

Ants (Hymenoptera: Formicidae) from Localities of the Russian Far East (Amgu, Velikaya Kema)

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Abstract—The Paleontological Institute (Russian Academy of Sciences) has a collection of isolated ant wing imprints from Cenozoic localities from the territory of Russia, which were collected at different times. I describe for the first time imprints from the Amgu (one imprint of a forewing) and Velikaya Kema (16 wings) localities (Far East, Early Oligocene). Representatives of Dolichoderinae (*Emplastus amguensis* sp. nov., *E. obliquus* sp. nov., *E. similis* sp. nov., and *Technomyrmex kemaensis* sp. nov.; six imprints), Formicinae (*Camponotus parvus* sp. nov. and *Lasius vulgaris* sp. nov.; four imprints), Myrmicinae (*Paraphaenogaster ussuriensis* sp. nov.; three imprints) and Formicidae incertae sedis (four imprints) are recorded. The cooccurrence of ant species characteristic of temperate and tropical climates, as well as a large proportion of endobionts, is noted.

Keywords: Oligocene, Miocene, fossil ants, Formicidae, ant wings, Far East

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INTRODUCTION

The collection of the Laboratory of Arthropods of the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN), which was collected in different geographical places at different times, includes imprints of isolated wings of Formicidae. Since wing characters are almost unused as taxonomic features for recent ants and their variability is poorly studied, the description of imprints of individual wings and the determination of their taxonomic affiliation is a fairly difficult task. Our original studies and generalization of information from other authors allow us to state that the wings of ants are of no less taxonomic value than for other well-flying groups of Hymenoptera (Brown and Nutting, 1949; Perfilieva, 2000, 2010, 2011, 2021). With this in mind, it seems relevant and adequate to describe the available imprints of isolated ant wings for a preliminary assessment of the taxonomic composition of the myrmecofauna of the localities where they are found.

MATERIALS AND METHODS

In this study, I describe one forewing imprint from the Amgu localities (Primorsky Krai, Tatar Strait, Amgu River, eastern Sikhote-Alin) and fore- and hindwing imprints of 16 specimens from the Velikaya Kema locality (Primorsky Krai, Terney District, Velikaya Kema Village, Kema River, eastern Sikhote-Alin), which are in the collection of the Arthropod

Laboratory of the Paleontological Institute, Russian Academy of Sciences (PIN RAS). The assessments of the age of localities on the basis of descriptions of floristic complexes by different authors differ. The Kizi Formation (Velikaya Kema) in the regional stratigraphic scheme corresponds to the Late Oligocene–Middle Miocene geochronological interval. However, some researchers consider this formation an invalid straton (Pavlyutkin et al., 2014). The floristic complex corresponds to the so-called “Engelhardian” flora, which for a long time was attributed to the Middle Miocene. However, according to the most recent studies of floristic complexes, Amgu and Velikaya Kema localities are older and should be attributed to the Early Oligocene. I give both points of view, but indicate the latest dating in the descriptions.

According to the floristic analysis by D.A. Lopatina (2004), the age of the Amgu locality is estimated as the end of the Late Oligocene–beginning of the Early Miocene, and the age of the Velikaya Kema locality is the second half of the Early Miocene–beginning of the Middle Miocene (Fig. 1). Previously, the Bolshaya Svetlovodnaya locality (Late Eocene) rich in ant imprints was described from this region (Fig. 1) (Dlussky et al., 2015). According to Lopatina, the climate and floristic conditions in this region changed markedly in the Eocene–Middle Miocene time interval. The flora of the Bolshaya Svetlovodnaya locality corresponds to mixed mesophytic forests with dominance of highly thermophilic deciduous broad-

leaved genera with a high moisture coefficient of the flora (i.e. predomination of subtropical and tropical plant components), which indicates rather high average annual temperatures (10–13°C). Climate cooling and drying at the turn of the Eocene–Oligocene in this area was pronounced and manifested in the replacement of formal flowering genera by extant ones. More recent flora of Amgu (Late Oligocene–Early Miocene) is characterized by the dominance of conifers; Taxodiaceae also played a significant role, with an admixture of elm and birch. According to Lopatina's ecological and floristic analysis, the climate was cooler (average annual temperatures 3–10°C) than in Svetlovodnaya: cooling at the Oligocene–Miocene boundary was even more pronounced than at the Eocene–Oligocene boundary. A decrease in the role of hygro- and hydrophytes and an increase in the proportion of mesophytes indicates a marked decrease in humidity. The Velikaya Kema locality dates back to the time of the Miocene temperature optimum (the end of the Early Miocene–beginning of the Middle Miocene). It is characterized by coniferous–broad-leaved forests with a noticeable role of beech, Taxodiaceae, and various evergreens. The proportion of subtropical and tropical elements of vegetation (persimmon, magnolia, and horse chestnut) is significant. There is a similarity between the vegetation of the Miocene thermal optimum (Velikaya Kema) and the forests of this region during the Late Eocene–Early Oligocene (Bolshaya Svetlovodnaya), which corresponds to climatic conditions with average annual temperatures of 10–13°C (Lopatina, 2004).

In relatively recent works of paleobotanists, Amgu and Velikaya Kema (Klyuch Tikhii) are recognized as Early Oligocene (Rupel); however, the floristic composition of these localities is somewhat different (Pavlyutkin et al., 2014; Bondarenko et al., 2019). Despite the significant difference in the dating of localities by Lopatina and the cited authors, the assessments of the floristic situation by all authors are comparable. Floristic analysis of macrofossils by Bondarenko et al. (2019) suggests the presence of a broad-leaved deciduous forest with a high proportion of conifers (up to 25%) with participation of evergreen subtropical components. The flora of Amgu has a greater proportion of evergreen subtropical plants (18 vs. 8.3% in Tikhii Klyuch), and the authors classify it as a transitional ecotone (from broad-leaved warm temperate to subtropical mixed forest). The broad-leaved deciduous forest of Velikaya Kema is classified by the authors as a warm-temperate type of vegetation.

Thus, all authors note the presence of a mesophytic broad-leaved deciduous forest with a high proportion of conifers and a significant participation of subtropical evergreen components during the period of sedimentation in the Amgu and Velikaya Kema localities. Apparently, the flora had the character of modern mountain subtropical forests without the participation

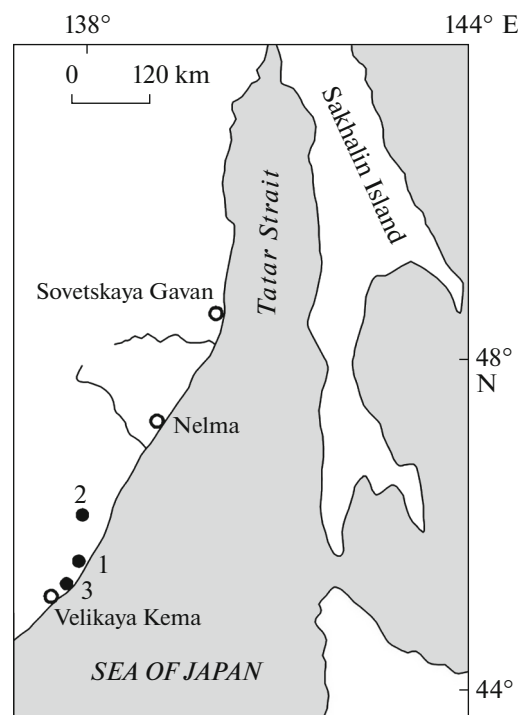


Fig. 1. Location of the studied localities: (1) Amgu, (2) Bolshaya Svetlovodnaya, (3) Velikaya Kema (by: Lopatina, 2004).

of lowland elements (absence of grasses). The climate at that time was characterized by rather high summer temperatures with a significant decrease in winter temperatures; i.e., seasonality in relation to the Eocene period increased.

The nomenclature of the venation of the forewing of ants according to A.P. Rasnitsyn (1980) is presented in Fig. 2a. Abbreviations of the names of the measurements used in the text and interpretation of the indices are as follows: FWL—forewing length; FWPt—distance between the bases of the wing and pterostigma; $Icu = [1Cu + (2M + Cu)]/1Cu$ reflects the position of the *cu-a* crossvein relative to the mediocubital (mcu) cell; $Icu_a = [(1M + Cu) + (2M + Cu)]/(1M + Cu)$ reflects the position of the *cu-a* crossvein relative to the wing base; $I(mcu) = (mcu \text{ cell height})/(mcu \text{ cell midline length})$ reflects the relative height of the mediocubital cell ($I(mcu) = 1$ indicates that the cell shape is close to a square; $I(mcu) > 1$ corresponds to a high and short cell, and $I(mcu) < 1$ corresponds to a low and long cell). The $I(mcu)$ index can be adequately used only for cells in which $RS + M$ is approximately parallel to $1Cu$ (i.e., trapezoidal, rectangular, square, and of parallelogram type). The radial cell index (I_r) is the ratio of lengths of cells $1 + 2r$ and $3r$.

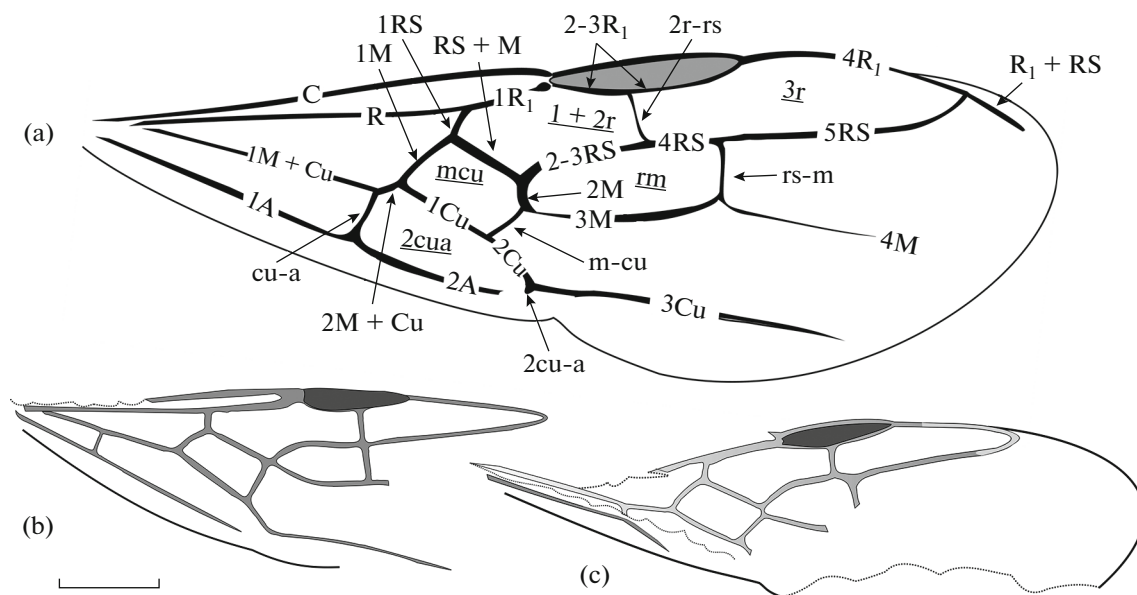


Fig. 2. (a) Nomenclature of the venation of the forewing of ants (by: Rasnitsyn, 1980); (b) *Emplastus amguensis* sp. nov., holotype PIN, no. 3135/1, forewing (mirror image), Amgu; (c) *E. obliquus* sp. nov., holotype PIN, no. 3136/9, forewing (mirror image), Velikaya Kema. Scale bar 1 mm.

SYSTEMATIC PALEONTOLOGY

Family Formicidae Latreille, 1809

Subfamily Dolichoderinae Forel, 1878

Genus (formal) *Emplastus* Donisthorpe, 1920

Type species. *Dolichoderus britannicus* Cockerell, 1915 (junior synonym: *Emplastus emeryi* Donisthorpe, 1920).

Diagnosis (for wings). Fossil ant imprints with signs of affiliation to the subfamily Dolichoderinae, whose preservation is not sufficient for describing a new orthotaxon or assigning to a known orthotaxon, yet with a certain set of traits. Forewings with three closed distal cells: 3r, rm, and mcu. Apex of 3r cell lies on wing margin; veins 1RS and 2r-rs departing from the radial vein at a right angle or with a slight slope. Mediocubital cell medium-sized, its distal edge not reaching level of base of pterostigma. $Icu > 1.45$, $Icu_a > 1.2$.

Species composition. To date, 12 fossil species have been described (AntWeb catalogue, August 2021): *E. macrops* Dlussky, Rasnitsyn et Perfilieva, 2015, *E. elongatus* Dlussky, Rasnitsyn et Perfilieva, 2015, and *E. biamoensis* (Perfilieva et Rasnitsyn, 2015) from the Upper Eocene of the Far East; *E. britannicus* (Cockerell, 1915), *E. hypolithus* (Cockerell, 1915), *E. gurnetensis* (Donisthorpe, 1920), and *E. kozlovi* Dlussky et Perfilieva, 2014 from the Upper Eocene of Great Britain; and *E. miocenicus* (Dlussky et Putyatina, 2014), *E. antiquus* (Mayr, 1867), *E. dubius* (Dlussky et Putyatina, 2014), *E. haueri* (Mayr, 1867), and *E. ocellus* (Heer, 1849) from the Miocene deposits of Croatia.

Remarks. Aneuretinae have a similar type of venation; however, in the wings of their recent representatives, the 3r cell is relatively longer in relation to other cells and the length of the entire wing than in dolichoderins. Today, the assignment of a wing with such venation to Aneuretinae can be rationally interpreted only in combination with other body characters, since it is impossible to assess the variability of venation of an entire subfamily by one (extant) species. The type of venation presented in this formal genus can be found in representatives of *Liometopum*, *Dolichoderus*, *Azteca*, *Technomyrmex*, and *Tapinoma*. However, the wing venation of representatives of these genera differs by the diverse shape of the mediocubital cell, the ratio of lengths of cells 1 + 2r and 3r, and/or the presence of a 4RS section in the rm cell (when rs-m is located much more distally to 2r-rs).

The wing venation of *Dolichoderus* is fairly variable: wings vary from the most complete type with a pentagonal radiomedial cell and well-expressed sections 2M and 4RS to a triangular rm cell with a stem (the 2RS + M section). The shape and relative dimensions of the mcu cell vary significantly. To identify the common venation patterns characteristic of representatives of this genus, additional studies are required.

The type of venation in some Myrmicinae is similar to that in *Emplastus*. However, extant Myrmicinae with a similar type of venation (*Pheidole*, *Messor*, *Myrmica*, *Pogonomyrmex*, and *Aphaenogaster*), in addition to the usually (but not always) open 3r cell, have distinctive features that allow their wing imprints to be attributed to orthotaxa. Therefore, the description of fossil Myrmicinae by the body imprints of ants with

wings will contribute to the correct assignment of wing imprints of this formal genus to Myrmicinae.

Emplastus amguensis Perfilieva, sp. nov.

Plate 10, fig. 1

E t y m o l o g y. From the location of the imprint at the Amgu River.

H o l o t y p e. PIN, no. 3135/1, forewing imprint; Primorsky Krai, Tatar Strait, Terney District, right bank of the Kudya River, a tributary of the Amgu River; Lower Oligocene, Granatnenskaya Formation.

D e s c r i p t i o n (Fig. 2b). The pterostigma is elongated. The radiomedial cell is triangular without a pronounced 2M section, without a stem, or the stem is as short as possible, almost not expressed; the cell length-to-width ratio is approximately 2.5. Crossveins 2r-rs and rs-m are on the same line. Medium-sized mediocubital cell is trapezoid, m-cu and 1M are almost of the same length (m-cu > 1M 1.1 times), 1Cu is 1.3 times as long as RS + M. The m-cu cell is elongated, its distal end does not reach the level of the pterostigma. The second cubital cell is not formed. The ratio of the lengths of the radial cells $I_r = 0.8$. $I_{cu} \sim 1.5$, $I_{cu-a} \sim 1.3$, $I(mcu) \sim 0.5$.

M e a s u r e m e n t s in mm. FWL ~ 7.0 . FWPt = 3.5, 3r cell length = 2, rm cell length = 1.1.

C o m p a r i s o n. A triangular radiomedial cell without stem is present in three species of this genus: *E. kozlovi* (FWL 7.8–8.8 mm in males), *E. haueri* (FWL 5.4 mm), and *E. miocenicus* (FWL 10.1 mm). The latter, in addition to its significantly larger size, differs from the new species in the rectangular shape of the mediocubital cell. *E. haueri* has a relatively short 3r cell and a smaller wing size. The greatest similarity is observed with *E. kozlovi* from the Eocene marls of Bembridge, but the relatively longer mediocubital cell in *E. amguensis* sp. nov. ($I(mcu)$ 0.7 and 0.5, respectively) has a different length ratio of 1M and m-cu. The wing sizes in the three species of this genus from Bolshaya Svetlovodnaya are somewhat smaller than in the new species (Dlussky et al., 2015).

R e m a r k s. Wing venation indicates affiliation to Dolichoderinae. Although individually the features of venation in *E. amguensis* sp. nov. and *E. kozlovi* are found in extant representatives of several genera of Dolichoderinae, a certain combination of venation features in these imprints is unique (triangular rm, absence of 4RS, trapezoid m-cu, and the ratio of 1M and m-cu, $I(mcu)$). Some extant *Tapinoma* have the most similar venation (e.g., specimen CASENT0109245, online catalog AntWeb.org), but, at the same time, a different shape of the mediocubital cell and a lower radial cell index ($I_r = 0.5$). There is also a strong similarity to the wing of the Aneuretinae; however, as noted above, in the absence of a body imprint, I do not consider this variant.

M a t e r i a l. Holotype.

Emplastus obliquus Perfilieva, sp. nov.

Plate 10, fig. 2

E t y m o l o g y. From the Latin *obliquus* (oblique, according to the characteristic shape of the mediocubital cell).

H o l o t y p e. PIN, no. 3136/9, forewing imprint; Primorsky Krai, Terney District, Velikaya Kema Village; Lower Oligocene, Kizi Formation.

D e s c r i p t i o n (Fig. 2c). The pterostigma is elongated. The radiomedial cell is quadrangular, without stem, with very short section 2M, about 1.9 times as long as wide. The crossvein rs-m is located distally to 2r-rs, so that 4RS and 2r-rs are of the same length. The medium-sized mediocubital cell is of a parallelogram type, so that the opposite sides are parallel and almost equal in length: $1M > m-cu$ 1.1 times; 1Cu and (RS + M) + 2M are of the same length. The m-cu cell is elongated, its distal end does not reach the level of the pterostigma. The second cubital cell is not formed. $I_r = 0.7$. $I_{cu} \sim 1.6$, $I_{cu-a} \sim 1.3$, $I(mcu) \sim 0.6$.

M e a s u r e m e n t s in mm. FWL 6.7–7.0. FWPt ~ 3.3 , 3r cell length = 1.9, rm cell length = 0.96.

C o m p a r i s o n. The measurements of the wings in three species of this genus from Bolshaya Svetlovodnaya are somewhat smaller than in the new species, and this imprint also differs significantly from all known *Emplastus* in the shape of the mediocubital cell.

R e m a r k s. A characteristic feature of the new species is the shape of the mediocubital cell, which is reflected in its name. The greatest similarity, including the shape of the m-cu cell, is observed with the wing venation of *Britaneuretus anglicus* (Cockerell, 1915) (Antropov et al., 2014). Some *Pachycondyla* have similar venation pattern; however, there are important differences: the proximal position of m-cu (the distal edge of the m-cu cell) relative to the pterostigma and cu-a, which are located at a distance from the m-cu cell, determine the affiliation of the wing to Dolichoderinae (or to the extinct genera of Aneuretinae, similarly to *Britaneuretus*).

M a t e r i a l. Holotype.

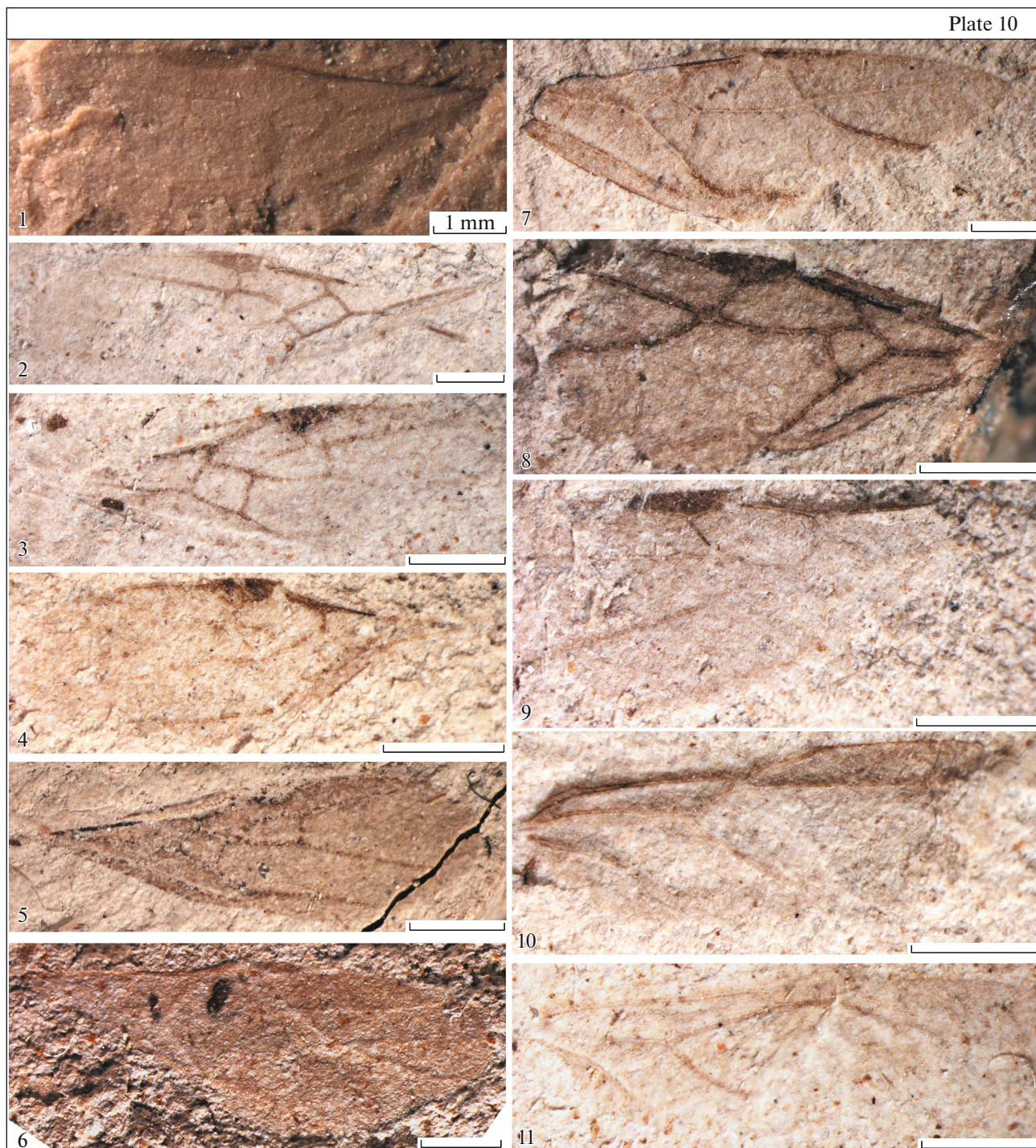
Emplastus similis Perfilieva, sp. nov.

Plate 10, fig. 3

E t y m o l o g y. From the Latin *similis* (like, similar).

H o l o t y p e. PIN, no. 3136/10, forewing imprint; Primorsky Krai, Terney District, Velikaya Kema Village; Lower Oligocene, Kizi Formation.

D e s c r i p t i o n (Fig. 3). The pterostigma is rounded. The 3r cell is closed, its apex is located close to the wing margin, the $R_1 + RS$ section is well-expressed. The radiomedial cell (rm) has no stem; there is a small zone of contact with the m-cu cell (the 2M section is very short), its length is 2.5 times its width. The transverse 2r-rs is slightly inclined with its lower end towards the apex of the wing. The m-cu cell is medium-sized, almost rectangular, 1M is equal to



Explanation of Plate 10

Fig. 1. *Emplastus amguensis* sp. nov., holotype PIN, no. 3135/1, forewing.

Fig. 2. *Emplastus obliquus* sp. nov., holotype PIN, no. 3136/9, forewing.

Fig. 3. *Emplastus similis* sp. nov., holotype PIN, no. 3136/10, forewing.

Figs. 4, 5. *Technomyrmex kemaensis* sp. nov., forewing: (4) specimen PIN, no. 3136/6; (5) holotype PIN, no. 3136/14.

Fig. 6. *Camponotus parvus* sp. nov., holotype PIN, no. 3136/359, forewing.

Figs. 7, 8. *Lasius vulgaris* sp. nov., forewing: (7) holotype PIN, no. 3136/3, female (?); (8) specimen PIN, no. 3136/7, male (?).

Fig. 9. *Paraphaenogaster ussuriensis* sp. nov., holotype PIN, no. 3136/1, forewing. Explanation: the dark branch from the pterostigma is not a vein, 2r-rs is light and is located distally to this artifact.

Figs. 10, 11. Formicidae inc. sed., hindwing: (10) specimen PIN, no. 3136/2; (11) specimen PIN, no. 3136/5.

Fig. 1—Amgu, figs. 2—11—Velikaya Kema; Lower Oligocene.

Scale bar 1 mm.

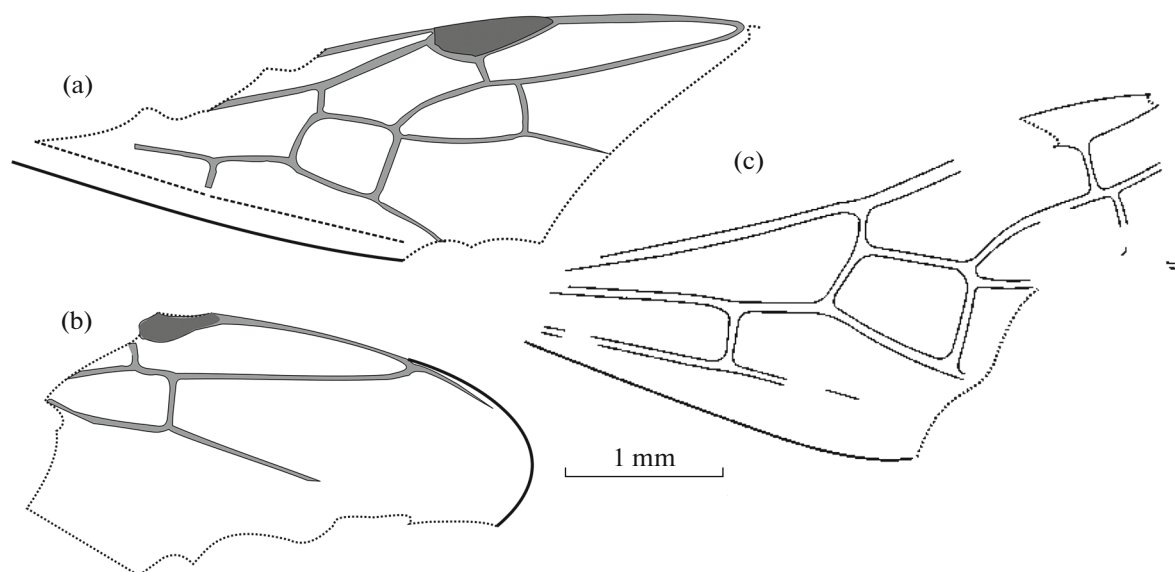


Fig. 3. *Emplastus* species: (a, b) *E. similis* sp. nov., forewings, Velikaya Kema: (a) holotype PIN, no. 3136/10, (b) specimen PIN, no. 3136/11 (mirror image); (c) *E. hypolithus* (Cockerell, 1915), holotype USNM 61411, Bembridge. Scale bar 1 mm.

m-cu and twice as long as 1RS. The rs-m crossvein is located much distally to 2r-rs but proximally to the level of the pterostigma apex, so that 4RS is well expressed. The crossvein cu-a is located at a distance from the m-cu cell. The second cubital cell is not formed. $Ir = 0.63$, $Icu = 1.3$, $Icu-a \sim 1.4$, $I(mcu) \sim 0.8$.

Measurements in mm. Holotype: FWL ~ 4.8 , FWpt = 2.8, 3r cell length = 1.7, rm cell length = 0.8.

Comparison. The wing is very similar in size and venation pattern to the wing of the holotype *Emplastus hypolithus* USNM 61411, from was described from the Eocene locality Bembridge, Great Britain (Fig. 3c). Small differences are observed in the wing sizes, in the relative length of the 2M + Cu and 4RS sections. Taking into account some differences in venation and due to the time interval separating these records, it is possible to describe a new species.

Remarks. The peculiarity of the described venation pattern is a combination of the characters that are each present in the wings of different extant dolichoderine genera, but do not occur together in any of them: the size of the wing is relatively small, the m-cu length is slightly greater than that of 1M, and the 4RS section is well-expressed. As a result, the assignment of the wing to the orthotaxon cannot yet be justified.

Material. Holotype (forewing) and imprint of the apical part of the wing, PIN, no. 3136/11.

Genus *Technomyrmex* Mayr, 1872

Type species. *Technomyrmex strenuous* Mayr, 1872; by monotypy.

Diagnosis (for wings). Forewings with closed distal cells (3r, rm, and m-cu). However, small males of

some species may have reduced distal rm and m-cu cells; in this case, the well-expressed bends of RS + M (at the point of departure of the reduced m-cu) and the free branch of M (at the point where the hypothetical rs-m passes into 4M) are retained. The radiomedial cell can be quadrangular (so that the 2M section is well expressed but is at least half as long as RS + M) or triangular with a very short stem (i.e. the 2RS + M section is short). A distinctive feature of the genus is the relatively small rectangular mediocubital cell. The second cubital cell is not formed. In small species, the hindwing has strongly reduced venation, without free M, all distal free branches are often represented by spectral veins or are reduced.

Species composition. The genus includes 94 extant species (AntWeb catalogue, August 2021), whose representatives are found on all continents. The greatest diversity of species is observed in the Old World (Africa and southern Asia), and only four species occur in the New World, two of which were, apparently, introduced by humans. They inhabit moist forests in warm-climate regions and build nests in the soil or on trees. Four fossil species have been described so far, two from Dominican amber (Brandão et al., 1999): *T. caritatis* Brandão et al., 1999 (worker) and *T. hispaniolae* (Wilson, 1985); *T. deletus* Emery, 1891 from Sicilian amber (worker) and *T. septentrionalis* Zhang, 1989 (male?) from the Miocene of China (Shanwong Formation, Shandong).

Technomyrmex kemaensis Perfilieva, sp. nov.

Plate 10, figs. 4, 5

Etymology. From the location of the imprint at the Kema River.

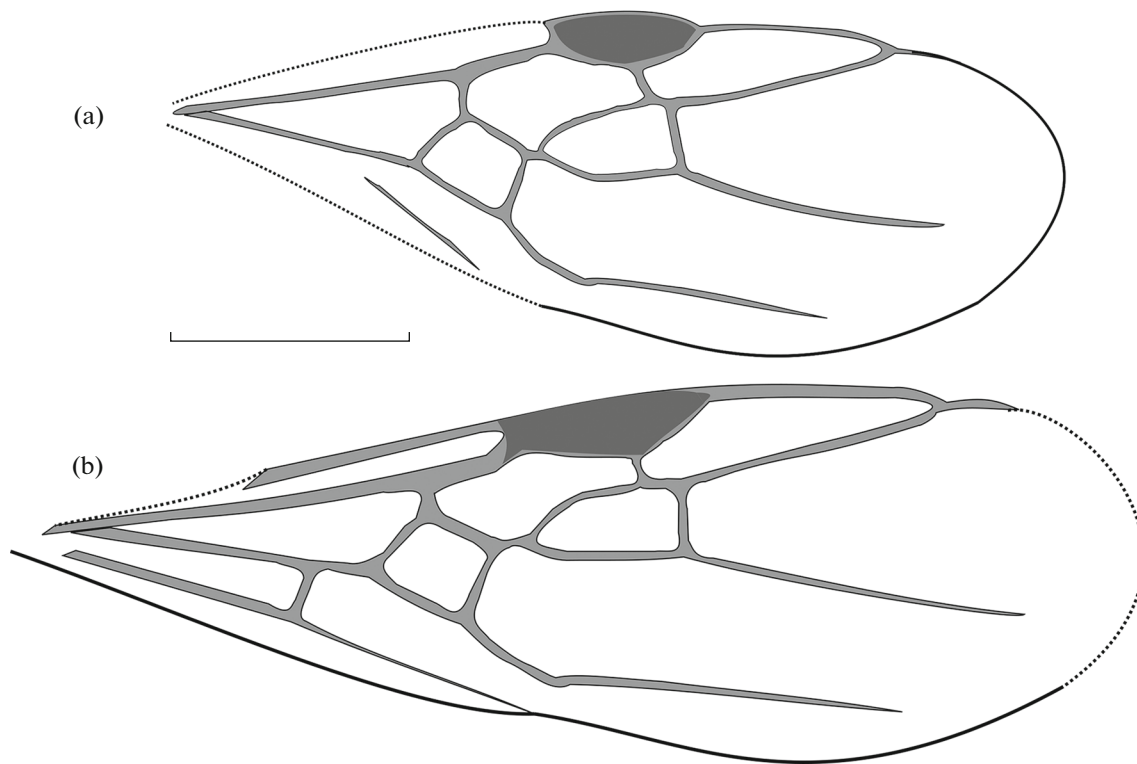


Fig. 4. *Technomyrmex kemaensis* sp. nov., forewing, Velikaya Kema: (a) specimen PIN, no. 3136/6, (b) holotype PIN, no. 3136/14. Scale bar 1 mm.

Holotype. PIN, no. 3136/14, imprint of forewing; Primorsky Krai, Terney District, Velikaya Kema Village; Lower Oligocene, Kizi Formation.

Description (Fig. 4). Wing with relatively large, rounded pterostigma. The 3r cell is closed, its apex is located on the edge of the wing, the R1 + RS section is located along the edge of the wing. The radiomedial cell is on a short stem, so that the 2RS + M section is no more than one quarter of the length of the rm cell. The rm cell length is 2.0–2.3 times its width. The 2-3RS section is curved. The transverse 2r-rs is slightly inclined with its lower end towards the apex of the wing. The mediocubital cell is relatively small, almost square in shape; 1M is 2 times longer than 1RS. The rs-m crossvein is located much more distally to 2r-rs but proximally to the level of the pterostigma apex, so that 4RS is well expressed. The crossvein cu-a is located not far from the mcu cell (in imprint no. 3136/6, cu-a is not seen). $Ir = 0.7$, $Icu = 1.7$, $Icu_a \sim 1.3$, $I(mcu) \sim 0.8$.

Measurements in mm. Holotype: FWL ~ 4.8 , FWPt = 2.1, 3r cell length = 1.3, 1M = m-cu = RS + M = 0.3, 2M + Cu = 0.3, 1M + Cu = 1, 1Cu = 0.5. Specimen PIN, no. 3136/6: FWL ~ 3.7 , FWPt = 1.6, 3r cell length = 1, 1M = m-cu = RS + M = 0.3, 1-2M + Cu = 0.9, 1Cu = 0.4.

Comparison. Wing imprints are available only in the Chinese *T. septentrionalis*, which is much larger (FWL = 6.7 mm).

Material. Holotype, imprints and counter-imprints of forewing, PIN, no. 3136/6.

Subfamily Formicinae Latreille, 1809

Genus *Camponotus* Mayr, 1861

Type species. *Formica ligniperda* Latreille, 1802, later designated by Bingham, 1903.

Diagnosis (for wings). Forewings with a closed 3r cell. The 1 + 2r cell is medium-sized, no longer than 3r. The radiomedial and mediocubital cells are absent. 1RS and 1M form a single straight line and are approximately equal in length. RS + M, which bounds the 1 + 2r cell, is smoothly curved and practically does not have an S-shaped bend. The second cubital cell is not formed.

Species composition. The genus includes more than 1000 extant species (1045 species, AntWeb catalog, August 2021) found on all continents. The greatest species diversity is observed in humid boreal ecosystems. To date, 31 fossil species from the Eocene to Miocene in localities of North America, Europe, and China have been described. Eocene: *C. cockerelli* (Donisthorpe, 1920) (Great Britain); *C. menzei* Mayr, 1868 (Baltic amber); *C. fuscipennis* Carpenter, 1930,

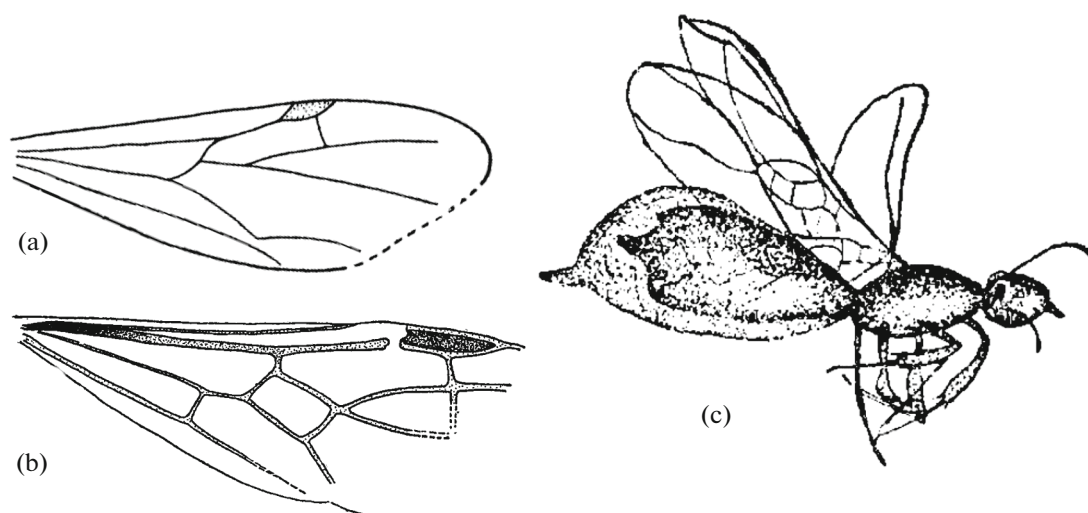


Fig. 5. Fossil specimens withdrawn from *Camponotus*: (a) *Myrmecites ullrichi* comb. nov. (*Camponotus ullrichi*, by: Bachmayer, 1960, text-fig. 8), (b) *Shanwangella palaeoptera* (*Camponotus palaeopterus*, by: Zhang, 1989, text-fig. 307), (c) *Camponotus* (?) *tokunagai* (by: Naora, 1933, text-fig. 19).

C. microcephalus Carpenter, 1930 *C. petrifactus* Carpenter, 1930, and *C. vetus* Scudder, 1877 (North America); *C. tokunagai* Naora, 1933 (amber, China). Oligocene: *C. vehemens* Förster, 1891 (Germany); *C. theobaldi* Ozdikmen, 2010, *C. compactus* Forster, 1891, *C. longiventris* Theobald, 1937, and *C. penninervis* Théobald, 1937 (France). Miocene: ten species from China—*C. ambon* Zhang, 1989, *C. ampullosus* Zhang, 1989, *C. curviansatus* Zhang, 1989, *C. gracilis* Zhang, 1989, *C. longus* Zhang, 1989, *C. microthoracicus* Zhang, 1989, *C. palaeopterus* (Zhang, 1989), *C. pictus* Zhang, Sun et Zhang, 1994, *C. plenus* Zhang, 1989, and *C. shanwangensis* Hong, 1984; four species from localities in Germany and Switzerland—*C. obesus* Python, 1935, *C. lignitus* (Germar, 1837), *C. heracleus* (Heer, 1849), and *C. oeningensis* (Heer, 1849); and one species from France, Croatia, Czech Republic, Austria, and North America, respectively: *C. crozei* Riou, 1999, *C. induratus* (Heer, 1849), *C. novotnyi* Samsinák, 1967, *C. ullrichi* Bachmayer, 1960, and *Paleosminthurus juliae* Pierce et Gibron, 1962 (transferred to *Camponotus*: Najt, 1987).

Remarks. *C. ullrichi* Bachmayer, 1960 should be excluded from the genus *Camponotus*. A schematic drawing of the wing and a photographic image of insufficiently good quality in the original publication do not allow unambiguously determining the taxonomic affiliation of the wing imprint. However, the open 3r and the proximal position of the branching of the free longitudinal branch of M relative to 2r-rs and the pterostigma, the mutual position of 1RS and 1M at an angle, the absence of the slope of 2r-rs, and other features point to the erroneous description of this wing as *Camponotus* (Fig. 5a) (Bachmayer, 1960). Most likely, it belongs to the subfamily Myrmicinae. There-

fore, here I transfer it to the formal genus of an unclear position—*Myrmecites ullrichi*, comb. nov.

The image and drawing of the Miocene *C. palaeopterus* (Zhang, 1989) are sufficiently distinct and detailed to rule out the affiliation of this ant to the genus *Camponotus*. Due to the presence of a radiomedial cell, its affiliation to Dolichoderinae is obvious (Fig. 5b). I believe that the original taxonomic position of this specimen (Zhang, 1989) should be restored: *Shanwangella palaeoptera* Zhang, 1989.

The affiliation of *C. tokunagai* Naora, 1933 is highly doubtful: the author's drawing of the wing not only does not correspond to *Camponotus* venation but is not comparable to any type of wing venation in ants (Fig. 5c). There are also doubts about the assignment of *C. microcephalus* Carpenter, 1930 to this genus, because 1RS in the wing drawing is at an angle to 1M; however, these statements require additional study of the material.

Camponotus parvus Perfilieva, sp. nov.

Plate 10, fig. 6

Etymology. From the Latin *parvus* (small).

Holotype. PIN, no. 3136/359, imprints and counter-imprints of the forewing of a male (?); Primorsky Krai, Terney district, Velikaya Kema Village; Lower Oligocene, Kizi Formation.

Description (Fig. 6). The pterostigma is small, rounded. The 3r cell is approximately 1.6 times longer than 1 + 2r. The 1RS section is approximately 1.9 times shorter than 1M. The RS + M and 5RS sections are smoothly curved. $Ir = 0.63$, $Icua = 1.5$.

Measurements in mm. FWL ~6; FWPt = 2.9; 3r cell length = 2.2.

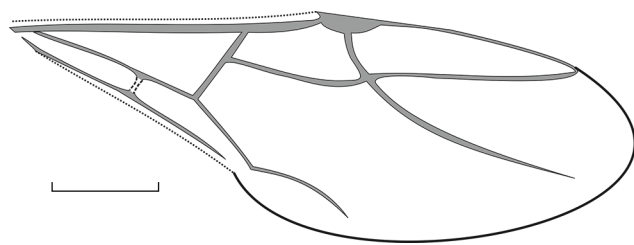


Fig. 6. *Camponotus parvus* sp. nov., holotype PIN, no. 3136/359, forewing (mirror image), Velikaya Kema. Scale bar 1 mm.

Comparison. Comparison of the features of the *Camponotus* wing imprints described to date is unproductive. First, the majority of the 28 fossil species (i.e., without the three imprints withdrawn from *Camponotus* in this paper) are described from females. Taking into account the pronounced sexual dimorphism in the size of sexual individuals in this genus, it is difficult to compare even the sizes of males and females from different localities. Since the wing length of the male *C. parvus* sp. nov. is 6 mm, it can be assumed that the size of females of this species may be 8–16 mm. Second, the standards of description and drawings of the majority of species described at the beginning of the last century do not allow comparison of the details of venation that are important for taxonomic purposes. Given these facts, our comparison shows that, among the known fossil representatives of *Camponotus*, there are three species with a relatively long 3r cell (Ir ca. 0.6): *C. curviansatus* (female, FWL = 10 mm), *C. longus* (female, FWL = 11.8 mm), and *C. gracilis* (male, FWL = 10.4 mm). However, the latter is much larger than *C. parvus* sp. nov. The synonymy of *C. parvus* sp. nov. with one of the two females of these two species cannot be ruled out without additional examination of the specimens.

Remarks. In the study of the wings of extant representatives of Formicinae, it was shown that males have relatively wider wings than females of this subfamily, regardless of the absolute size of individuals (Perfilieva, 2007, 2021). From these data, I assume that the wing imprint of *C. parvus* sp. nov. belongs to a male.

Material. Holotype.

Genus *Lasius* Fabricius, 1804

Type species. *Formica nigra* (L., 1758), later designated Bingham, 1903.

Diagnosis (for wings). Forewings with two distal cells: 3r and m-cu. There is no radio medial cell. The m-cu cell in small males may be absent due to the reduction of the crossvein m-cu. The 1 + 2r and 3r cells are medium-sized, the latter is usually relatively longer than the former. The m-cu cell is trapezoid, usually medium-sized, sometimes relatively small; 1M

and m-cu are approximately equal in length, 1Cu is slightly longer than the 1RS + M section. The 2RS + M section, as a rule, is smoothly curved, without S-shaped bend. The 2r-rs is straight and explicitly tilted with its lower end to the top of the wing; 5RS and the free branch of M emerge from the same point, the bend of the latter is noticeably greater than that of 5RS.

Species composition. Currently, there are 127 extant species of *Lasius* inhabiting the Holarctic region and 22 fossil species (AntWeb catalog, August 2021). Two species are known from the Eocene of the United States: *L. glom* LaPolla and Greenwalt, 2015 and *L. peritulus* (Cockerell, 1927). Four fossil species are known from Baltic amber: *L. punctulatus* Mayr, 1868, *L. pumilus* Mayr, 1868, *L. schiefferdeckeri* Mayr, 1868, and *L. nemorivagus* Wheeler, 1915 (Dlussky, 2011). In the Oligocene deposits of France, *L. epicentrus* Théobald, 1937 (male) was found. Miocene representatives of the genus have been described from different localities: Croatia—*L. occultatus* (Heer, 1949), *L. globularis* (Heer, 1949), *L. longaevus* (Heer, 1949), *L. ophthalmicus* (Heer, 1949), *L. anthracinus* (Heer, 1867), and *L. longipennis* (Heer, 1849) (Dlussky and Putyatina, 2014); China—*L. inflatus* (Zhang, 1989), *L. truncatus* Zhang, 1989 (female), *L. validus* Zhang, 1989, and *L. mordicus* Zhang, 1989 (Zhang, 1989); Russia—*L. vetulus* Dlussky, 1981 and *L. tertarius* Zalessky, 1949; Poland—*L. oblongus* Assmann, 1870; France—*L. crispus* Théobald, 1935, as well as *L. chambonensis* Théobald, 1935 from the Pliocene deposits.

Remarks. One or both species known from the Upper Eocene deposits of the Isle of Wight, the formal taxon *Leucotaphus donisthorpei* Dlussky et Perfilieva, 2014, and *L. gurnetensis* (Cockerell, 1915), may also belong to *Lasius* (Antropov et al., 2014).

Lasius vulgaris Perfilieva, sp. nov.

Plate 10, figs. 7, 8

Species name. From the Latin *vulgaris* (typical, common).

Holotype. PIN, no. 3136/3, imprints and counter-imprints of the forewing of a female (?); Primorsky Krai, Terney District, Velikaya Kema Village; Lower Oligocene, Kizi Formation.

Description (Fig. 7). The 1 + 2r and 3r cells are medium-sized, the latter being relatively longer than the former. The m-cu cell is trapezoid, medium-sized; 1M and m-cu are approximately equal in length, 1Cu is approximately 1.9 times longer than the 1RS + M section; 2RS + M and 5RS sections are slightly convex, almost straight lines, without bends. The 2r-rs is straight and clearly oblique. $Ir = 0.6$, $I(mcu) = 0.8$, $Icu \sim 2-2.2$. Icu cannot be calculated because the base of the wing has not been preserved.

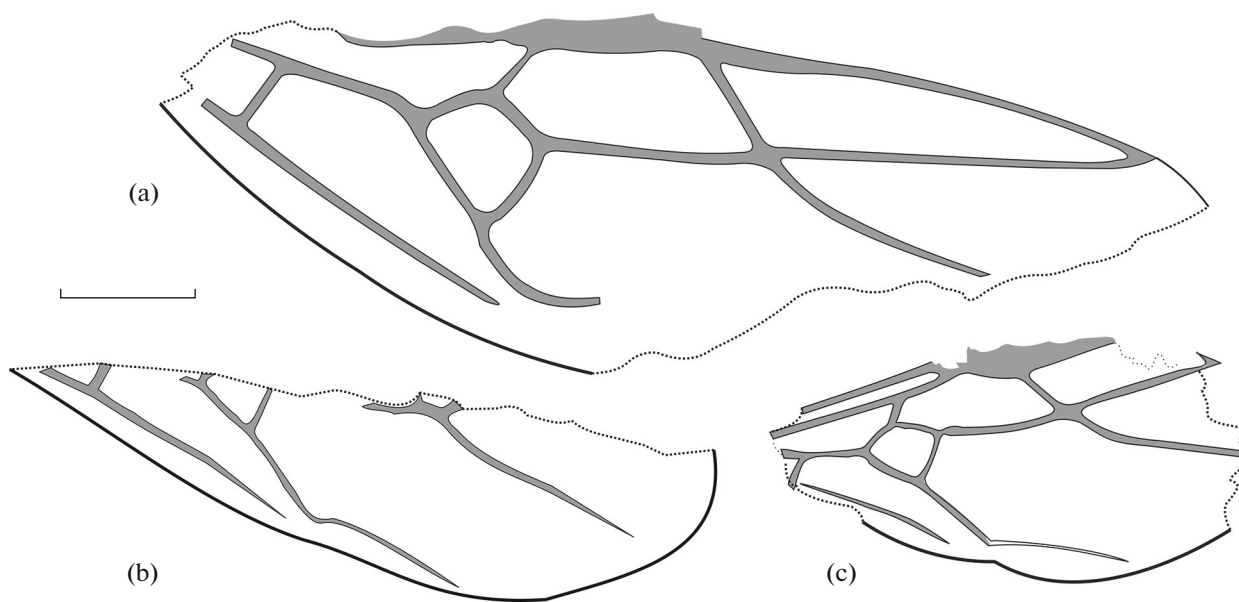


Fig. 7. *Lasius vulgaris* sp. nov., forewing: (a) holotype PIN, no. 3136/3, female (?), (b) specimen PIN, no. 3136/8, male (?), (c) specimen PIN, no. 3136/7, male (?) (mirror image); Velikaya Kema. Scale bar 1 mm.

Measurements in mm. FWL (female, holotype) ~9–9.5 (the length of the visible part of the imprint from cu-a to the top of the 3r cell is ca. 6.6), FWL (males, specimens nos. 3136/7 and 8) ~5–5.4 (the length of the visible part of the imprint from cu-a to the top of the 3r cell is ca. 3.2).

Comparison. Wing measurements of the majority of the described fossil *Lasius* species and two *Leucotaphus* species differ from the described species. Wing measurements in the Oligocene *L. epicentrus* are similar; however, the wing pattern is insufficiently detailed for analysis. Of particular interest is the comparison with other Miocene species of a suitable size class: *L. anthracinus* and *L. occultatus* have a higher *mcu* cell, in *L. ophthalmicus* cu-a is located much farther from the *mcu* cell, *L. validus* and *L. chambonensis* have a relatively shorter 3r cell. Chinese *L. truncatus* is without wings; therefore, comparison cannot be performed. *Leucotaphus donisthorpei* differs in its relatively small *mcu* cell.

Remarks. Judging by the proportions of the wings, the smaller wings belong to the males, and the larger ones belong to the female. Since other features of venation are very similar, I consider it possible to combine the three imprints into one species. The absolute sizes of the wings were calculated from the reconstructions performed on the basis of the analysis of the shape of the wings of extant *Lasius*.

Material. In addition to the holotype, specimen PIN, no. 3136/7 is an imprint (or counter-imprint) of the central part of the forewing of a male (?), and specimen PIN, no. 3136/8, is an incomplete imprint of the lower part of the forewing of a male (?).

Subfamily Myrmicinae Lepeletier De Saint-Fargeau, 1835

Genus (formal) *Paraphaenogaster* Dlussky, 1981

Type species. *Paraphaenogaster microphthalma* Dlussky, 1981, Miocene of the North Caucasus.

Diagnosis (for wings). Forewings with a reduced *rm* cell. The third radial cell is usually open: the free branch of *RS* is long, does not reach *R*₁; however, in rare cases, they are connected, so that 3r is closed. The crossvein 2r-rs is strictly vertical in relation to the lower margin of the pterostigma or slightly inclined with its lower end to the base of the wing, relatively short. The radiomedial cell is absent due to the complete reduction of the crossvein rs-m. The 2RS + M and 3RS segments are well defined; as a result, the free branch of M branches off much proximally to 2r-rs. The *mcu* cell is trapezoidal, medium-sized. The second cubital cell is not formed.

Species composition. Eleven fossil species were described from the Upper Eocene to the Middle Miocene. From the Upper Eocene of Great Britain, *P. hooleyana* Dlussky et Perfilieva, 2014 (Isle of Wight, Bembridge) is known. Six species from the Upper Oligocene of Germany (Enspel): *P. bizeri* Jessen, 2020, *P. freihauti* Jessen, 2020, *P. loosi* Jessen, 2020, *P. schindleri* Jessen, 2020, *P. wettlauferi* Jessen, 2020, and *P. wuttkei* Jessen, 2020. From the Miocene of China: *P. dumetorum* (Lin, 1982). From the Lower Miocene of Croatia (Radoboy): *P. tertiaria* (Heer, 1849) and *P. jurinei* (Heer, 1849). From the Middle Miocene of the Stavropol Krai (Russia, Vishnevaya Balka): *P. microphthalma* Dlussky, 1981.

Remarks. It is advisable to consider representatives including in the analysis of this genus three Miocene species from China, which are assigned to

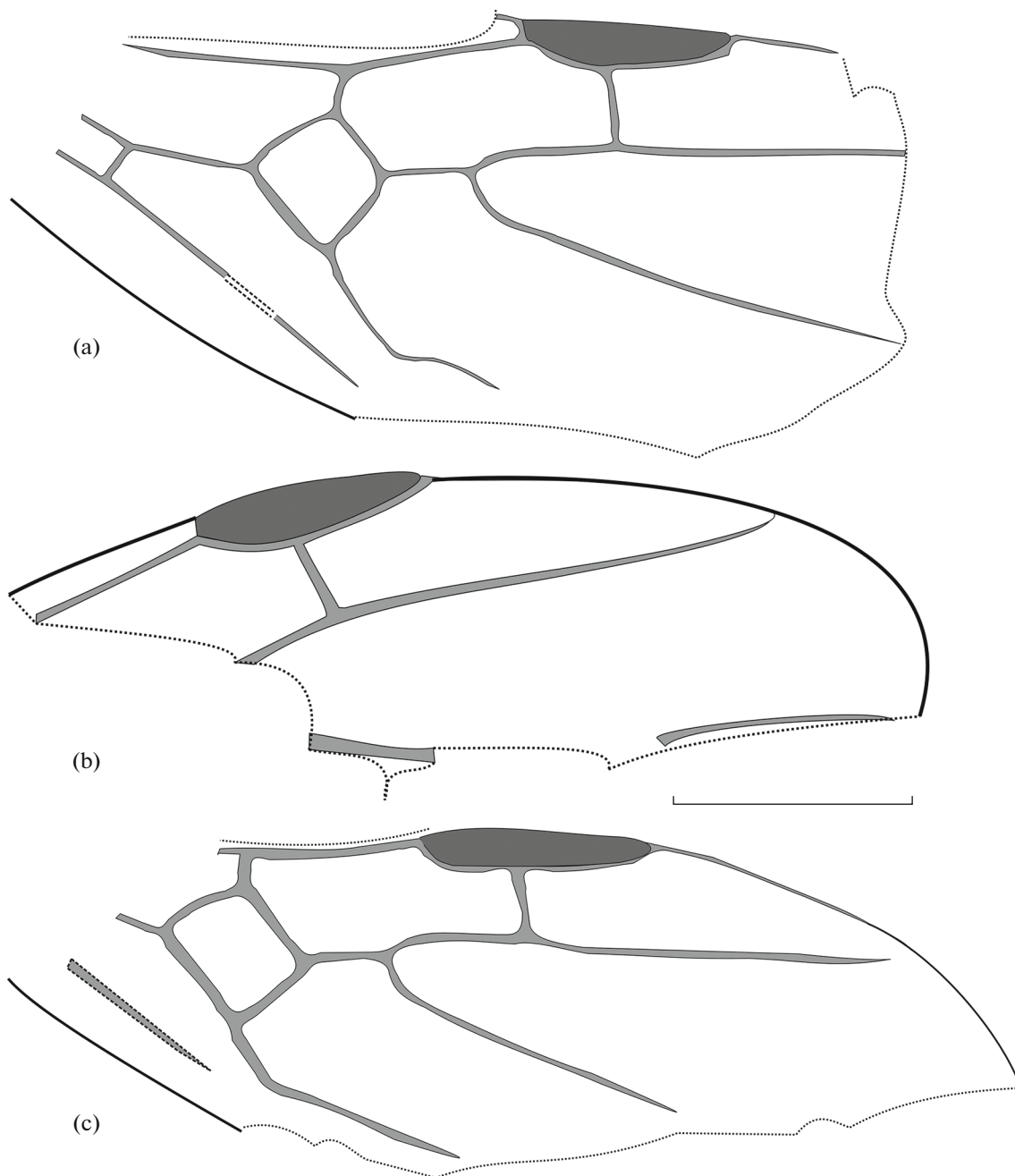


Fig. 8. *Paraphaenogaster ussuriensis* sp. nov., forewing: (a) holotype PIN, no. 3136/1, (b) specimen PIN, no. 3136/362 (mirror image), (c) specimen PIN, no. 3136/4, Velikaya Kema. Scale bar 1 mm.

Aphaenogaster: *A. lapidescens* Zhang, 1989, *A. paludosa* Zhang, 1989, and *A. shanwangensis* (Hong, 1984). *P. hooleyana* Dlussky et Perfilieva, 2014 has the most deviant wing venation among all other species, namely, a relatively short 3RS section. In our opinion, the formal character of the genus needs to be revised on the basis of the currently fairly representative paleontological material, including males, winged females, and workers. Accordingly, its composition should be revised. This work is planned for the near future.

Paraphaenogaster ussuriensis Perfilieva sp. nov.

Plate 10, fig. 9

Etymology. From the historical name of the geographical region, the Ussuri region.

Holotype. PIN, no. 3136/1, impressions and counter-impressions of the forewing; Primorsky Krai, Terney district, Velikaya Kema Village; Lower Oligocene, Kizi Formation.

Description (Fig. 8). The pterostigma is oblong. The top of the 3r cell is poorly visible, so it is

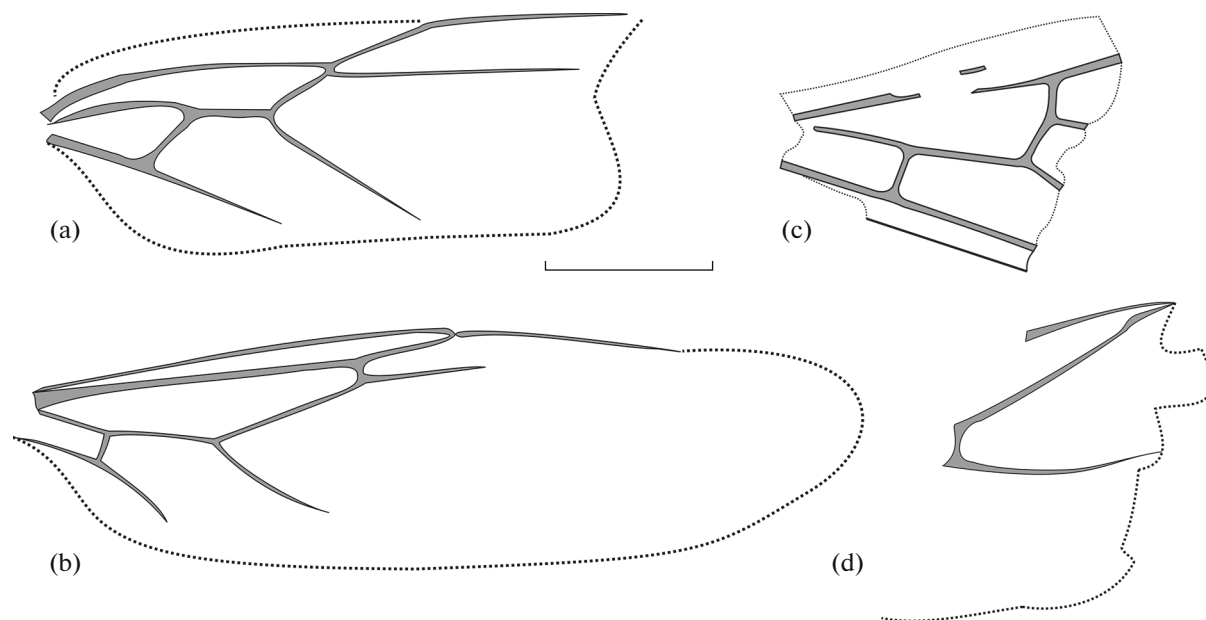


Fig. 9. Imprints assigned to Formicidae inc. sed.: (a) specimen PIN, no. 3136/2, hindwing; (b) specimen PIN, no. 3136/5, hindwing; (c) specimen PIN, no. 3136/12 (mirror image); (d) specimen PIN, no. 3136/13, Velikaya Kema. Scale bar 1 mm.

difficult to determine whether or not it is closed. The mediocubital cell is medium-sized, trapezoid, the 1M and m-cu are of the same length, the 1Cu section is 1.1–1.4 times as long as 1RS + M. The transverse 2r-rs is vertical. The free branch of M departs from 2RS + M much more proximally than 2r-rs, so that the length of 2RS + M is ~1.7 times shorter than that of 3RS. $Icu = 2.1$, $I(mcu) = 1$.

Measurements in mm. Holotype: FWL ~5, 1R1 ~0.7, 1Cu ~0.5.

Comparison. The wings of the new species are smaller than the wings of all species described to date (except *P. hooleyana*, which has a unique venation that distinguishes it from all other *Paraphaenogaster*, see above). The ratio of different vein segments specific for the new species (mcu shape, 2RS + M/3RS ratio, etc.) should also be noted.

Remarks. Three incomplete wing imprints, assigned by us to this species, are almost of the same size and are very similar in the venation pattern.

Material. In addition to the holotype, specimen PIN, no. 3136/4, imprints and counter-imprints of the forewing without proximal part, and specimen PIN, no. 3136/362, distal part of the wing.

* * *

Almost complete imprints and counter-imprints of two hindwings of different ant species from Velikaya Kema, specimens PIN, nos. 3136/2 and 5 (Plate 10, figs. 10, 11) were identified as Formicidae inc. sed.; the length of both wings is ~5.2 mm (Figs. 9a, 9b). Both specimens have a reduced free branch of M. In

the wing of specimen no. 3136/2, rs-m is relatively short, its length is approximately equal to the length of the 2M + Cu segment, the 1RS vein is not well-expressed, cu-a is relatively long (~0.4 mm) (see Fig. 9a) (Plate 10, fig. 10). In the wing of specimen 3136/5, rs-m is relatively long, about 1.5 times as long as the 2M + Cu section, the 1RS vein well-expressed, and cu-a is relatively short (~0.2 mm) (Fig. 9b; Plate 10, fig. 11).

Imprint of the base of the forewing, specimen PIN no. 3136/12: according to the position of cu-a relative to the base of the wing and the mcu cell, the wing obviously has a mediocubital cell and may belong to representatives of Formicinae, Dolichoderinae, or Myrmicinae (Fig. 9c). FWL ~4.8 mm, the length of the visible part of the wing imprint is ~2 mm.

Imprint of the apical part of the wing, specimen PIN no. 3136/13 (the apex of 3r is poorly seen). Most likely, the wing does not belong to a representative of Formicinae (Fig. 9d). FWL ~4 mm, the length of the visible part of the wing imprint is ~1.7 mm.

DISCUSSION

Given the small number of ant imprints available from the Amgu and Velikaya Kema localities, only a preliminary analysis of the features of these records can be made. The simultaneous presence of elements of myrmecocomplexes of the temperate zone and tropical thermophilic species shows that the situation known as “Wheeler’s dilemma”—found in the rich locality of this region in the Late Eocene (Bolshaya Svetlovodnaya) is also observed here in the Early Oligocene, although with a different taxonomic composi-

tion. For example, in Svetlovodnaya of the Late Eocene, these were the temperate *Formica* and, apparently, *Lasius* alongside the thermophilic *Gesomyrmex* and Myrmecinae, and in the Velikaya Kema locality these were *Lasius* and *Technomyrmex*, respectively. Representatives of *Technomyrmex* (before our record) were known to appear in the fossil record in the Late Oligocene (Sicilian amber). Apparently, this thermophilic representative of the myrmecofauna, which is currently distributed in the tropical and subtropical regions of the Old World (species introduced by humans in the New World), previously had a much wider range (Sicilian amber, Velikaya Kema, Dominican amber, and Shangwong). Our data are consistent with the presented floristic conclusion about a warmer climate in this area in the early Oligocene than at present.

The high species diversity of this oryctocenosis should be noted: 14 imprints of the forewings correspond to seven different species of three subfamilies. Of interest is a significant number of individuals (seven specimens) and the predominance in terms of taxonomic diversity (five species) of ants associated with an arboreal lifestyle—all species of Dolichoderinae and *Camponotus*, against a background of a smaller proportion of myrmecines, represented by one species of *Paraphaenogaster*, and in the complete absence of geobionts and poneromorph stratobionts. Such a ratio of life forms is characteristic of inclusions in resins and is found in sedimentary deposits only in the North American localities Green River (Early Eocene) and Florissant (Terminal Eocene). The high proportion of dendrobionts confirms the idea of paleobotanists about the pronounced forest character of the Amgu and Velikaya Kema flora without an admixture of plain components; however, so far the absence of poneromorphs can be explained only by the small number of records of ants from these localities.

The subfamily Myrmicinae is represented in the localities described in this paper by the only species of the formal genus *Paraphaenogaster*. Species of this genus are found in the oryctocenoses of Europe from the Upper Eocene to the Miocene, as well as in the Miocene locality Shangwong (China). Their representation is often very high. In the late Eocene Bembridge, myrmecines are very scarce (less than 1% of imprints); however, three-quarters of all imprints of Myrmicina belong to this genus. Six species of *Paraphaenogaster* were described from the Late Oligocene locality Enspel (Germany). As much as 80% of all myrmecines, which account for approximately one-third of all imprints, are observed in the Late Oligocene Rotte (Germany). All Myrmicinae (accounting for 40% of the imprints) in the Miocene Vishnevaya Balka (Stavropol) are represented by imprints of several species of this genus, and in the Middle Miocene Shangwong, four out of five Myrmicinae imprints belong to one *Paraphaenogaster* species. However, in the rich locality of the Late Eocene of the Far East

(Bolshaya Svetlovodnaya), there are no *Paraphaenogaster* among the myrmecine imprints, which account for 21% of all imprints. Apparently, the presence of this genus should be interpreted as a later “acquisition” of the local myrmecofauna. Thus, according to the available data, it can be preliminarily concluded that the myrmecofauna of the Velikaya Kema locality is more similar to that of the Chinese Shangwong locality than to the myrmecofauna of the geographically closer but older Late Eocene locality Bolshaya Svetlovodnaya.

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CONFLICT OF INTEREST

The author declares that she has no conflicts of interest.

REFERENCES

- Antropov, A.V., Belokobylskij, S.A., Compton, S.G., et al., The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the Insect Limestone (Late Eocene) of the Isle of Wight, UK, *Earth Environ. Sci. Trans. R. Soc. Edinburgh*, 2014, vol. 104, nos. 3–4, pp. 335–446.
- AntWeb. Version 8.64.2. California Acad. Sci. <https://www.antweb.org>. Accessed August 13, 2021.
- Bachmayer, F., Insektenreste aus den Congerenschichten (Pannon) von Brunn-Vösendorf (südl. von Wien) Niederösterreich, *Sitzungsber. Österr. Akad. Wiss. Math.-Naturwiss. Kl., Abt. I*, 1960, vol. 169, pp. 11–16.
- Bondarenko, O.V., Blokhina, N.I., and Utescher, T., Major plant biome changes in the Primorye Region (Far East of Russia) during the Paleogene, *Bot. Pac.*, 2019, vol. 8, no. 1, pp. 3–18.
- Brandão, C.R.F., Baroni, UrbaniC., Wagensberg, J., et al., *Technomyrmex* in Dominican amber (Hymenoptera: Formicidae), with a reappraisal of Dolichoderinae phylogeny, *Entomol. Scand.*, 1999, vol. 29, pp. 411–428.
- Brown, W.L. and Nutting, W., Wing venation and the phylogeny of the Formicidae, *Trans. Am. Entomol. Soc.*, 1949, vol. 75, nos. 3–4, pp. 113–132.
- Dlussky, G.M., The ants of the genus *Lasius* Fabricius (Hymenoptera, Formicidae) from the Late Eocene European ambers, *Vestn. Zool.*, 2011, vol. 45, no. 3, pp. 209–222.
- Dlussky, G.M. and Putyatina, T.S., Early miocene ants (Hymenoptera, Formicidae) from Radoboj, Croatia, *N. Jb. Geol. Paläontol. Abh.*, 2014, vol. 272, no. 3, pp. 237–285.

- Dlussky, G.M., Rasnitsyn, A.P., and Perfilieva, K.S., The ants (Hymenoptera: Formicidae) of Bol'shaya Svetlovodnaya (Late Eocene of Sikhote-Alin, Russian Far East), *Caucasian Entomol. Bull.*, 2015, vol. 11, no. 1, pp. 131–152.
- Lopatina, D.A., Vegetation and climate of the Eocene–Miocene of eastern Sikhote-Alin according to paleobotanical analysis data, *Tikhookean. Geol.*, 2004, vol. 23, no. 3, pp. 98–112.
- Najt, J., Le Collembole fossile *Paleosminthurus juliae* est un Hyménoptère, *Rev. Fr. Entomol. (N. Ser.)*, 1987, vol. 9, pp. 152–154.
- Pavlyutkin, B.I., Chekryzhov, I.Yu., and Petrenko, T.I., *Geologiya i flory nizhnego oligotsena Primor'ya* (Geology and Floras of the Lower Oligocene of Primorye), Vladivostok: Dal'nauka, 2014.
- Perfilieva, K.S., Wing anomalies in sexual ants (Hymenoptera, Formicidae) with different mating strategies, *Zool. Zh.*, 2000, vol. 79, no. 11, pp. 1311–1312.
- Perfilieva, K.S. Characterization of the variability of quantitative traits of wings using some ant species (Hymenoptera, Formicidae) as an example, *Usp. Sovr. Biol.*, 2007, vol. 127, no. 2, pp. 147–156.
- Perfilieva, K.S., New data on the wing morphology of the Cretaceous Sphecomyrminae ants (Hymenoptera: Formicidae), *Paleontol. J.*, 2011, vol. 45, no. 3, pp. 275–283.
- Perfilieva, K.S., Distribution and differentiation of fossil *Oecophylla* (Hymenoptera: Formicidae) species by wing imprints, *Paleontol. J.*, 2021, vol. 55, no. 1, pp. 76–89.
- Perfilieva, K.S., Trends in the evolution of wing venation in ants (Hymenoptera, Formicidae), *Zool. Zh.*, 2010, vol. 89, no. 8, pp. 965–977.
- Rasnitsyn, A.P., Origin and evolution of Hymenoptera insects, in *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Trans. Paleontol. Inst. USSR Acad. Sci.), Moscow: Nauka, 1980, vol. 174.
- Zhang, J., *Fossil Insects from Shanwang, Shandong, China*, Jinan: Shandong Sci. Technol. Publ. House, 1989.

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