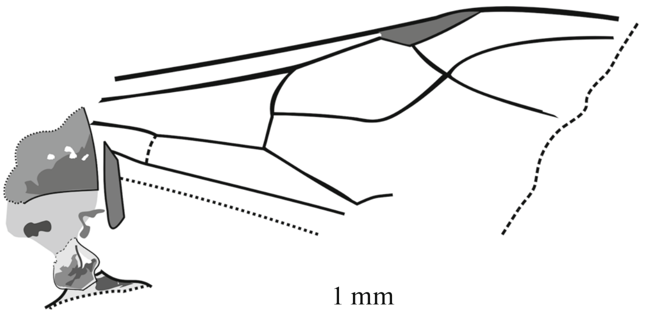


Fig. 7. *Oecophylla taurica* sp. nov., holotype PIN, no. 4204/32.

Description (Fig. 7). Forewing, part of a petiole and hind part of a alitrunk. The alitrunk is poorly visible. Only the posterior part of the petiole is visible. Apparently, the petiole is elongated; the node is poorly developed. The forewing lacks mediocubital and radiomedial cells. The forewing has diagnostic characters of *Oecophylla*: vein 5*RS* considerably concave within the cell 3r, crossvein 2*r-rs* strongly shifted toward the base of the pterostigma, and the convex S-like outline of the segment *RS* + *M*. The position of the vein *cu-a*: Icua = 2.2.

Measurements in mm. The forewing length is ca. 7.6.

Comparison. The imprint from the Tarkhanian of Crimea is distinct in the more proximal position of cu-a in the forewing (Icua = 2.2, in other fossil species ca. 1.6) and relatively long cell 3r.

Remarks. This imprint, despite its size small for *Oecophylla*, should be considered as a female based on the characteristics of the petiole and the relative width of the forewing. The discovery of such small weaver ant females is interesting in an ecological faunistic context. For instance, as an adaptation to co-habitation of various species of dendrobionts, including other species of weaver ants, such as took place in the Late Eocene biocoenoses of the Isle of Wight, Great Britain (Antropov et al., 2014).

Material. Holotype.

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