

The Ants (Hymenoptera: Formicidae) of Bol'shaya Svetlovodnaya (Late Eocene of Sikhote-Alin, Russian Far East)

Муравьи (Hymenoptera: Formicidae) Большой Светловодной (поздний эоцен, Сихотэ-Алинь, Дальний Восток, Россия)

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Key words: Hymenoptera, Formicidae, Late Eocene, Russian Far East, ant assemblage, Cenozoic, equable climate, *Gesomyrmex*.

Ключевые слова: Hymenoptera, Formicidae, эоцен, мирмекокомплекс, муравьи, Приморский край, климат, кайнозой.

Abstract. The ant fossils of the Bol'shaya Svetlovodnaya (Late Eocene of Sikhote-Alin, Russian Far East) are studied. A total of 80 specimens are identified as Formicidae. The location is quite diverse in composition of ant: described 15 genera and 9 subfamilies. A generic level comparison reveals Svetlovodnaya ants as more similar to European rather than North American ant fauna. Unusually high proportion Myrmicinae (21.4%) for the known deposits of Europe, where these ants become abundant only in the Miocene. A distinctive feature of the Svetlovodnaya ant assemblage under comparison with the European and North American ones is the lack of highly dominating species. Presences of strictly tropical and temperate taxa support the equable climate concept as applicable to the Late Eocene climate of the Sikhote-Alin area.

New genera and species are described from the Bol'shaya Svetlovodnaya: Aneuretinae – *Paraneuretus dubovikoffi* sp. n., Dolichoderinae – *Dolichoderus pinguis* sp. n., *Emplastus macrops* sp. n., *Emplastus elongates* sp. n., *Emplastus dubius* sp. n., *Liometopum incognitum* sp. n., Formicinae – *Formica biamoensis* sp. n., *Formica paleosibirica* sp. n., *Gesomyrmex magnus* sp. n., *Gesomyrmex macrops* sp. n., *Gesomyrmex incertus* sp. n., Myrmeciinae – *Ypresiomyrma orientalis* sp. n., Amblyoponinae – *Casaleia orientalis* sp. n., Ponerinae – *Pachycondyla oligocenica* sp. n., *Pachycondyla aberrans* sp. n., Proceratiinae – *Proceratium petrosus* sp. n., Myrmicinae – *Agastomyrma laticeps* sp. n., *Biamomyrma zherikhini* sp. n., *Biamomyrma lata* sp. n., *Biamomyrma rugosa* sp. n., *Myrmecites sibiricus* sp. n., *Myrmecites dubius* sp. n., *Myrmecites major* sp. n., also at least two species of *Lasius* and one species of *Cerapachyinae*.

Резюме. В статье приведены результаты исследования позднеэоценового местонахождения

Большая Светловодная Приморского края (Сихотэ-Алинь, Дальний Восток, Россия). Восемьдесят отпечатков насекомых из Большой Светловодной можно с уверенностью отнести к Formicidae. Из них 56 были определены до подсемейства, 45 до уровня рода и 43 отпечатка имеют видовую принадлежность. Всего описано 26 видов муравьев из 15 родов 9 подсемейств, из которых 2 рода и 23 вида являются новыми для науки. Наибольшую долю отпечатков (41.1% от всех определенных до подсемейства Formicidae) составляют экземпляры, отнесенные к подсемейству Formicinae. На втором месте по обилию особей находится подсемейство Myrmicinae (21.4%), затем последовательно Dolichoderinae (17.9%) и Ponerinae (7.1%). Оставшиеся подсемейства Aneuretinae, Proceratiinae и Myrmeciinae представлены каждое одним-двумя экземплярами. Произведено сравнение мирмекокомплексов разных частей света сходного с Большой Светловодной возраста. На родовом уровне мирмекокомплекс местонахождения в Приморском крае ближе к европейским фаунам, чем к американским. По соотношению представителей разных подсемейств и жизненных форм Большая Светловодная наиболее близка к европейскому позднеолигоценному местонахождению Ротт (Rott, Германия), против ожиданий сходства с североамериканскими позднеэоценовыми отложениями Green River и олигоценным Florissant. В то же время фауна тафоценоза Светловодной отличается от всех эоценовых и олигоценных отложений Европы необычайно высокой долей представителей подсемейства Myrmicinae. Состав родов мирмицин достаточно специфичен для Светловодной. Осторожная оценка показывает

схожесть мирмекофауны Большой Светловодной и китайских местонахождений по характерному отсутствию явных доминирующих групп как по числу экземпляров, так и видов. Наличие наравне с обычными обитателями умеренного климата (*Lasius* и *Formica*) муравьев теплых тропиков *Aneuretinae*, *Gesomyrmex* и *Myrmeciinae* свидетельствует в пользу того, что во времена захоронения климат этой местности был значительно более ровный и мягкий.

Из местонахождения описаны новые виды: *Aneuretinae* – *Paraneuretus dubovikoffi* sp. n., *Dolichoderinae* – *Dolichoderus pinguis* sp. n., *Emplastus macrops* sp. n., *Emplastus elongates* sp. n., *Emplastus dubius* sp. n., *Liometopum incognitum* sp. n., *Formicinae* – *Formica biamoensis* sp. n., *Formica paleosibirica* sp. n., *Gesomyrmex magnus* sp. n., *Gesomyrmex macrops* sp. n., *Gesomyrmex incertus* sp. n., *Myrmeciinae* – *Ypresiomyrma orientalis* sp. n., *Amblyoponinae* – *Casaleia orientalis* sp. n., *Ponerinae* – *Pachycondyla oligocena* sp. n., *Pachycondyla aberrans* sp. n., *Proceratiinae* – *Proceratium petrosium* sp. n., *Myrmicinae* – *Agastomyrma laticeps* sp. n., *Biamomyrma zherikhini* sp. n., *Biamomyrma lata* sp. n., *Biamomyrma rugosa* sp. n., *Myrmecites sibiricus* sp. n., *Myrmecites dubius* sp. n., *Myrmecites major* sp. n., а также имеются представители как минимум двух видов *Lasius* и одного вида *Cerapachyinae*.

Introduction

The rich insect fossil site Bol'shaya Svetlovodnaya (= Biamo) has been explored by V.V. Zherikhin with colleagues in 1974 and 1976. The insectiferous diatomites are formed in a small lake near an active volcano. The deposits are referred to as either Maksimovka [Lopatina, 2003, 2004] or Salibez Formation [Pavlyutkin, Petrenko, 2010]. The age estimations vary as Eocene or Oligocene [Lopatina, 2004], Priabonian (the uppermost stage of Eocene) [Pavlyutkin, Petrenko, 2010], or the upper half of Eocene (M.A. Akhmetiev, personal communication, 2014). Zherikhin [1998] compared Svetlovodnaya with the famous Lagerstätten Bembridge Marls, the Isle of Wight in southern England, and Florissant in Colorado, USA, which are both considered currently as the latest Eocene (younger than the Baltic amber within Priabonian [Evanoff et al., 2001; Antropov et al., 2014; Ross, Self, 2014]. The insect fauna is reviewed by Zherikhin [1998], he presents some floristic information as well, and the aquatic fauna and environments are briefly analyzed by Zherikhin [2002].

The insect assemblage of Svetlovodnaya is known based on 1700 fossils including 470 hymenopterans (28%), other dominating orders being (35%), Homoptera¹ (17%), Coleoptera (8%), and Heteroptera (5%). One hundred fifteen fossil ants are collected comprising almost 7% of all insects and 24% of hymenopterans. Study of the ant assemblage of Svetlovodnaya is important, the first, because the end of Eocene was the time just before the Eocene/Oligocene global cooling which triggered transition from

the Mesozoic through Early Paleogene Greenhouse Climate toward the Oligocene through Holocene (current time) Icehouse Climate, and ants are possible to shed more light on the climate they existed in. The second, the ant fossil assemblages of the Eocene, and particularly of the latest Eocene (Priabonian) are rather well studied in the Europe and North America (Dlussky, Perfilieva [Antropov et al., 2014] and references therein). The present study of the first rich East Asian ant fauna of supposedly Priabonian age is intended to add to a global understanding the ant evolution that time. In turn, this might help revealing the biotic transformations at the green/ice house climatic boundary.

Material and methods

The insects are collected at small outcrop in a narrow valley upstream the Barachek stream a right tributary of the Bol'shaya Svetlovodnaya (former Biamo) River; Pozharsky District, Primorskiy Region, SE Russia. The collection no. 3429 is kept at the A.A. Borissiak Paleontological Institute (PIN), Russian Academy of Sciences. At the second visit (1976) several beds have been identified in the outcrop, with the bed 2 and bed 5 being insectiferous. The ant fossils no. 3429/1105–1144 are collected in the bed 1, and 3429/1145–1207 lower in the bed 5. The fossils no. 101–112 are collected in 1974 and not known to come from a particular bed. No permits were required for the described study, which complied with all relevant regulations. The fossil specimens were photographed using digital camera, and enlarged prints were hand traced by pencil with the visual control of the specimen under stereomicroscope. The resulted draft drawing was scanned and improved finally using the program CorelDraw X5. In the line drawings, lines trace visible sclerite boundaries, dashed lines – supposed sclerite boundaries, and dotted lines – visible margins of incomplete sclerites. Filled contours denote sclerites with the original matter preserved even if chemically modified. Measurements of larger structures (total body length, length of alitrunk, forewing, etc.) are made using ocular micrometer of microscope. Smaller details (petiole length, height and width, maximum eye diameter etc.) are measured after digital pictures.

Measurements are referred to as follows: AL – alitrunk (mesosoma) length from junction with head to that with petiole; ED – maximum eye diameter; F3L – hind femur length; FWL – fore wing length; HL – head length without mandibles; HW – maximum head width; Icu = $[1Cu + (2M + Cu)] / 1Cu$; Icu = $[(1M+Cu) + (2M + Cu)] / (1M + Cu)$; MdL – mandible length; PptH – maximum postpetiole height; PptL – postpetiole length; PptW – maximum postpetiole width; PtH – maximum petiole height; PtL – petiole length; PtW – maximum petiole width; SctL – scutum length; SctlL – scutellum length; SctlW – scutellum width; SctW – scutum width; SL – scape length.

Nomenclature of the wing venation (Fig. 1) in general follows Dlussky [2009]. The other morphological terminology is after Bolton [1994]. Index of Icu is particularly helpful in the distinguishing of *Dolichoderinae* and *Poneromorpha*, especially in the case of incomplete wings.

¹Taxon is considered as a classic variant, because of original definition of fossil insects of Svetlovodnaya. Recent phylogenetic analysis using mitochondrial DNA suggest that Homoptera may be a monophyletic group after all, a sister group of Heteroptera [Song et al., 2012].

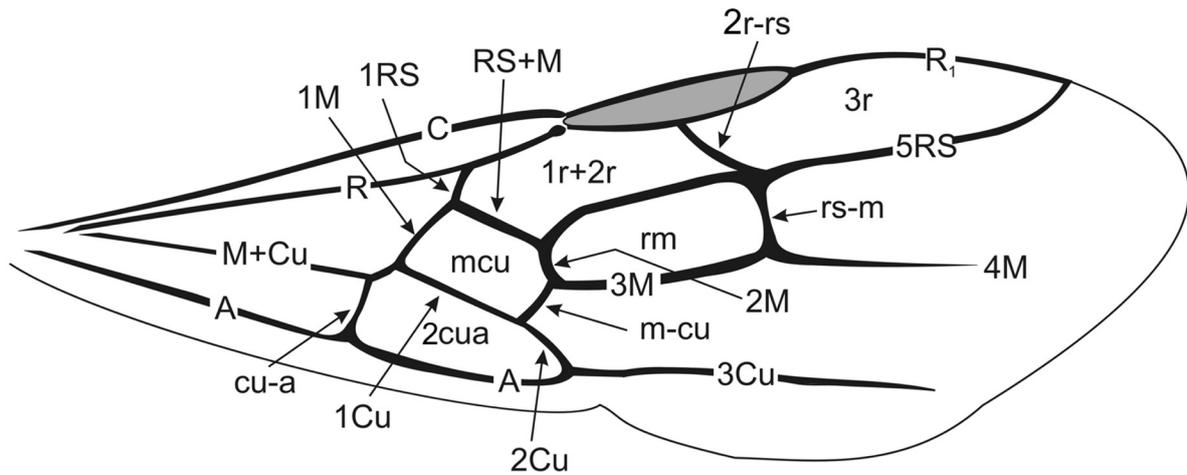


Fig. 1. Wing venation of *Gnampptogenys europaea* Mayr, 1868 to show venational symbols used. Designations: C, R, RS, M, Cu, A – longitudinal veins; 1RS, RS+M, 2M, etc. – their sections; 2r-rs, r-m, m-cu, etc. – crossveins; 1r+2r, rm, m-cu, 2cua – cells.

Рис. 1. Номенклатура жилкования на примере переднего крыла *Gnampptogenys europaea* Майр, 1868. Обозначения: C, R, RS, M, Cu, A – продольные жилки; 1RS, RS+M, 2M и т.д. – отрезки продольных жилок; 2r-rs, r-m, m-cu и т.д. – поперечные жилки; 1r+2r, rm, m-cu, 2cua – ячейки.

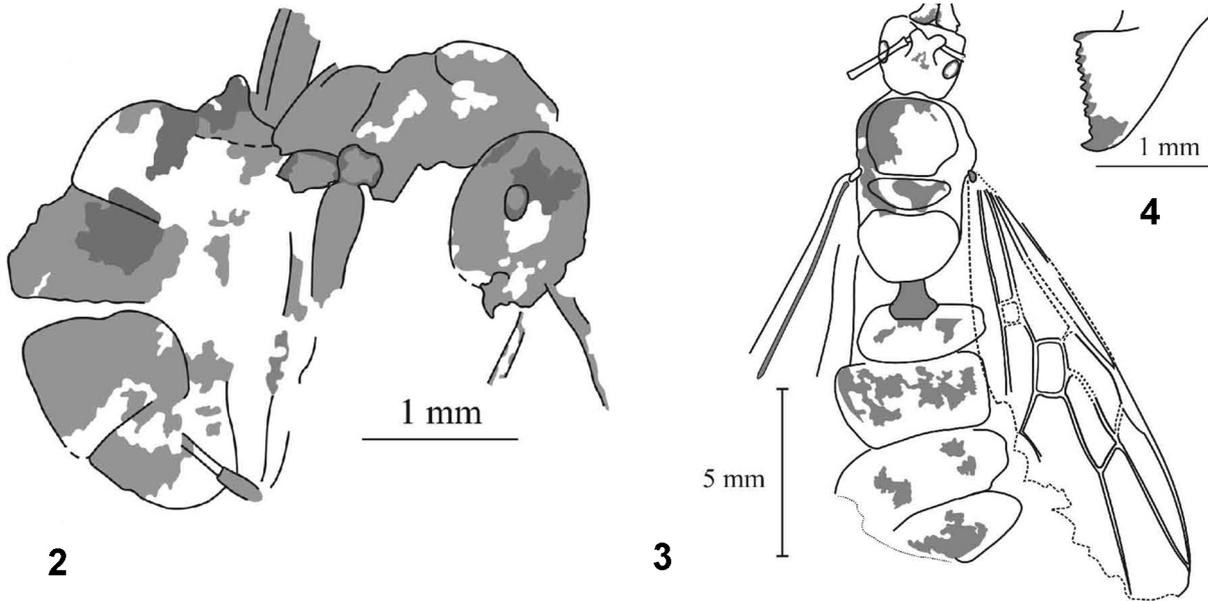
Subfamily Aneuretinae Emery, 1913
Genus *Paraneuretus* Wheeler, 1915

Type species *Paraneuretus tornquisti* Wheeler, 1915, by original designation.

Diagnosis (for fossil imprints). Worker. Waist consisting of 1 segment (petiole); gaster without constriction between 1st and 2nd gastral (abdominal III and IV) segments. Petiole with node and long peduncle. Head longer than wide. Eyes situated nearly at the middle of head sides. Mandibles long, narrow, triangular, bent downwards at their tips, with straight external and finely denticulate apical borders. Antennae 12-segmented, long and slender; funiculi not enlarged towards their tips, all the joints

much longer than broad. Propodeum without teeth or denticles, rounded in side view. Legs long and slender, all the tibiae with distinctly pectinated spurs. Sting long and well-developed. Gyne. Head subrectangular with rounded occipital corners. Antennae geniculate, 12-segmented, with long scape. Scape attached at some distance from clypeus. Mandibles large, triangular, with sharp teeth on the masticatory margin. Petiole elongate, without scale, or nodiform (only at females). Forewing with usual pterostigma and closed cells 1+2r, 3r, rm, m-cu. Cell rm quadrangular. Cell 3r long, about one third of wing length.

Species included. *Paraneuretus tornquisti* Wheeler, 1915 and *P. longicornis* Wheeler, 1915; Baltic amber, Late Eocene [Wheeler, 1915].



Figs 2–4. *Paraneuretus dubovikoffi* sp. n. 2 – holotype PIN 3429/1155, worker; 3 – paratype PIN 3429/1145, gyne; 4 – counterprint of mandible of holotype.

Рис. 2–4. *Paraneuretus dubovikoffi* sp. n. 2 – голотип PIN 3429/1155, рабочий; 3 – паратип PIN 3429/1145, самка; 4 – обратный отпечаток мандибул голотипа.

Paraneuretus dubovikoffi sp. n.
(Figs 2–4)

Material. Holotype PIN 3429/1155, lateral imprint of worker. Paratype: PIN 3429/1145, gyne with forewings. Biomo.

Description. Worker. Body length 6 mm. Head with rounded occipital margin. Eyes comparatively small, oval, situated slightly behind midlength of head; gena nearly 1.5 times as long as maximum eye diameter. Pronotum convex in side view. Mesopropodeal constriction distinctive. Propodeum rounded in side view. Propodeal dorsum shorter than declivity. Petiole with high node and short peduncle. Gyne. Body length about 17–18 mm. Head wider (without mandibles) than long, narrower at its base than apically, with feebly convex sides. Occipital margin concave, but perhaps it is result of deformation during fossilization. Anterior margin of clypeus stright. Eyes comparatively small, oval, situated on the midlength of head; maximum eye diameter about 0.4 times head length. Mandibles large, triangular, with large apical tooth and numerous denticles on the masticatory margin. Scape protrudes beyond the occipital margin of the head, shorter than head length. Mesosoma wider than head. Scutum shorter than wide, not over-hanging pronotum in dorsal view. Scutellum transverse. Petiole longer than wide, with node and peduncle. Gaster oval. Forewing with usual pterostigma and closed cells 1+2r, long 3r, quadriangular rm, pentagonal mcu; 2M and 3M sections almost equal. Transverse veins 2r-rs and rs-m are closely disposed, that 4RS is reduced.

Measurements of holotype, mm: AL 1.75; HL 1.1; ED 0.23; PtL 0.51. Gyne: AL 5.6; HL 2.2; HW 2.45; ED 0.6; SL = 2; SctL 2.3; SctW 2.7; SctL 0.9; SctLW 2.4; MdL 1.2; FWL 14.3.

Comparison. Differs worker from *P. tornquisti* in having body size less (body length of *P. tornquisti* 8–10 mm), less slender habitus and lower propodeum.

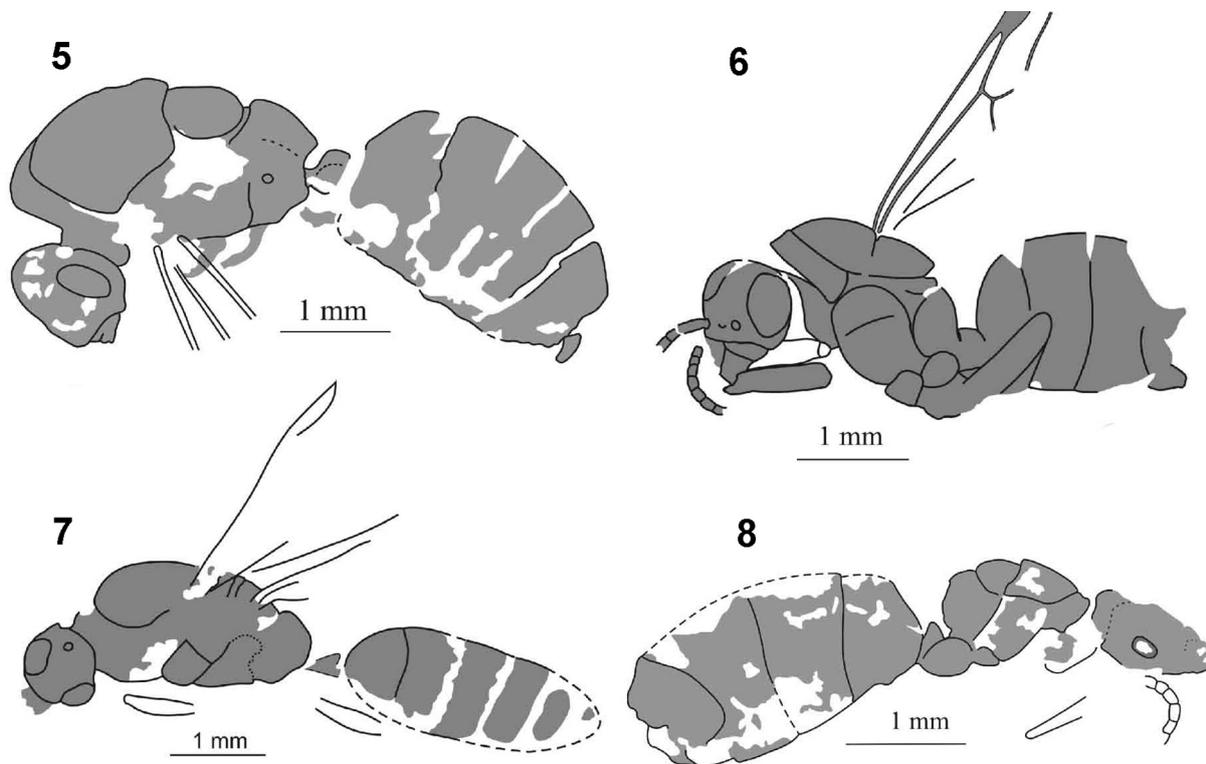
Notes. Forewing of gyne has quadriangular rm, that differs the specimen from all known winged aneuretines (both extant and extinct). We describe winged gyne as Aneuretinae due to the following combination of features: long pedunculate petiole with compact body. Because of doubts that two species of Aneuretinae are in the same place, we describe both specimens into one species.

Etymology. After Dmitry A. Dubovikoff who was the first identified worker ant as Aneuretinae.

Subfamily Dolichoderinae Forel, 1878
Genus *Dolichoderus* Lund, 1831

Type species *Formica attelaboides* Lund, 1831, by monotypy.

Diagnosis (for fossil imprints). Waist consisting of 1 segment (petiole); gaster without constriction between 1st and 2nd gastral (abdominal III and IV) segments. Head elliptical or oval, widest behind midlength of head sides; sometimes retort-shaped or subrectangular with rounded occipital corners, but never rectangular and longer than wide as in *Protazteca* Carpenter, 1930. Eyes of moderate size. Antennae of gynes and workers 12-segmented; antennae of males 13-segmented, with very short scape.



Figs 5–8. Species of genera *Dolichoderus* and *Emplastus*.

5 – *Dolichoderus pinguis* sp. n., holotype PIN 3429/1134, male; 6 – *Emplastus macrops* sp. n., holotype PIN 3429/1187, male; 7 – *Emplastus elongatus* sp. n., holotype PIN 3429/1115, male; 8 – *Emplastus dubius* sp. n., holotype PIN 3429/109, gyne.

Рис. 5–8. Виды родов *Dolichoderus* и *Emplastus*.

5 – *Dolichoderus pinguis* sp. n., голотип PIN 3429/1134, самец; 6 – *Emplastus macrops* sp. n., голотип PIN 3429/1187, самец; 7 – *Emplastus elongatus* sp. n., голотип PIN 3429/1115, самец; 8 – *Emplastus dubius* sp. n., голотип PIN 3429/109, самка.

Mandibles triangular, dentate. Propodeum bispinate, bidentate, or distinctly angular in side view, always with concave declivity. Petiole of various form. Forewing with cells 1+2r, 3r, rm and mcu closed; rm usually triangular. Cell 3r touching wing margin. Icu > 1.45. Integument thick, often coarsely sculptured. Male genitalia small, not permanently external.

Species included. The genus *Dolichoderus* comprises 132 species and 20 subspecies in the modern fauna [Bolton, 2015]. The vast majority of them are distributed in the Neotropical, Indo-Australian, and Australian Regions. Only 9 species are known from the Oriental Region, 4 from the Nearctic Region and 2 from the Palearctic Region, and none have been recorded from the Afrotropical Region. A total of 47 extinct species have been described. The oldest species *D. kohlsi* Dlussky et Rasnitsyn, 2002 is recorded from the Middle Eocene Green River Formation, USA [Dlussky, Rasnitsyn, 2003]. Nearly half of the fossil species (24) have been described from Late Eocene European ambers [Dlussky, 2002, 2008].

Dolichoderus pinguis sp. n.
(Fig. 5)

Material. Holotype PIN 3429/1134, male. Biamo.

Description. Male. Body length 6.3 mm. Head wider than long, with convex occipital margin. Eye large, ovate, 0.5 times as long as head. Scutum elongate, nearly twice as long as scutellum. Propodeum with weakly convex dorsum and concave declivity. Petiole nodiform with short peduncle.

Measurements of holotype, mm: AL 2.3; HL 1; ED 0.5; SctL 1.3; SctIL 0.7.

Comparison. All fossil congeners being described after female sex, a reliable comparison of the only available male is impossible. A peculiar structure of petiole of the new species is comparable to that of *Dolichoderus kutschieri* Dlussky, 2008 from the Late Eocene Bitterfeld amber.

Etymology. Pinguis is the Latin for fat.

Morphogenus *Emplastus* Donisthorpe, 1920

Type species *Emplastus emeryi* Donisthorpe, 1920 (= *Dolichoderus britannicus* Cockerell, 1915), by original designation.

Diagnosis (for fossil imprints). Gynes and males of fossil ants not preserved well enough to fit orthotaxa, and with following combination of traits: size medium; head subrectangular with rounded occipital corners; mandibles triangular with denticulate masticatory margin; propodeum rounded in side view, petiole in side view with thick scale (gynes) or triangular (males). Forewing with cells 1+2r, 3r, rm and mcu closed; cell 3r with apex touching wing fore margin, 1RS vertical to R or slightly proclined. Icu > 1.45, Icu_a > 1.2. Gaster without constriction between 1st and 2nd segments.

Species included. *Emplastus britannicus* Cockerell, 1915, *E. hypolithus* Cockerell, 1915, *E. gurnetensis* Donisthorpe, 1920, and *E. kozlovi* Dlussky et Perfilieva, 2014. Bembridge Marls, Isle of Wight, UK; Late Eocene or Early Oligocene [Cockerell, 1915; Donisthorpe, 1920; Antropov et al., 2014].

Emplastus macrops sp. n.
(Fig. 6)

Material. Holotype PIN 3429/1187, male. Biamo.

Description. Male. Body length 5 mm. Head with rounded occipital corners and convex occipital margin. Anterior clypeal margin straight. Eyes oval, very large, occupied most part of head sides. Gena about as long as scape thickness. Scape short, not reaching occipital margin, about as long as 1–3 funicular segments together. 1st and 2nd funicular segments nearly as long as wide; following 5 segments longer than wide; distal segments not preserved. Mandibles well developed, triangular. Mesosoma nearly 2.5 times longer than head. Pronotum narrow, along midline less than 0.3 times as long as scutum. Scutum and scutellum convex in side view. Scutum about 0.4 times as long as alitrunk, not over-hanging pronotum in dorsal view. Propodeum rounded in side view. Petiole short, apparently triangular in side view. Wing venation not preserved.

Measurements of holotype, mm: AL 1.9; HL 0.77; ED 0.57; SL 0.27; SctL 0.74; SctIL 0.59; PtL 0.24.

Comparison. Differs from other described species in having very large eyes.

Notes. Poorly preserved specimen PIN 3429/1193 (male, body length 4.5 mm) may belong to this species as well.

Etymology. Macrops is the Latin for “with large eyes”.

Emplastus elongatus sp. n.
(Fig. 7)

Material. Holotype PIN 3429/1115, male. Biamo.

Description. Male. Body length 6.3 mm. Head wider than long, with rounded occipital corners and convex occipital margin. Anterior clypeal margin feebly rounded. Eyes oval, large; head 1.8 times longer than maximum eye diameter. Ocelli large. Mesosoma elongate, twice longer than high and more than 3 times longer than head. Scutum strongly convex, 2.3 times shorter than mesosoma. Propodeum rounded in side view. Petiole triangular in side view, more long than high. Wing venation not preserved.

Measurements of holotype, mm: AL 2.5; HL 0.75; HW 0.78; ED 0.4; SctL 1.1.

Comparison. Differs from other described species except *E. macrops* sp. n. by large eyes. Differs from *E. macrops* sp. n. by more elongate mesosoma and more convex scutum.

Etymology. Elongatus is the Latin for elongated.

Emplastus dubius sp. n.
(Fig. 8)

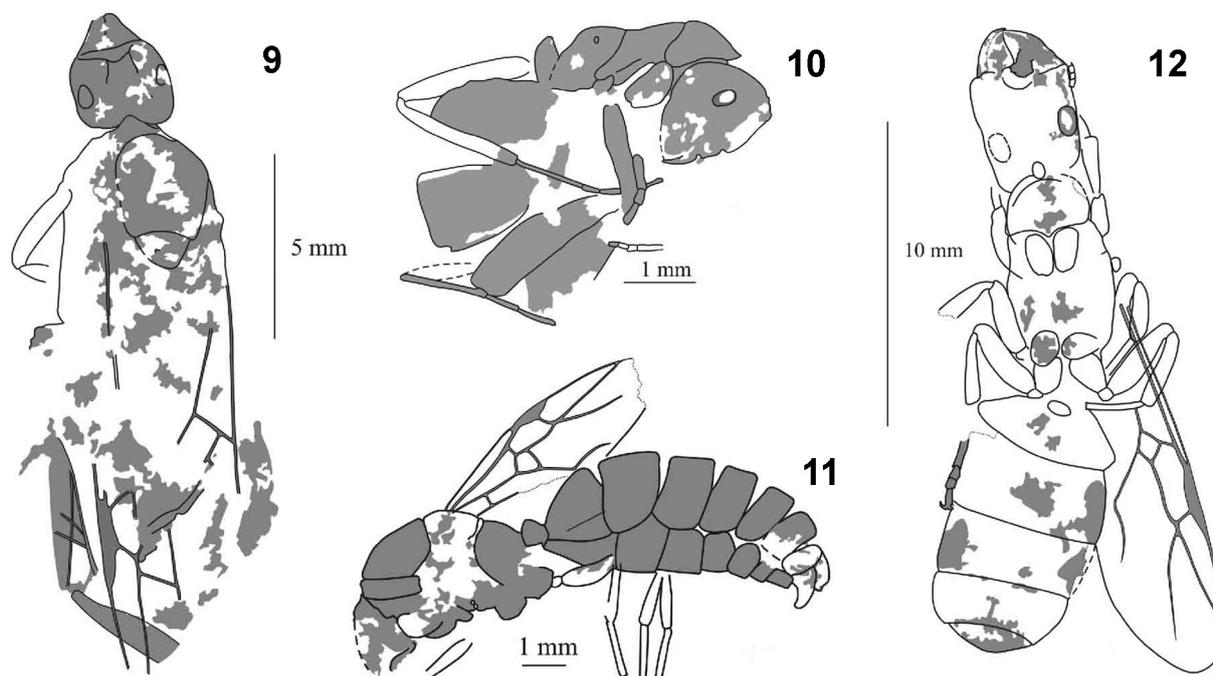
Material. Holotype PIN 3429/109, gyne. Biamo.

Description. Gyne. Body length 5.05 mm. Posterior margin of head convex. Eyes comparatively small, oval, displaced forward; gena shorter than maximum eye diameter. Mesosoma 1.4 times as long as high. Scutum comparatively short, only 1.1 times as long as scutellum. Propodeum straight in side view. Petiole with small scale inclined forward.

Measurements of holotype, mm: AL 1.4; HL 1; ED 0.22; SctL 0.54; SctIL 0.49.

Comparison. *Emplastus britannicus* and *E. gurnetensis* are also described after the female sex: they differ from *E. dubius* sp. n. in having petiolar scale thicker and higher. *Emplastus britannicus* additionally differs in being bigger (body length 6–8.5 mm).

Etymology. Dubius is the Latin for uncertain, doubtful.



Figs 9–12. Species of genera *Liometopum*, *Formica* and *Gesomyrmex*.

9 – *Liometopum incognitum* sp. n., holotype PIN 3429/1157, gynes; 10 – *Formica biamoensis* sp. n., holotype PIN 3429/1141, worker; 11 – *Formica paleosibirica* sp. n., holotype PIN 3429/107, male; 12 – *Gesomyrmex magnus* sp. n., holotype PIN 3429/101, gynes.

Рис. 9–12. Виды родов *Liometopum*, *Formica* и *Gesomyrmex*.

9 – *Liometopum incognitum* sp. n., голотип PIN 3429/1157, самка; 10 – *Formica biamoensis* sp. n., голотип PIN 3429/1141, рабочий; 11 – *Formica paleosibirica* sp. n., голотип PIN 3429/107, самец; 12 – *Gesomyrmex magnus* sp. n., голотип PIN 3429/101, самка.

Genus *Liometopum* Mayr, 1861

Type species *Formica microcephala* Panzer, 1798, by monotypy.

Diagnosis (for fossil imprints). Size large or medium. Head of gynes wider than long, with concave occipital margin. Antennae geniculate in both sexes, 12-segmented in gynes and workers and 13-segmented in males. Scape of male short. Declivous part of propodeum stright or convex (not concave) in side view. Petiole with scale in gynes and triangulate in side view in males. Male genitalia large, not involved. Forewing with closed cells 1+2r, 3r, rm and mcu. Cell 3r with apex removed from fore margin of wing. Icu > 1.45.

Species included. Seven living species distributed in temperate and subtropic zones of Eurasia and North America [Shattuck, 1992]. Seven fossil species have been described: *L. oligogenicum* Wheeler, 1915 (Baltic amber, Late Eocene), *L. miocenicum* Carpenter, 1930, *L. scudderi* Carpenter, 1930 (Florissant, USA, Oligocene), *L. eremicum* Zhang, 1989, *L. patamophilum* Zhang, 1989, *L. lubricum* Zhang, Sun et Zhang, 1994 (Shanwang, China, Miocene), and *L. imhoffii* Heer, 1849 (Radoboj, Croatia, Miocene) [Carpenter, 1930; Heer, 1849; Wheeler, 1915; Zhang, 1989; Zhang et al., 1994].

Liometopum incognitum sp. n.

(Fig. 9)

Material. Holotype PIN 3429/1157, dorsal imprint of gynes. Biamo.

Description. Gynes. Body length 14.5 mm. Head 0.8 times as

long as wide, with rounded occipital corners and concave occipital margin. Anterior margin of clypeus concave. Frontal carinae short, divergent. Eyes oval, situated on the midlength of head; maximum eye diameter about 0.35 times head length. Scutum 1.1 times as long as wide. Scutellum transverse. Wing venation incompletely preserved: cell rm closed as implied by presence of rs-m, rs-m meeting RS distal of 2r-rs.

Measurements of holotype, mm: HL 2.1; HW 2.6; ED 0.6; SctL 2.6; SctW 2.4.

Comparison. Differs from *L. miocenicum* and *L. scudderi* from Oligocene deposits of Florissant [Carpenter, 1930] in the shape of the head of gynes (the head in these species is longer than wide, with a straight occipital margin). Differs from *L. patamophilum*, *L. lubricum* (Shanwang, Miocene), *L. imhoffii* (Radoboj, Miocene) and recent *L. microcephalum* Panzer, 1798 and *L. orientale* Karavaiev, 1927 in having rs-m and 2r-rs distant on RS and no coinciding as in the above species. *Liometopum eremicum* (Shanwang, Miocene) differs in being half as big as the new species (being 7.1 long) and having eyes much shifted forwards.

Etymology. Incognitum is the Latin for unknown.

Dolichoderinae incertae sedis

The collection studied includes 4 fossils belonging unquestionably to Dolichoderinae but impossible to reveal their generic identity due to their imperfect preservation state. Specimens PIN 3429/106, 111 and 1117 might belong to one of the species described above, and specimen PIN 3429/1114 differ from all of found in Biamo in being bigger (body length ca. 13 mm).

Subfamily Formicinae Latreille, 1809**Genus *Formica* Linnaeus, 1758**

Type species *Formica rufa* Linnaeus, 1758; by subsequent designation by Curtis, 1839: 752.

Diagnosis (for fossil imprints). Head of gyne and worker usually longer than wide, with rounded occipital angles. Anterior margin of clypeus rounded or angulate. Eyes situated above middle of head sides, gena of gynes and workers much longer than maximum eye diameter. Mandibles triangular, dentate in gynes and workers. Antennae 12-segmented in gynes and workers and 13-segmented in males. Scape protruding beyond posterior margin of head. Second to fifth joints of funiculus of gynes and workers 1.5–2 times as long as wide. Antennal insertion near posterior margin of clypeus. Hind coxae closely set. Forewing with closed cells 1+2r, 3r and mcu, free branches 5RS and 4M leaving cell 1+2r from common knot. 5RS and 4M curved approximately equally. Section 2-3RS often S-shaped. Icu > 1.45. Male and gyne size subequal.

Species included. Bolton's online catalogue [Bolton, 2015] gives 175 species and 25 subspecies of *Formica* distributed in the Palearctic and Nearctic, as well as 55 extinct species and 1 subspecies distributed in Eocene, Oligocene and Miocene. However, fossil species need a revision, for some of them well might be found synonyms and some other belonging elsewhere.

***Formica biamoensis* sp. n.**

(Fig. 10)

Material. Holotype PIN 3429/1141, lateral imprint of worker. Biamo.

Description. Worker. Body length about 7.5 mm. Head oval. Eyes comparatively small, oval, markedly displaced backwards. Head 5 times as long as maximum eye diameter. Gena 2.5–3 times as long as maximum eye diameter. Mandible with acute apical tooth; teeth of masticatory margin not preserved. Funicular segments longer than wide. Mesosoma slender. Pronotum weakly convex in side view. Promesonotal constriction shallow. Propodeum angulated in side view; dorsal side nearly as long as declivous side. Petiole with thick vertical scale; in side view with convex posterior side and rounded top.

Measurements of holotype, mm: AL 2.25; HL 1.4; ED 0.28.

Comparison is difficult to provide, for all other fossil workers are described after amber specimens using characters not available for our rock fossil. In general appearance, the new species is more similar to *Formica flori* Mayr, 1868 and *F. gustawi* Dlussky, 2003 from the Baltic amber which differ in having scale thicker and eyes smaller.

Etymology. After the former name of the type locality (Biamo).

***Formica paleosibirica* sp. n.**

(Fig. 11)

Material. Holotype PIN 3429/107, lateral imprint of male. Paratypes: PIN 3429/1105, imprint of male without head; PIN 3429/1133, lateral imprint of male without wings and gaster. Other specimens: PIN 3429/1131 and 3429/1189, forewings.

Description. Male. Body length about 10–13 mm. Head trapezoid, 0.94 times as long as wide, with rounded occipital corners and weakly convex occipital margin. Anterior margin of clypeus rounded. Eyes oval, large, convex; head twice as long

as maximum eye diameter. Scape protruding beyond posterior margin of head, 1.3 times as long as head. Scutum convex in side view, does not overhang pronotum, 1.5 times as long as scutellum. Propodeum gradually rounded in side view. Petiole triangulated in side view, nearly as long as wide and high. Genitalia with stipes triangular, rounded apically, 1.5 times as long as wide near the base. Forewing venation as in genus. Cell 3r 3.7–4.7 times as long as wide. Cell 1+2r 2–2.5 times as long as wide. Cell mcu trapezoid. Icu = 2.6–2.7.

Measurements, mm. Holotype PIN 3429/107: AL 3.9; SctL 1.9; SctL 1.3; PtL 0.6; PtH 0.6; FWL 6.3. Paratype 3429/1105: AL 3.4; PtL 0.5; PtW 0.51; FWL 6.5. Paratype 3429/1133: AL 3.3; HL 1; HW 1.1; ED 0.48; SL 1.3. Specimen PIN 3429/1131: FWL 6.1. Specimen PIN 3429/1189: FWL 6.7.

Comparison. By now, only 3 extinct *Formica* males are described in sufficient detail: Baltic amber *F. flori* and *F. gustawi* [Dlussky, 2003] and *F. ungeri* Heer, 1849 from the Miocene of Radoboj in Croatia [Dlussky, Putyatina, 2014]. *Formica paleosibirica* sp. n. differs from the two former species in having genitalia with stipes apex more rounded, and from *F. ungeri* in having propodeum lateral contour rounded rather than forming rounded obtuse angle.

Notes. For the present, it can be neither confirmed nor excluded that the above described worker and males belong to one and the same species.

Etymology. From the Latinized Greek palaios (ancient) and Siberia.

Formica sp.

The collection under description reveals 2 fragmentarily preserved wings PIN 3429/110 and 3429/1152 and the male head PIN 3429/1135 which most probably represent *Formica* as well but differ from *F. paleosibirica* sp. n. in being much bigger.

Genus *Gesomyrmex* Mayr, 1868

Type species *Gesomyrmex hoernesii* Mayr, 1868, by monotypy.

Diagnosis (for fossil imprints). Gyne. Antennae geniculate, 10-segmented, with very short scape. Clypeus extends back between antennal sockets. Antennal insertions widely separated, situated close to the posterior clypeal margin. Frontal lobes close to antennal insertions. Mandibles massive, triangular, with 4–10 teeth. Palp formula 6, 4. Posterolateral corners of the head and propodeum without spines. Petiole with thick scale. Fore wings with closed cells 1+2r, 3r and mcu. Veins RS and M after 2r-rs usually partly united and form short section RS+M. Posterior margin of cell 3r (formed by RS) convex or S-formed.

Species included. Six extant species are known which are distributed in the Oriental tropics [Mayr, 1868]. Six fossil species are known: *Gesomyrmex hoernesii* Mayr, 1868 (Baltic amber, Late Eocene), *G. germanicus* Dlussky, Wappler et Wedmann, 2009, *G. flavescens* Dlussky, Wappler et Wedmann, 2009 (Eckfeld, Germany, Middle Eocene), *G. pulcher* Dlussky, Wappler et Wedmann, 2009, *G. breviceps* Dlussky, Wappler et Wedmann, 2009, *G. curiosus* Dlussky, Wappler et Wedmann, 2009 (Grube Messel, Germany, Middle Eocene) [Mayr, 1868; Dlussky

et al., 2009]. *Gesomyrmex expectans* Théobald, 1937 (Kleinkembs, France, Oligocene) and *G. miegi* Théobald, 1937 (Haut-Rhin, France, Oligocene) excluded from *Gesomyrmex* [Dlussky et al., 2009]. Three new species are described below.

Notes. Living species of *Gesomyrmex* are arboreal ants constructing nests in tree twigs [Wheeler, 1930; Cole, 1949].

Gesomyrmex magnus sp. n.
(Fig. 12)

Material. Holotype PIN 3429/101, print and counterprint of gyne. Biamo.

Description. Gyne. Body length 20.5 mm. Head subrectangular, about 1.25 times longer than wide, with nearly parallel sides, and rounded occipital corners. Anterior clypeal margin projected as small rounded lobe. Eyes ovate; head 4.4 times longer than maximum eye diameter. Scape not visible, however position of preserved three 1st funicular segments indicate that it was very short, not reaching middle of eye. Funicular segments 1–3 a little longer than wide. Mandible massive, triangular, with acute apical tooth; dentition of masticatory margin not visible. Mesosoma about as wide as head. Metacoxae approximated but not contact. Legs comparatively short and thick. Gaster ovate. Forewing with closed cells 1+2r, 3r and mcu. Cell 1+2r about 3 times longer than wide. Cell 1+2r 3 times longer than wide. Cell 3r 5 times longer than wide. Section RS+M after 2r-rs about as long as 3–4 vein thickness. Cell mcu small, rhomboidal.

Measurements of holotype, mm: AL 7.7; HL 4.2; HW 3.3; ED 0.95; FWL 12.5.

Comparison. Differs from all known living and fossil gynes of *Gesomyrmex* by size. Body length of all other species less than 11 mm.

Etymology. Magnus is the Latin for large.

Gesomyrmex macrops sp. n.
(Fig. 13)

Material. Holotype PIN 3429/1162, incomplete dorsal print of gyne.

Description. Gyne. Body length 9.7 mm. Head subrectangular, about 1.4 times longer than wide, with feebly concave sides, convex occipital margin and rounded occipital corners. Anterior clypeal margin projected as small rounded lobe. Eyes ovate, large: head about 3 times longer than maximum eye diameter. Scape does not reach posterior margin of eye, head about 3 times longer than scape. Mandibles triangular with 4 teeth on the masticatory margin. Scutum nearly as long as scutellum. Petiole low, about as long as high. Legs comparatively short and thick. Gaster ovate. Wings not preserved.

Measurements of holotype, mm: AL 2.7; HL 1.7; HW 1.25; SL 0.55; ED 0.55.

Comparison. Differs from other species of Svetlovodnaya by large eyes. *Gesomyrmex germanicus* (Eckfeld, Germany, Middle Eocene) and *G. pulcher* (Grube Messel, Germany, Middle Eocene) also have large eyes (2.6–3 times less than head length) but they differ from the new species by the form of head. *Gesomyrmex germanicus* has head with convex sides and *G. pulcher* has head with distinctively concave posterior margin. Also *G. pulcher* is less (body length 4.8 mm).

Etymology. Macrops is the Latin for “with large eyes”.

Gesomyrmex incertus sp. n.
(Fig. 14)

Material. Holotype PIN 3429/1183, PIN 3429/1164 (counterprint of the same specimen), head of gyne.

Description. Gyne. Head subrectangular, 1.5 times longer than wide, with nearly parallel sides, rounded occipital corners and concave occipital margin. Anterior clypeal margin projected as rounded lobe. Eyes oval, situated on the midlength of head; head 3.8 times longer than maximum eye diameter. Mandible massive, triangular, with acute apical tooth and small blunt denticles on the masticatory margin.

Measurements of holotype, mm: HL 2.4; HW 1.6; ED 0.65.

Comparison. Differs from all known species of *Gesomyrmex* by combination of elongate head with concave occipital margin and position of eyes.

Notes. In spite of key characters of genus not preserved, preserved head of described specimen in general habitus is most similar to known species of *Gesomyrmex*. That is why we placed it to this genus.

Etymology. Incertus is the Latin for doubtful.

Genus *Lasius* Fabricius, 1804

Type species *Formica nigra* Linnaeus, 1758; by subsequent designation by Bingham, 1903: 338.

Diagnosis (for fossil imprints). Waist consisting of 1 segment (petiole) with scale; gaster without constriction between 1st and 2nd gastral (abdominal III and IV) segments. Head with rounded occipital angles. Anterior margin of clypeus rounded. Eyes situated above middle of head sides, gena of gynes and workers much longer than maximum eye diameter. Mandibles of gynes and workers triangular, dentate. Antennae 12-segmented in gynes and workers and 13-segmented in males; scape protruding beyond posterior margin of head. Second to fifth joints of funiculus of gynes and workers 1–1.4 times as long as wide (except in the subgenus *Dendrolasius* Fabricius, 1804). Antennal insertion near posterior margin of clypeus. Hind coxae broadly separated. Forewing with closed cells 1+2r, 3r and usually mcu, free branches 5RS and 4M leaving cell 1+2r from common knot. 4M strongly curved basally. Section 2RS+M (under 1+2r cell) straight or weakly convex. Icu > 1.45. Gynes 1.5–2.2 times as large as males (except in the subgenus *Austrolasius* Fabricius, 1804).

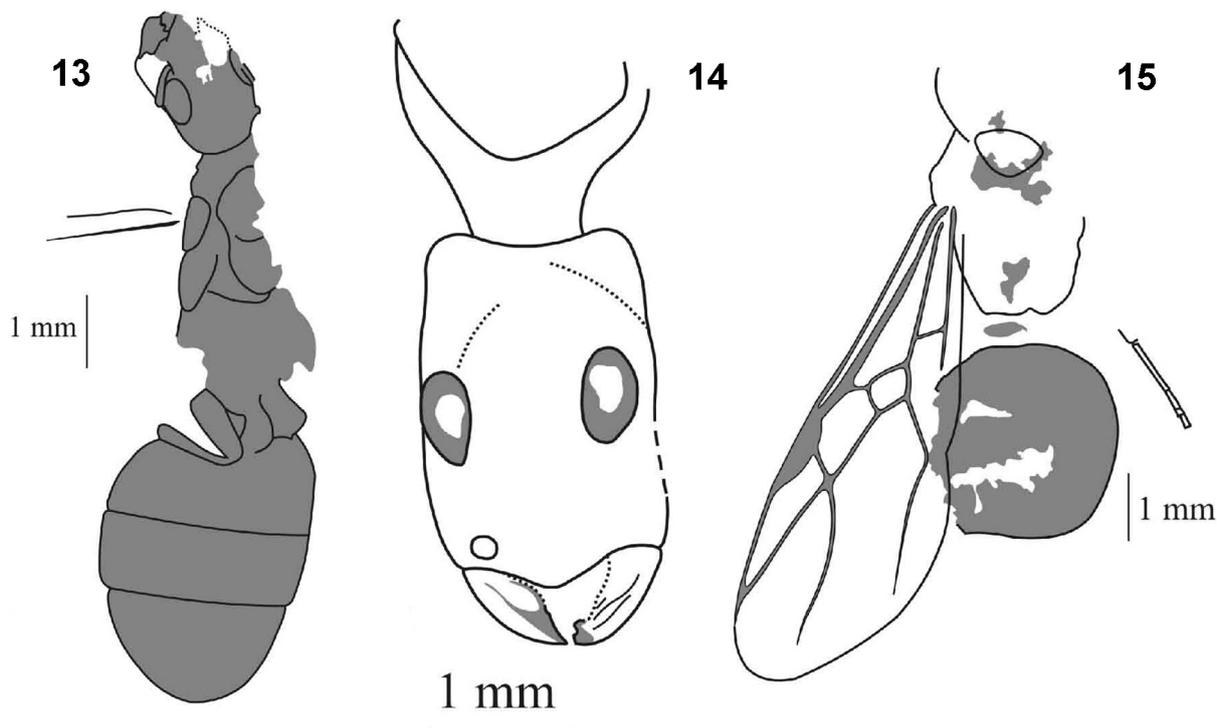
Species included. According Bolton's online catalogue [Bolton, 2015] a total of 114 extant valid species and subspecies of *Lasius* distributed in the Palearctic and Nearctic are known to date. Bolton's catalogue also includes a checklist of 25 extinct species and subspecies distributed in Eocene, Oligocene and Miocene. Fossil taxa badly need in revision, for some of them are possibly deserve synonymization, and some other belong elsewhere.

Notes. There are 11 fossils in the collection studied with the wing venation and general appearance characteristic of the genus. Judging from the size, they represent two species. Unfortunately, the preservation state is not sufficient to provide their formal description, so we present only their registration numbers and measurements available.

Lasius sp. A
(Fig. 15)

Material. PIN 3429/1108 (?♀), 3429/1122 (fragment of wing), 3429/1130 (♀), 3429/1156 (fragment of wing).

Measurements, mm: PIN 3429/1108: FWL 7; PIN 3429/1130: BL ~7; AL 2.5; FWL 7.6.



Figs 13–15. Species of genera *Gesomyrmex* and *Lasius*.

13 – *Gesomyrmex macrops* sp. n., holotype PIN 3429/1162, gyne; 14 – *Gesomyrmex incertus* sp. n., holotype PIN 3429/1183, PIN 3429/1164 (counterprint of the same specimen), head of gyne, drawing from both print and counterprint; 15 – *Lasius* sp. A, PIN 3429/1130, gyne.

Рис. 13–15. Виды родов *Gesomyrmex* и *Lasius*.

13 – *Gesomyrmex macrops* sp. n., голотип PIN 3429/1162, самка; 14 – *Gesomyrmex incertus* sp. n., голотип PIN 3429/1183, PIN 3429/1164 (обратный отпечаток голотипа), голова самки, реконструкция по обоим отпечаткам; 15 – *Lasius* sp. A, PIN 3429/1130, самка.

Lasius sp. B
(Fig. 16, 17)

Material. PIN 3429/102 (♀), 3429/1111 (♂), 3429/1121 (fragment of wing), 3429/1159 (fragment of wing), 3429/1167 (fragment of wing), 3429/1177 (♀), 3429/1200 (♀).

Measurements, mm. Gynes PIN 3429/102: AL 2.1; FWL 4.2. PIN 3429/1177: AL 2; PIN 3429/1200: AL 2. Male PIN 3429/1111: AL 1.7.

Subfamily Myrmeciinae Emery, 1877
Genus *Ypresiomyrma* Archibald, Cover et Moreau, 2006

Type species *Ypresiomyrma orbiculata* Archibald, Cover et Moreau, 2006, by original designation.

Diagnosis. Gyne. Large ants (body length more than 15 mm). Waist consisting of 1 segment (petiole). Petiole lacking anterior peduncle; node conical, well developed; attached to 1st gastral segment without notable constriction, length, height subequal. Gaster normal in proportions, not notably slender as in *Avitomyrmex* Archibald, Cover et Moreau, 2006, without constriction between 1st and 2nd gastral (abdominal III and IV) segments. 1st gastral segment bell-shaped, 0.69–0.96 times as long as 2nd. Mandibles triangular, shorter than head capsule length. Eyes, where known, large, well developed, placed at or anterior to cephalic mid-length. Propodeal dorsum rounded in lateral view, without projections. Forewing with closed cells 1+2r, 3r, rm and mcu.

Species included. *Ypresiomyrma rebekkae* Rust, Andersen, 1999 from Ølst and Fur Formations (Denmark, Eocene, earliest Ypresian) [Rust, Andersen, 1999], *Y. orbiculata* Archibald, Cover et Moreau, 2006, and *Y. bartletti* Archibald, Cover et Moreau, 2006 from the McAbee locality [Archibald et al., 2006]; Kamloops Group, unnamed formation; Canada, Eocene, Ypresian and the species described below.

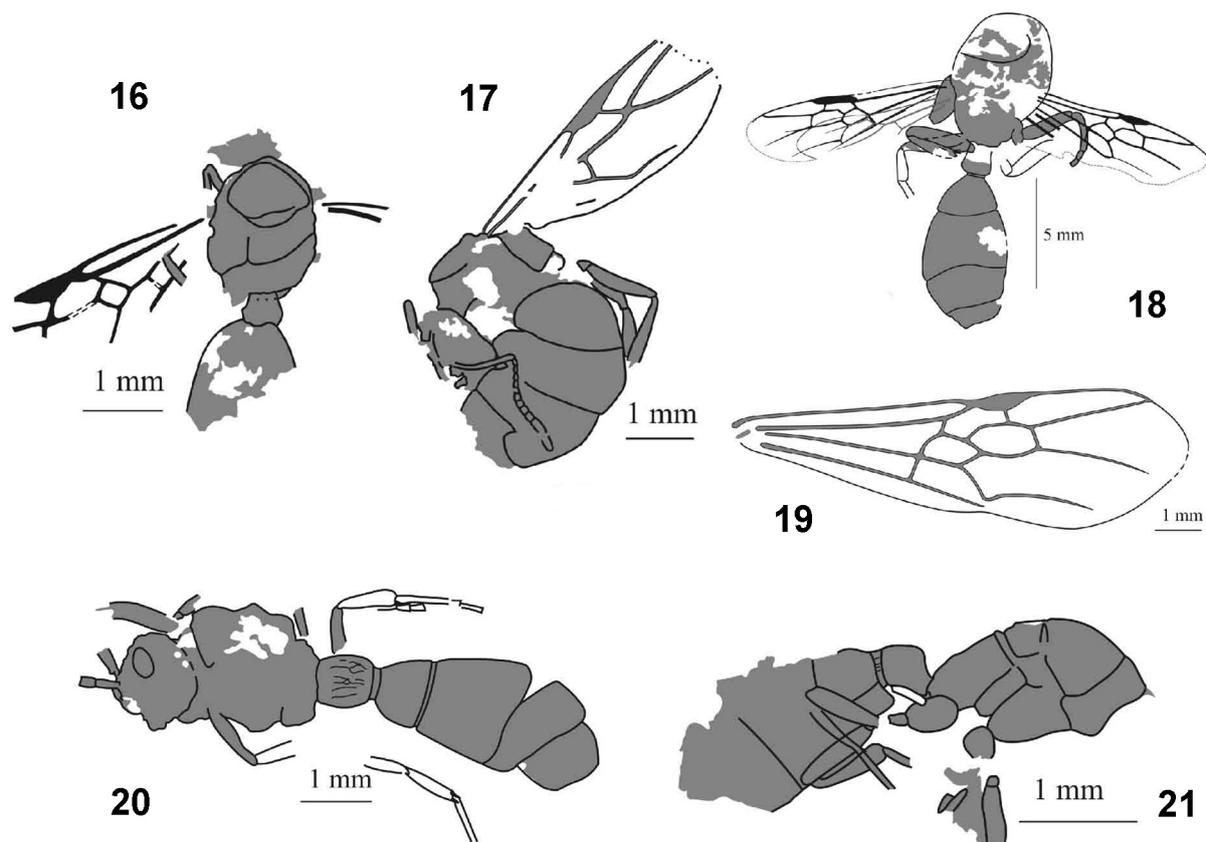
Ypresiomyrma orientalis sp. n.
(Fig. 18, 19)

Material. Holotype PIN 3429/1109 (print and counterprint), dorsal imprint of gyne without head. Paratype: PIN 3429/1198, forewing.

Description. Gyne. Judging by the remained parts body length approximately 17.5 mm. Mesosoma robust, 1.5 times as long as wide. Petiole nodiform, a little longer than wide. 1st gastral (abdominal III) segment 0.8 times as long and 0.7 times as wide as 2nd gastral (abdominal IV) segment. Forewing with closed cells 1+2r, 3r, rm and mcu. Cell 3r elongated, 4.5–5 times as long as wide. Cell 1+2r shorted, 2–2.2 times as long as wide. The meeting of crossvein rs-m and RS is distal to 2r-rs, section 4RS nearly as long as cross-vein rs-m. Section 2-3RS bent to form rounded obtuse angle in its basal third and so cell rm hexagonal, twice as long as wide. Transverse rs-m position at level of pterostigma top. Section 1M 2–2.5 times as long as 1RS. Cell mcu pentagonal. Cross-veins cu-a and section 1M meet M+Cu at the same point, essentially forming a single crossvein, so Icu = 1.

Measurements, mm. Holotype PIN 3429/1109: AL 6; PtL 1.4; PtW 1.3; FWL 9.8. Paratype PIN 3429/1198: FWL 9.6.

Comparison. Wing venation and short the 1st gastral



Figs 16–21. Species of genera *Lasius*, *Ypresiomyrma*, *Casaleia* and *Cerapachyinae inc. gen.*

16–17 – *Lasius* sp. B: 16 – PIN 3429/1111, male, 17 – PIN 3429/102, gyne; 18–19 – *Ypresiomyrma orientalis* sp. n.: 18 – holotype PIN 3429/1109, gyne, left forewing from counterprint, 19 – PIN 3429/1198, forewing; 20 – *Cerapachyinae inc. gen.*, PIN 3429/1132, gyne or worker; 21 – *Casaleia orientalis* sp. n., holotype PIN 3429/1174, gyne.

Рис. 16–21. Виды родов *Lasius*, *Ypresiomyrma*, *Casaleia* и *Cerapachyinae inc. gen.*

16–17 – *Lasius* sp. B: 16 – PIN 3429/1111, самец, 17 – PIN 3429/102, самка; 18–19 – *Ypresiomyrma orientalis* sp. n.: 18 – голотип PIN 3429/1109, самка, левое переднее крыло реконструировано по обратному отпечатку, 19 – PIN 3429/1198, переднее крыло; 20 – *Cerapachyinae inc. gen.*, PIN 3429/1132, самка или рабочий; 21 – *Casaleia orientalis* sp. n., голотип PIN 3429/1174, самка.

segment indicate unquestionably a position of the fossils in the subfamily Myrmecinae. The gaster lacking a constriction between the 1st and the 2nd segments in combination with a robust body are further characteristic of the genus *Ypresiomyrma*. The new species well differs from *Y. rebekkae* in much less size of the petiolar node. No reliable difference from the North American species are found because of different (lateral) burial position of *Y. bartletti* and *Y. orbiculata* and incomplete presentation of their wings. Yet a distinct species status of the new species is beyond doubts because all other congeners are distinctly more old (known from the Early and Middle Eocene).

Etymology. *Orientalis* is the Latin for eastern.

Subfamily Cerapachyinae Forel, 1893

Cerapachyinae incertae generis
(Fig. 20)

Material. PIN 3429/1132, gyne or worker. Biamo.

Description. Gyne or worker. Body length 7.3 mm. Body elongated. Waist consisting of 1 segment (petiole); gaster with distinctive constriction between 1st and 2nd gastral (abdominal III and IV) segments. Head as long as wide. Eye ovate, moderate size. Antennal insertions approximate. Petiole sessile, nearly rectangular in dorsal view, with weakly convex sides, 1.2 times as long as wide,

with longitudinal rugae. 1st gastral segment 0.56 times as long as 2nd. Pygidium without spines or teeth.

Measurements, mm: AL 2; HL 1.1; HW 1.1; ED 0.41; PtL 0.88; PtW 0.74.

Notes. Peculiar petiolar form combined with the approximate antennal bases are characteristic of some *Cerapachyinae* and unknown in other ants. At the same time, incomplete preservation state of the unique fossil permits neither its attribution to a genus nor description a new one. There are 7 cerapachyine species in the fossil record, 3 described from the Late Eocene ambers (*Procerapachys annosus* Wheeler, 1915, *P. favosus* Wheeler, 1915, *P. sulcatus* Dlussky, 2009 [Dlussky, 2009]) and 4 from the Early Miocene Dominican amber (*Acanthostichus hispaniolicus* de Andrade, 1998, *Cylindromyrmex antillanus* de Andrade, 1998, *C. electrinus* de Andrade, 1998 and *C. inopinatus* de Andrade, 2001 [Wheeler, 1915; de Andrade, 1998, 2001; Dlussky, 2009]).

Subfamily Amblyoponinae Forel, 1893

Morphogenus *Casaleia* Pagliano et Scaramozzino, 1990

Type species *Protamblyopone inversa* Dlussky, 1981, by original designation.

Diagnosis (for fossil imprints). Gyne. Petiole essentially sessile, with steep broad anterior face but without distinctly descending posterior face, markedly broadly attached to 1st gastral (abdominal III) segment. Helcium protruding from very high on anterior face of 1st gastral segment; 1st gastral segment above the helcium without free anterior face. Dorsum of mesosoma convex in side view. Mandible triangulate. Eyes rather large, situated nearly at midlength of head sides. Antenna 12-segmented. Petiole trapezoid in dorsal view, broadly attached to 1st gastral segment, nearly 40% as wide as 1st gastral segment. Forewing with closed cells 1+2r, 3r, rm and mcu. Icu < 1.4.

Species included. *Casaleia inversa* (Dlussky, 1981) (Chon-Tuz, Kirgizia, Middle Miocene), *C. longiventris* (Heer, 1849) (Radoboj, Croatia, Early Miocene), and *C. eocenica* Dlussky et Wedmann, 2012 (Messel, Germany, Middle Eocene) [Heer, 1849; Dlussky, 1981; Dlussky, Wedmann, 2012].

Casaleia orientalis sp. n.
(Fig. 21)

Material. Holotype PIN 3429/1174, imprint of gyne without head. Biamo.

Description. Gyne. Judging by the remained parts the length of a body ca. 5 mm. Waist consisting of 1 segment (petiole); gaster with constriction between 1st and 2nd gastral (abdominal III and IV) segments. Petiole without free posterior surface, broadly attached to 1st gastral segment, in lateral view separated from gaster only by constriction. Helcium in profile attached to upper part of anterior surface of 1st gastral segment. Mesosoma 1.6 times as long as high. Scutum convex in side view, twice as long as scutellum. Propodeum nearly straight in side view. Petiole with rounded antero-dorsal corner in side view.

Measurements of holotype, mm: AL 1.75; PtL 0.52; SctL 0.74.

Comparison. Petiole structure and its attachment to the gaster are uniquely characteristic of Amblyoponinae, and the convex dorsal contour of mesosoma implies a position of the new species to the genus *Casaleia*. Reliable comparison to other congeners is problematic because the previously described species are described after fossils buried in dorsal aspect.

Etymology. *Orientalis* is the Latin for eastern.

Subfamily Ponerinae Lepeletier, 1835
Genus *Pachycondyla* F. Smith, 1858

Type species *Formica crassinoda* Latreille, 1802, by subsequent designation of Emery, 1901: 42.

Diagnosis (for impression fossils). Waist of 1 segment (petiole) of different shape narrowly attached to 1st gastral (abdominal III) segment, with a distinctly descending posterior face. Gaster usually with constriction between 1st and 2nd gastral (abdominal III and IV) segments. Helcium projects from very low down on the anterior face of 1st gastral segment, the latter usually with a high vertical anterior face above the helcium. Head less than 1.7 times shorter than mesosoma. Antennal sockets closely approximated. Frons of gyne and worker width less than 25% of head width. Mandible of gyne and worker subtriangular with dentate masticatory margin, less than 65% of head length. Male with very reduced and not opposable mandibles. Middle

and hind tibiae each with a large pectinate spur and a small simple spur. Pretarsal claws simple. Petiole with thick scale or high node. Pygidium of male with distinct terminal spine. Forewing usually with closed cells 1+2r, 3r, rm and mcu. Crossvein cu-a meet M+Cu near distal angle of mcu: Icu < 1.45.

Species included. The genus includes 261 extant valid species [www.antweb.org, accessed 1 January 2013]. Also 12 described fossil species can be placed with confidence in *Pachycondyla*: *P. labandeirai* Dlussky et Rasnitsyn, 2003 (Green River Formation, USA, Middle Eocene); *P. succinea* Mayr, 1868, *P. gracilicornis* Mayr, 1868 and *P. baltica* Dlussky, 2003 (Baltic amber, Late Eocene); *P. conservata* Dlussky, 2009 (Rovno amber, Late Eocene); *P. tristis* Dlussky, 2009 (Bitterfeld amber, Late Eocene), *P. eocenica* Dlussky et Wedmann, 2012, *P. lutzi* Dlussky et Wedmann, 2012, *P. messeliana* Dlussky et Wedmann, 2012, *P. parvula* nom. n. (= *P. minuta* Dlussky et Wedmann, 2012, non MacKay et MacKay, 2010 [MacKay, MacKay, 2010]), *P. petiolosa* Dlussky et Wedmann, 2012, and *P. petrosa* Dlussky et Wedmann, 2012 (Grube Messel, Germany, Middle Eocene). Two new species are described below. Besides, there is a specimen PIN 3429/112, a male or female without head, wings and metasomal apex, which probably represent the third congener, which is left unnamed because of insufficient preservation. It differs in size (AL = 3.4 mm) and in lower petiolar node.

Pachycondyla oligocenica sp. n.
(Fig. 22)

Material. Holotype PIN 3429/1112, lateral imprint of male.

Description. Male. Judging by the remained parts the length of a body ca. 7 mm. Head nearly as long as wide, with rounded occipital margin. Eyes large, ovate, convex. Anterior margin of clypeus convex. Mandibles without teeth, not opposable. Mesosoma 1.5 times as long as high. Parapsidal furrows present. Propodeum gradually convex in side view. Petiole with high node, rounded in side view. 1st gastral segment nearly as long as 2nd. Constriction between 1st and 2nd gastral segments distinct. Forewing with closed cells 1+2r, 3r, rm, and mcu. Cell 3r nearly 4 times as long as wide. Cell rm pentagonal, 2.5 times as long as wide, and not reach level of pterostigma top. The meeting of crossvein rs-m and RS is distal to 2r-rs: section 4RS distinct. Cell mcu pentagonal, longer than wide. 1M nearly 2.5 times as long as 1RS. 1M and crossvein cu-a meet M+Cu at one point, appearing as a single crossvein.

Measurements of holotype, mm: AL 2.3; HL 0.95; HW 0.95; ED 0.5; PtH 0.65; PtL ~0.5; FWL 4.1.

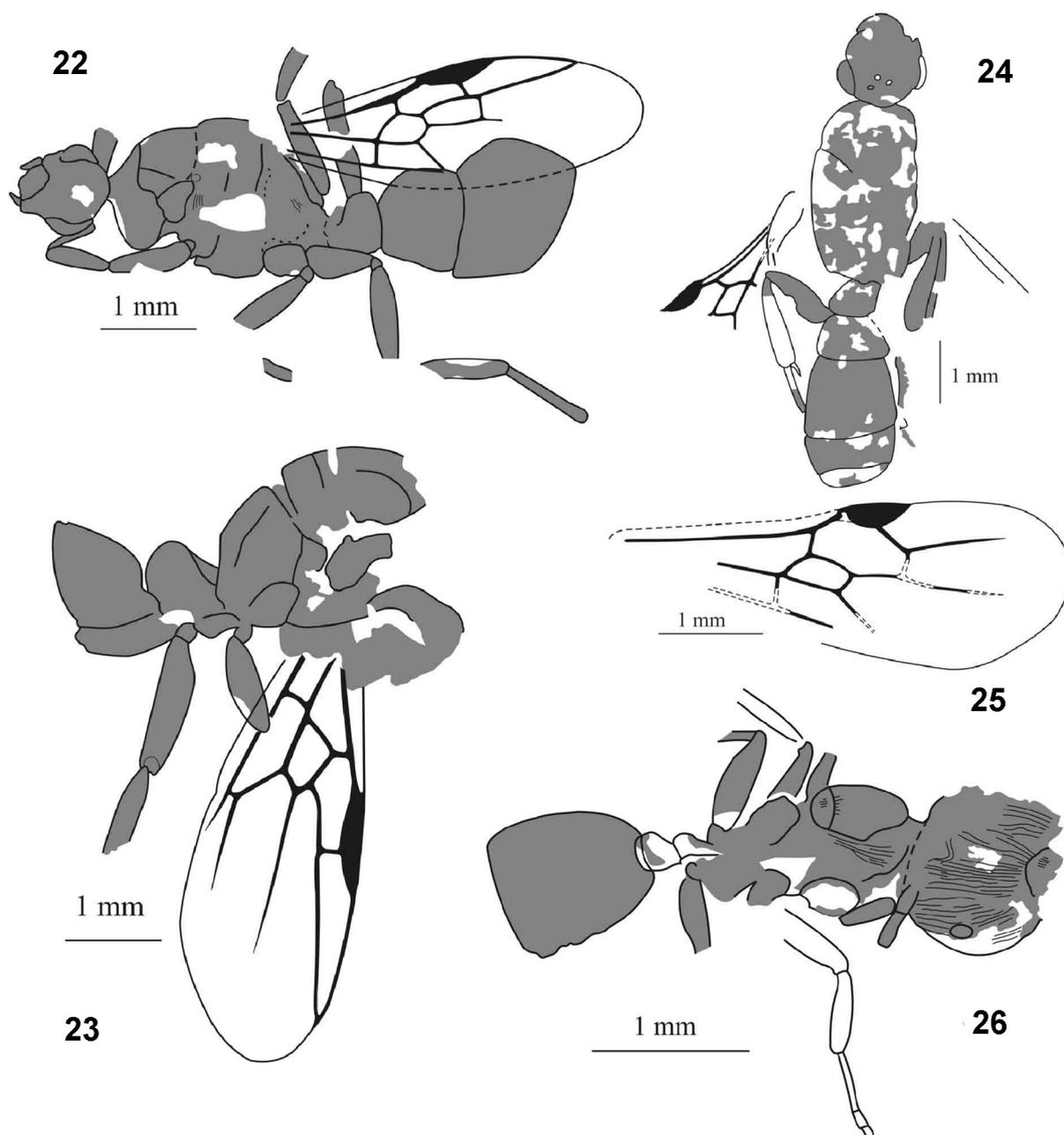
Comparison. Only 2 fossil males of *Pachycondyla* are known: *P. succinea* and *P. baltica* (both from Late Eocene European ambers). Both species differs from *P. oligocenica* sp. n. by size (their body length 3.5–4.5 mm).

Etymology. From the name of the epoch (Oligocene).

Pachycondyla aberrans sp. n.
(Fig. 23)

Material. Holotype PIN 3429/104, lateral imprint of male or gyne without head and top of gaster.

Description. Male or gyne. Judging by the remained parts the length of a body ca. 6–7 mm. Parapsidal furrows present. Propodeum angulated in side view. Petiole with high node, rounded in side view. Forewing with closed cells 1+2r, 3r, mcu and 2cua. Closed cell rm is absent (rs-m reduced). Cell 3r 4.7 times as long as wide. Cell mcu pentagonal, longer than wide. 1M nearly



Figs 22–26. Species of genera *Pachycondyla*, *Proceratium* and *Agastomyrma*.

22 – *Pachycondyla oligocenica* sp. n., holotype PIN 3429/1112, male; 23 – *Pachycondyla aberrans* sp. n., holotype PIN 3429/104, male or gyne; 24–25 – *Proceratium petrosus* sp. n.: 24 – holotype PIN 3429/103, male, 25 – reconstruction of forewing based on print and counterprint; 26 – *Agastomyrma laticeps* sp. n., holotype PIN 3429/1178, PIN 3429/1173 (counterprint of the same specimen), gyne, drawing from both print and counterprint.

Рис. 22–26. Виды родов *Pachycondyla*, *Proceratium* и *Agastomyrma*.

22 – *Pachycondyla oligocenica* sp. n., голотип PIN 3429/1112, самец; 23 – *Pachycondyla aberrans* sp. n., голотип PIN 3429/104, самец или самка; 24–25 – *Proceratium petrosus* sp. n.: 24 – голотип PIN 3429/103, самец, 25 – переднее крыло восстановлено по прямому и обратному отпечаткам; 26 – *Agastomyrma laticeps* sp. n., голотип PIN 3429/1178, PIN 3429/1173 (обратный отпечаток того же экземпляра), самка, реконструкция по обоим отпечаткам.

3 times as long as 1RS. The meeting of crossvein cu-a and M+Cu is proximal to the 1M and 1Cu fork, being separated from it by two widths of vein.

Measurements of holotype, mm: AL 2.5; PtL 0.6; F3L 1.4; FWL ~5.7.

Comparison. Loss of cell rm rarely occurs in Ponerinae. Yet this character is known in *Pachycondyla* and in the extant *Buniapone amblyops* Emery, 1887.

Etymology. *Aberrans* is the Latin for deviate, aberrant.

Pachycondyla parvula nom. n.

Pachycondyla minuta: Dlussky et Wedmann, 2012: 735 (non *Pachycondyla minuta* MacKay et MacKay, 2010), Middle Eocene of Messel, Germany [MacKay, MacKay, 2010; Dlussky, Wedmann, 2012].

Material. Holotype: FIS MeI 10638, lateral imprint of gyne (the construction of the mesosoma undoubtedly indicates that it is a gyne: the mesonotum is distinctly divided in scutum and scutellum). Paratypes: gynes,

FIS Mel 10167, FIS Mel 12250. Other specimens: gynes, FIS Mel 10093, FIS Mel 13789, FIS Mel 14219.

Type locality and horizon. Grube Messel, Hesse, Germany. Messel Formation, Middle Eocene, c. 47 Ma [Mertz, Renne, 2005].

Etymology. From the Latin parvulus (small, tiny).

Ponerinae incertae sedis

There are 2 more specimens (PIN 3429/112 and 1168) which belong to Ponerinae but cannot be described formally because of imperfect preservation state. These unquestionably represent 2 species distinct from each other as well as from all Ponerinae described above.

Subfamily Proceratiinae Emery, 1895

Genus Proceratium Roger, 1863

Type species *Proceratium silaceum* Roger, 1863, by monotypy.

Diagnosis (for impression fossils). Males. Waist of 1 segment (petiole) of different shape narrowly attached to 1st gastral (abdominal III) segment, with a distinctly descending posterior face. Gaster with constriction between 1st and 2nd gastral (abdominal III and IV) segments. Eyes large, rounded. Ocelli relatively small. Clypeus narrow, with weakly produced anterior margin. Frontal carinae short. Antennal insertions exposed, close to posterior clypeal margin. Antennae 13-segmented, filiform, with short scape. Mandibles triangular, touching when closed, without teeth on masticatory margin. Parapsidal furrows present. Each tibia with 1 spur. Petiole with node. Helcium attached approximately to center of anterior surface of 1st gastral segment. 2nd gastral segment much longer than 1st, trapezoidal in side view, with strongly convex dorsal surface, such that entire body is arched, its tip directed down. Pygidium without terminal spine. Forewing with incomplete set of veins: closed cell rm reduce because 2-3RS absent.

Species included. There are 77 species in the recent fauna, distributed on all continents, but predominantly in the tropics [Bolton, 2015]. Five species are known in the southern Palearctic [Bolton et al., 2006]. Up until now, 5 fossil species have been described: *P. denticulatum* Lattke, 1991, *P. dominicanum* Baroni Urbani et de Andrade, 2003, *P. gibberum* Baroni Urbani et de Andrade, 2003, *P. poinari* Baroni Urbani et de Andrade, 2003 (Dominican amber, Early Miocene) and *P. eocenicum* Dlussky, 2009 (Baltic amber, Late Eocene) [Lattke, 1991; Baroni Urbani, de Andrade, 2003; Dlussky, 2009].

Proceratium petrosium sp. n.

(Fig. 24, 25)

Material. Holotype PIN 3429/103, dorsal imprint of male.

Description. Male. Body length 7.5 mm. Head with gradually rounded occipital margin, without occipital corners. Head including eyes 1.08 times as wide as long. Eyes large, convex; head 2.2 times as long as maximum eye diameter. Ocelli large. Mesosoma elongate, 1.7 times as long as wide. Petiole with node. Hind tibia with 1 pectinate spur. 1st gastral (abdominal III) segment 0.57 times as long, and 0.78 times as wide as 2nd (abdominal IV) segment. Forewing with closed cells 1+2r+rm and mcu. Cell 1+2r+rm big, 1.9 times as long as wide. Transverse 2r-rs elongated and inclined. Cell mcu quadrangular, nearly twice as long as wide. Section 1M 1.35 times as long as 1RS. The meeting of crossvein cu-a and

M + Cu is proximal to the 1M and 1Cu fork, being separated from it by a distance approximately equal to vein width.

Measurements of holotype, mm: AL 2.9; HL 1.3; HW (including eyes) 1.4; ED 0.58; PtL 0.61; FWL 4.4.

Comparison. A comparison with the recent species of *Proceratium* is not possible because males of this genus are poorly known. The only known male of fossil species is *P. eocenicum* described from Baltic amber [Dlussky, 2009]. It differs from *P. petrosium* in size (body length 2.2–2.7 mm) and closed cell 3r of forewing.

Etymology. From the Latinized Greek petros (stone).

Subfamily Myrmicinae Lepeletier, 1835

Genus Agastomyrma gen. n.

Type species *Agastomyrma laticeps* sp. n.

Diagnosis (for fossil imprints). Gyne. Head very big and broad. Scutum does not overhang pronotum. Propodeum without teeth or spines. Petiole with node and peduncle. Also see diagnosis of type species.

Species included. One species described below.

Comparison. Differs from other fossil genera of Myrmicinae in combination of big and broad head, unarmed propodeum, and pedunculate petiole.

Etymology. From Latin agastus (pleasing) and Greek Myrmica (ant).

Agastomyrma laticeps sp. n.

(Fig. 26)

Material. Holotype PIN 3429/1178, PIN 3429/1173 (counterprint of the same specimen), gyne.

Description. Gyne. Body length ca. 4 mm. Head very large, 0.86 times as long as wide, with weakly convex sides, rounded occipital corners and straight occipital margin. Eyes comparatively small, oval, situated in the middle of the sides of the head. Gena longer, than maximum eye diameter. Scutum longer than wide and 3 times as long as scutellum. Propodeum unarmed. Petiole with rounded node and comparatively long peduncle, 1.7 times as long as high. Postpetiole a little longer than high. Gaster oval. Head and evidently mesosoma densely longitudinally striated.

Measurements of holotype, mm: AL 1.3; HL 0.9; HW 1; ED 0.14; SctL 0.46; SctlL 0.15; PtL 0.25; PtH 0.15; PptL 0.27; PptH 0.25.

Etymology. Laticeps is the Latin for “with wide head”.

Genus Biamomyrma gen. n.

Type species *Biamomyrma zherikhini* sp. n.

Diagnosis (for fossil imprints). Gyne. Petiole nodiform, sessile. Postpetiole bell-shaped, markedly broadly attached to 1st gastral (abdominal IV) segment. 1st gastral (abdominal IV) segment without tergo-sternal fusion. Scape comparatively short, not reaching the occipital margin. Mandibles triangular, dentate. Scutum does not overhang pronotum. Forewing with closed cells 3r, 1+2r, rm and mcu.

Species included. Three species described below.

Comparison. Differs from other fossil Myrmicinae in combination of bell-shaped postpetiole, short scape, and complete forewing venation. Outwardly similar to *Agroecomyrmex* Wheeler, 1915. However key character of *Agroecomyrmicinae* is completely fused tergite and

sternite of 1st gastral (abdominal IV) segment, whereas *Biamomyrma* **gen. n.** has 1st gastral segment without tergosternal fusion.

Notes. The material available does not permit identifying a number of the antennal segment in *Biamomyrma*: *B. zherikhini* **sp. n.** displays only 3 basal flagellar segments, in *B. lata* **sp. n.** flagellum is detached and preserves clearly 8 segments which are not necessarily include the basalmost flagellar segment(s). *Biamomyrma rugose* **sp. n.** clearly preserves 9 flagellar segments, but the apicalmost one have its apex ill-preserved, thus leaving doubts if it is really apical segment.

Etymology. From former name of locality (Biamo) and Greek Myrmica (ant).

Biamomyrma zherikhini **sp. n.**
(Fig. 27)

Material. Holotype PIN 3429/108 (print and counterprint), gyne.

Description. Gyne. Body length ca. 9 mm. Head 1.1 times as long as wide, with nearly parallel sides, rounded occipital corners and weakly concave occipital margin. Anterior margin of clypeus with rounded lobe. Scape short. Funiculus without clava. Scutum longer than wide, twice as long as scutellum. Propodeum without teeth or spines. Propodeal declivity concave in side view. Form of petiole not visible. Postpetiole massive, shorter than high. Gaster oval. Head, mesosoma, petiole and postpetiole coarsely longitudinally rugose. Forewing with closed cells 3r, 1+2r, rm and mcu. Cell 3r shorted 3.7 times as long as wide. The meeting of crossvein rs-m and RS is a little distal to 2r-rs. Cell rm triangular with a short stem, twice as long as wide. Cell mcu quadrangular, trapeziform. Section 1M 1.5 times as long as section 1RS. Icu = 1.75.

Measurements of holotype, mm: AL 2.6; HL 1.5; HW 1.4; SctL 0.87; SctL 0.41; FWL 4.5.

Etymology. In honor of the paleontologist V.V. Zherikhin who collected ants from Bol'shaya Svetlovodnaya.

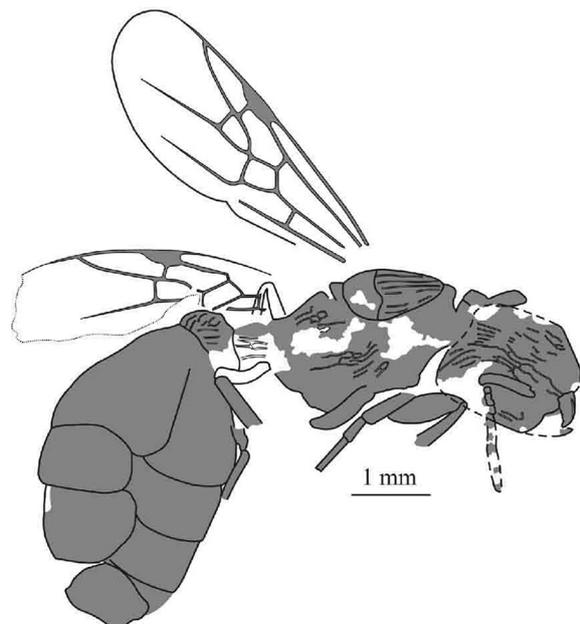


Fig. 27. *Biamomyrma zherikhini* **sp. n.**, holotype PIN 3429/108, gyne.

Рис. 27. *Biamomyrma zherikhini* **sp. n.**, голотип PIN 3429/108, самка.

Biamomyrma lata **sp. n.**
(Fig. 28)

Material. Holotype PIN 3429/1149 (print and counterprint), gyne.

Description. Gyne. Body length ca. 6 mm. Head nearly as long as wide, with weakly convex sides, rounded occipital corners, and weakly concave occipital margin. Anterior margin of clypeus with rounded lobe. Eyes comparatively small, oval, situated backward midlength of head. Scape short, nearly half as long as head. Funiculus with distinctive 3-segmented clava; basal funicular segments wider than long. Mesosoma very broad. Scutum transverse, 0.7 times as long as wide. Scutellum a little wider than long. Propodeum without teeth or spines. Postpetiole very large. Gaster oval. Occipital corners, sides of pronotum and petiole with coarse cellular sculpture, head, most part of mesosoma and postpetiole very coarsely longitudinally and reticulately rugose. 1st gastric segment sharply longitudinally striated.

Measurements of holotype, mm: AL 2; HL 1.4; HW 1.4; SL 0.76; SctL 0.9; SctW 1.3; SctL 0.5; SctW 0.6; PptH 1.

Comparison. Differs from other species in very broad mesosoma and transverse scutum.

Etymology. Lata is the Latin for broad.

Biamomyrma rugosa **sp. n.**
(Fig. 29)

Material. Holotype PIN 3429/1172 and 1169 (counterprint of the same specimen), gyne.

Description. Gyne. Body length ca. 5 mm. Head very big, 0.9 times as long as wide. Antenna 10-segmented. Scape short, nearly half as long as head. Funiculus gradually incrassate towards apex but without differentiated club. 2–5 funicular joints nearly as long as wide. Scutum nearly 3 times as long as scutellum, its dorsum straight in side view. Propodeum weakly convex in side view. Petiole with ventral tooth, sessile, longer than high; its dorsum gradually convex in side view. Postpetiole comparatively small. Gaster oval. Pronotum, mesopleura, petiole and postpetiole reticulately rugose, head, scutum and scutellum longitudinally rugose.

Measurements of holotype, mm: AL 1.5; HL 0.9; HW 1; SL 0.47; SctL 0.8; SctL 0.3; PtL 0.42; PptH 0.54.

Comparison. Differs from other species in comparatively small postpetiole.

Etymology. Rugosa is the Latin for rugose, wrinkled.

Morphogenus *Myrmecites*
Dlussky et Rasnitsyn, 2003

Type species *Myrmecites rotundiceps* Dlussky et Rasnitsyn, 2003.

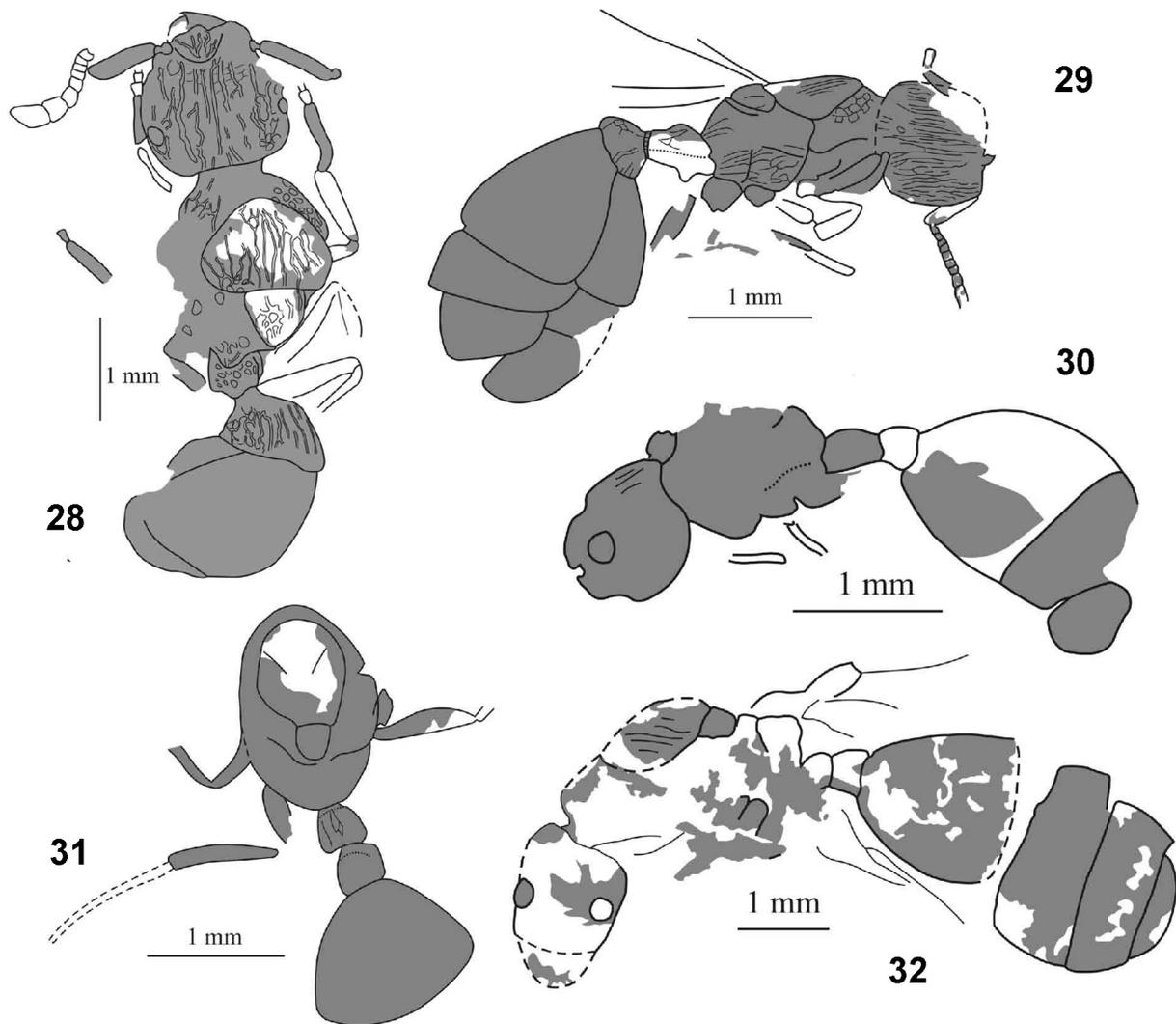
Diagnosis. Ant impression fossils with waist 2-segmented and comparatively short, petiole sessile, postpetiole narrowly attached to gaster, and propodeum unarmed, which cannot be identified more precisely.

Species included. Only type species described from Green River Formation, USA, Middle Eocene [Dlussky, Rasnitsyn, 2003].

Myrmecites sibiricus **sp. n.**
(Fig. 30)

Material. Holotype PIN 3429/1120 (+/-), gyne. Paratype PIN 3429/1127, gyne.

Description. Gyne. Body length 4–4.5 mm. Eyes situated in front of lateral midlength of head. Mesosoma nearly 1.5 times as long as high. Propodeal dorsum and declivity form rounded



Figs 28–32. Species of genera *Biamomyrma* and *Myrmecites*.

28 – *Biamomyrma lata* sp. n., holotype PIN 3429/1149, gyne; 29 – *Biamomyrma rugosa* sp. n., holotype PIN 3429/1172 and 1169 (counterprint of the same specimen), gyne, drawing from both print and counterprint; 30 – *Myrmecites sibiricus* sp. n., holotype PIN 3429/1120, gyne; 31 – *Myrmecites dubius* sp. n., holotype PIN 3429/1116, gyne; 32 – *Myrmecites major* sp. n., holotype PIN 3429/1113, gyne.

Рис. 28–32. Виды родов *Biamomyrma* и *Myrmecites*.

28 – *Biamomyrma lata* sp. n., голотип PIN 3429/1149, самка; 29 – *Biamomyrma rugosa* sp. n., голотип PIN 3429/1172 и 1169 (обратный отпечаток того же экземпляра), самка, реконструкция по обоим отпечаткам; 30 – *Myrmecites sibiricus* sp. n., голотип PIN 3429/1120, самка; 31 – *Myrmecites dubius* sp. n., голотип PIN 3429/1116, самка; 32 – *Myrmecites major* sp. n., голотип PIN 3429/1113, самка.

angle in side view. Propodeal dorsum much shorter than declivity. Declivity straight in side view. Petiole sessile, longer than high and longer than postpetiole. Petiolar dorsum gradually rounded in side view. Postpetiole nearly as long as high. Some rugae are visible on the head of both imprints.

Measurements, mm. Holotype PIN 3429/1120: AL 1.1; HL 0.9; PtL 0.36; PptL 0.27. Paratype PIN 3429/1127: AL 1.25; HL 0.8; PtL 0.32; PptL 0.24.

Comparison. Differs from *M. rotundiceps* in more compact mesosoma and elongated petiole.

Etymology. Name from locality (Siberia).

Myrmecites dubius sp. n.

(Fig. 31)

Material. Holotype PIN 3429/1116 (+/-), gyne without head.

Description. Gyne. Body length ca. 4.5 mm. Eyes situated in front of lateral midlength of head. Mesosoma 1.5 times as long

as wide. Scutum does not overhang pronotum, 1.3 times as long as wide. Parapsidal furrows present. Scutellum a little longer than wide. Petiole comparatively short, a little longer than wide. Postpetiole a little wider than long and a little longer than petiole. Petiolar dorsum rugulose.

Measurements of holotype, mm: AL 1.5; SctL 0.77; SctW 0.64; SctL 0.26; SctW 0.24; PtL 0.31; PtW 0.35; PptL 0.33; PptW 0.35.

Comparison. Differs from *M. sibiricus* sp. n. in short petiole.

Etymology. Dubius is the Latin for uncertain.

Myrmecites major sp. n.

(Fig. 32)

Material. Holotype PIN 3429/1113 (+/-), gyne.

Description. Gyne. Body length 8.3 mm. Head longer than wide, with rounded occipital corners and weakly concave occipital margin. Eyes situated in front of lateral midlength of

head. Propodeal dorsum and declivity form rounded right angle in side view. Propodeal dorsum shorter than declivity, straight in side view. Declivity straight in side view. Petiole sessile, nearly as long as high and shorter than postpetiole. Postpetiole higher than long. Gaster oval. Some longitudinal rugae are visible on scutum.

Measurements of holotype, mm: AL 2.7; HL ~1.3; HW 1.2; PtH 0.38; PptL 0.36; PptH 0.51.

Comparison. Differs from other known species in size: body length of other known species less than 5.5 mm.

Etymology. Major is the Latin for big.

Myrmicinae incertae sedis

Four fossils (PIN 3429/1146, 1151, 1160, 1163) unquestionably belong to Myrmicinae but cannot be attributed to a genus because of poor preservation state. It cannot be excluded as well that they might belong to above described species.

Formicidae incertae sedis

As many as 24 ant fossils (PIN 3429/1110, 1126, 1128, 1138, 1139, 1142, 1144, 1147, 1148, 1150, 1153, 1154, 1158, 1166, 1171, 1175, 1179, 1184, 1185, 1188, 1190, 1192, 1202, 1207) cannot be ascribed even to a particular subfamily. Of them, 22 have 1-segmented petiole and no constriction between the 1st and the 2nd gastral segments and so belong to the formicoid assemblage of subfamilies (Aneuretinae + Dolichoderinae + Formicinae).

Discussion

The collection under study consists of 115 fossils preliminary identified as ants. In fact, 35 of them are fragmentary and doubtfully ants, so only 80 are considered as Formicidae now. Of them, 56 were found identifiable up to subfamily level, 45 to generic, and 42 to species level. Finally, described are 26 species representing 15 genera and 9 subfamilies.

The most abundant subfamily is Formicinae with 8 species of 3 genera (23 fossils out of 56 identified to the generic level, 41.1%). The second is Myrmicinae, with at least 8 species, 4 genera, and 12 specimens (21.4%). Following are Dolichoderinae (no less, than 6, 4, 10, and 17.9%, respectively), and Ponerinae (at least 3, 2, 4, 7.1%). The remaining subfamilies Aneuretinae, Amblyoponinae, Cerapachyinae, Proceratiinae and Myrmeciinae are represented with 1 species and 1 or 2 fossils each. Taking into account 22 fossils identified as Formicomorpha, and sorting the others to 3 main groups, we have a total of 57 specimens (73.1%) for Formicomorpha (Aneuretinae + Dolichoderinae + Formicinae), 12 specimens (15.4%) for Myrmicinae, and 6 (7.7%) for Poneromorpha (Amblyoponinae + Ponerinae + Proceratiinae).

The results obtained make possible to compare the assemblage of Svetlovodnaya to other known Cenozoic ant faunas. Cenozoic ant assemblages are known from many sites in Europe, Asia, North and South America, and yet only a fraction are sufficiently rich to permit a meaningful comparison. This particularly concern Asia. Particularly, only 8 fossils of 7 species are currently known

in the Sakhalin amber [Dlussky, 1988] which is dated as the Middle Eocene now [Kodrul, 1999]. The Chinese ants in the Middle Miocene Fushun amber [Hong, 2002] are peculiar and very interesting. However, they are so poorly described that cannot be used in comparison. The only tentative inference available to be drawn is apparent absence of dominant species there: all species are established based on 1, rarely 2 specimens. Another rich Chinese ant fauna from the Middle Miocene of Shanwang in Shandong Province [Zhang, 1989; Zhang et al., 1994] is also difficult to be taken into comparison because of clearly selective approach employed. Indeed, only females are described whilst all ant assemblages other than from ambers are dominated with males. No data on the numerical relation of the Shanwang ant species is provided as well.

The best studied are currently the fossil ant faunas of Europe. This particularly concerns the Priabonian (Late Eocene) ambers (succinites) of the Baltic group: true Baltic, Bitterfeldian (Saxony, Germany), Scandinavian (Denmark), and Rovno ambers (Ukraine, Belarus and Poland) [Dlussky, Rasnitsyn, 2009]. Described as entire faunas are also the one from the Middle Miocene of Stavropol (Cis-Caucasian [Dlussky, 1981]), Late Eocene (Priabonian) of the Bembridge Marls (north in Isle of Wight, UK [Antropov et al., 2014]) and the Early Miocene of Radoboj in Croatia [Dlussky, Putyatina, 2014]. Ants of the Middle Eocene of Grube Messel and Eckfeld Maar in Germany are described only in part [Lutz, 1986; Dlussky et al., 2008, 2009; Dlussky, 2012; Dlussky, Wedmann, 2012]. However, complete lists of ants identified up to subfamily are available for these fossil sites. Additionally, G.M. Dlussky was able to compile lists of genera of ants in the Aquitanian (latest Oligocene or earliest Miocene, depending on a stratigraphic scheme accepted) of Rott and in Ruscinian (Late Pliocene) of Willershausen, both in Germany. These data are based on the collections kept, respectively, at the Steinmann Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, and Geowissenschaftlicher Zentrum der Georg-August-Universität Göttingen. Unfortunately, the rich ant faunas of Aix-en-Provence in France (Late Oligocene, Chattian [Théobald, 1937]) and Oeningen in Germany (Late Miocene [Heer, 1849, 1867]) cannot be involved into analysis until a revision.

In Americas, sufficient information is available about ants in the Early or Middle Eocene of the Green River Formation (Middle Ypresian to Earliest Lutetian of western USA, 53.5–48.5 Ma) [Dlussky, Rasnitsyn, 2003] and the latest Eocene Florissant Formation (ca. 34 Ma; Colorado, USA [Carpenter, 1930]). There are data available about the Early Miocene (ca. 20 Ma) ants in the Mexican [Solórzano Kraemer, 2007] and Dominican ambers (many publications dealing with particular taxa, but with no review) which cannot provide any complete picture of the fauna. The information available attests their ant fauna as essentially Neotropical which differs so much from the Eurasian and North American ant assemblages that its comparison with the one under present study is hardly possible. We don't consider it further here.

The least known currently is the past Afrotropical ant fauna. A limited collection (39 specimens only) of ants is described long ago from the Sicily amber [Emery, 1891].

Table 1. Subfamily participation in main ant fossil sites (%).

Таблица 1. Доли представителей разных подсемейств муравьев в важнейших ископаемых комплексах (%).

Subfamilies / Подсемейства	Asia / Азия	Europe / Европа									North America / Северная Америка	
	Svetlovodnaya / Светловодная	Messel / Мессель	ambers / янтари			Bembridge / Бембридж	Rott / Ротт	Radoboj / Радобой	Stavropol / Ставрополь	Willershausen / Виллерхаузен	Green River / Грин-Ривер	Florissant / Флориссант
			Baltic* / Балтийский	Bitterfeld / Биттерфельдский	Rovno / Ровенский							
Formiciinae	0	48.3	0	0	0	0	0	0	0	0	0	0
Aneuretinae	3.5	0	+	0.2	0	0.1	0	0	0	0	2.9	0
Dolichoderinae	17.9	10.4	55.9	52.9	53.2	8.5	28.1	9.4	3.9	0	71.6	62.6
Formicinae	41.1	30.6	39.6	34	39	88.2	35.1	84.9	52.6	86.8	2.9	32.5
Myrmicinae	21.4	1.4	2.8	9.5	4.6	0.4	35.1	2	40.8	13.2	2	4.8
Poneromorpha	10.7	8.4	1.3	1.3	1.6	2.8	0	3.7	2.6	0	9.8	0
Myrmeciinae	3.6	1.4	+	0.1	0	0	1.8	0	0	0	10.8	0
Pseudomyrmecinae	0	0.5	0.3	1.3	1.5	0	0	0	0	0	0	0
Cerapachyinae	1.8	0.2	0.1	0.3	0.2	0	0	0	0	0	0	0
Specimens examined	56**	432***	1948	1105	1202	630	57	350	76	106	102	5592

Notes. * – crosses denote subfamilies recorded only in non-representative collections of Baltic amber; ** – number of specimens identified at least up to subfamily level; *** – in Messel, the figure refers to the number of specimens collected except Formiciinae which precise number is not recorded; the total number of Messel ants is roughly estimated as 900.

Примечание. * – для балтийского янтара крестами показаны подсемейства, найденные только в нерепрезентативных коллекциях; ** – число экземпляров, определенных по меньшей мере до уровня подсемейства; *** – для Месселя указанное количество всех изученных экземпляров не включает Formiciinae, точное число которых не зафиксировано. Приближенное число изученных муравьев в Месселе 900.

This amber is considered now as Early Eocene (29–34 Ma) in age [Skalski, Veggiani, 1990]. The assemblage is unusual in composition including participation of subfamilies, and resembles the modern Afrotropical ant faunas most of all [Dlussky, 2005; Dlussky, Rasnitsyn, 2007]. No other Cenozoic ant assemblages are known yet in the region.

The most striking feature of the Svetlovodnaya ant assemblage revealed under comparison with the European and North American ones is the lack of one or a few highly dominating species. Other studied European and North American assemblages always display a few dominating species and many others represented by rare to unique specimens only. The examples are species of *Titanomyrma* Archibald et al., 2011 (= *Formicium* Westwood, 1854) in the Middle Eocene of the Messel and Eckfeld [Archibald et al., 2011], responsible for, respectively, 48 and 43% of all ants there [Wappler, 2003; Wedmann, 2005]. In the Late Eocene ambers of Europe, 17 ant species (10%) account for 85–94 per cent of all ant fossils, with the share of the most common species *Ctenobethylus goepperti* Mayr, 1868 varying from 26% in the Scandinavian up to 52% in the Baltic amber, whilst the second most common species, *Lasius schiefferdeckeri* Mayr, 1868 takes from 15 to 24.5% of the Baltic and Bitterfeldian ants, respectively [Dlussky, Rasnitsyn, 2009]. In the Bembridge marls, 51% of all ant fossils belong to 2 species of *Oecophylla* F. Smith, 1860 [Antropov et al., 2014]. *Lasius* fossils represent a half of all ants in Radoboj [Dlussky, Putyatina, 2014] and 40%

in Stavropol deposits [Dlussky, 1981]. North American assemblages give a similar pattern. *Eoformica pinguis* Scudder, 1877 accounts for 40% and *Dolichoderus kohlsi* for a quartet of all ant fossils in the Green River [Dlussky, Rasnitsyn, 2003]. Similarly, *Protazteca elongata* Carpenter, 1930, *Liometopum miocenicum* Carpenter, 1930 and *Lasius peritulus* Cockerell, 1927 each take a quarter of all ant fossils in the Florissant [Carpenter, 1930].

Table 1 displays data on participation of ant subfamilies in the fossil assemblages in Eurasia and North America. The table considers new information accumulated since Dlussky, Rasnitsyn [2007, 2009]. For the Baltic amber, the figures represent data up to early 2014 and based on the representative (sensu Dlussky and Rasnitsyn [2009]) samples only, that is, the collections known to be compiled with no prior selection in favor of, or against, particular kinds of fossils (e.g., rare vs. common, big and spectacular vs. small and ordinarily looking, representing particular taxa, etc.). Subfamilies known from the non-representative Baltic collections only are marked with a cross (+). Bolton [2003] has recently splitted Ponerinae into several subfamilies called jointly the Poneromorph subfamilies: we treat all of them as the entire group because of their similar morphology and ecology in spite of their possible polyphyly.

The table demonstrates dominance of the formicomorph ants in all assemblages considered there. This evolutionary success may be ascribed, at least in part, to an important innovation obtained by formicomorphs.

Characteristic of them, besides the 1-segmented petiole, is a specialized construction of proventriculus which makes them possible to store a considerable amount of liquid in the crop. As a result, aphid excretates play important role in the formicomorph diet, and this was the case at least since the Late Eocene [Perkovsky, 2006, 2007, 2008]. In partial correlation with this feature, characteristic of the vast majority of the living formicomorph ants, and probably of extinct ones as well, is their foraging activity on and above the ground surface, in contrast to poneromorphs which generally prefer to forage within a substrate. Arnoldi [1937] has classified the former group as herpetobionts, hortobionts and dendrobionts (foraging on the earth surface, in herb level and on trees, respectively), and the latter group as stratobionts (foraging within leaf litter) and geobionts (foraging in soil). The classification and terminology proposed was found easy and helpful, it is widely accepted by Russian myrmecologists [Kupyanskaya, 1990; Zakharov, 1994; Zryanin, 2010] and employed herein as well.

At the same time, different formicomorph subfamilies played dominant role in different past assemblages. Prevailing in the Middle Eocene of Europe were extinct giant Formiciinae, a sister group of the remaining Formicomorpha (that is, Aneuretinae, Dolichoderinae и Formicinae) according Bolton [2003] which died out by the end of Eocene. Formiciinae are known in the Middle Eocene in North America as well [Archibald et al., 2011], although they have never been as numerous there as in Europe. Dominating in the North American Eocene, in Green River and Florissant, have been Dolichoderinae. In contrast, in the rock fossil (non-amber) European assemblages of Cenozoic Formicinae always outweigh Dolichoderinae.

At first glance the data about the Eocene ambers contradict to the above inference: participation of Dolichoderinae surpasses that of Formicinae there. However, this is most probably a result of taphonomical processes that distort shares of particular taxa in the source communities (cf. Rasnitsyn, Zherikhin [2002] and Martínez-Delclòs et al., [2004] for the review of amber taphonomy). Particularly, the ants subjected to direct burial in sediments are primarily winged casts trapped into water mainly at the nuptial flight, with those of larger body size having higher chance of successful burial and subsequent discovery by a paleontologist. In contrast, the worker ants of medium to small size have higher probability to be trapped into resin of an amber tree, and particularly those who used to visit those trees regularly. The Late Eocene amber dominant species *Ctenobethylus goeperti* (Dolichoderinae) and *Lasius schiefferdeckeri* (Formicinae) took jointly more than half of all ant inclusions there. They were most probably specialized dendrobionts which formed trails towards aphid colonies on the tree, as their common (10–13%) syninclusions of multiple workers and workers with aphids suggest (our observations). As a result, exclusion of these two species changes participation of Dolichoderinae and Formicinae in the respective amber assemblages considerably. In the Baltic amber ant assemblage, participation of Dolichoderinae is 55.9% and of Formicinae 39.6%, and with *C. goeperti*

and *L. schiefferdeckeri* being excluded, the figures change to 11.5 and 22.6%, respectively. Formicinae take a distinct prevalence. Additionally, the European Eocene ant assemblages in sediments often include many *Oecophylla* fossils (10.4% of all ants but *Formicium* in Messel, and 51% in Bembridge Marls) which are distinctly underrepresented in the amber assemblages (0.2% in representative samples, 0.6% in the overall collection of the Bitterfeldian amber) because of two main taphonomical features. The first of them is that *Oecophylla* is a comparatively big insect (body length of workers of amber *O. brischkei* Mayr, 1868 being 4.5–8 mm) which makes it easier to free itself of a resin trap comparing smaller ants. More important, however, is that the weaver ants populate broadleaf trees where they weave leaves together with silk produced by their larvae to make nest. This makes *Oecophylla* a rare visitor of conifer amber trees.

Unlike Formicomorpha, Poneromorpha and Myrmicinae are ecologically classifiable as predominantly geo- and stratobionts rarely employing trophobiosis with aphids and other plant sucking insects. In tropical forests, Myrmicinae account for 74% of leaf litter ants [Ward, 2000]. In temperate forests, 80% of myrmicine ants are foraging within the leaf litter, soil and/or lower herb layer. As to Poneromorpha, it was only mid-Eocene when these ants override Myrmicinae in species and specimen diversity in Europe [Dlussky, Wedmann, 2012]. In the Late Eocene, abundance of myrmicine ants surpassed that of poneromorphs but left low yet until grew considerably in majority of the Oligocene and Miocene assemblages (Radoboj excluded). Similar is the pattern observed in the North America: in the late Early Eocene (Ypresian) of Green River (see Smith et al. [2010] and references therein for age), Poneromorpha prevail over Myrmicinae unlike the terminal Eocene of Florissant where only two fossils of a sole poneromorph species is recorded thus far.

The Svetlovodnaya assemblage reminds most closely the Rott one (Aquitanian, that is latest Oligocene or earliest Miocene in Germany) in its subfamily level composition, for the shares of both Formicinae and Myrmicinae is higher there comparing Dolichoderinae. However, a comparatively high participation of poneromorphs gives it a distinctly older appearance.

A generic level comparison reveals Svetlovodnaya ants as more similar to European rather than North American ants. All formicomorph genera there are recorded in Europe, whilst *Gesomyrmex* is known neither in contemporary nor in past American ant faunas. Equally, *Protazteca*, the most abundant ant in the terminal Eocene of Florissant in Colorado, has been never recorded in the Old World deposits including Svetlovodnaya. The same holds true for *Klondikia* Dlussky et Rasnitsyn, 2003 and *Kohlsimyrmex* Dlussky et Rasnitsyn, 2003 which are not uncommon in the Early Eocene of Green River, nor *Elaeomyrmex* Carpenter, 1930, *Miomymex* Carpenter, 1930 and *Petraeomyrmex* Carpenter, 1930 characteristic of the Florissant. At the same time, a composition of Myrmicinae in Svetlovodnaya differs from those both in Europe and North America. *Agastomyrma* **gen. n.** and *Biamomyrma* **gen. n.** are not recorded elsewhere. In contrast, the morphogenus

Paraphaenogaster Dlussky, 1981 [Dlussky, 1981] based on a specific wing venation, is absent from the Svetlovodnaya and widespread in Europe (three quarters of all myrmecines in the Bembridge Marls, four fifth in Rott, and all Myrmicinae in Stavropol and Willershausen). However, its absence from Svetlovodnaya could be due to insufficient material: in the Shanwang assemblage (Middle Miocene of China), four of five myrmecine fossils have their wing venation characteristic of *Paraphaenogaster*.

One more feature in common with the past European faunas is the simultaneous occurrence in Svetlovodnaya of the ant genera which are currently characteristic of the Holarctic and the tropics. These are *Formica* and *Lasius*, now populated the temperate Eurasia and North America and only high mountains elsewhere [Wheeler, 1922, 1927], from one side, and *Gesomyrmex* known exclusively in the Old World tropics now [Dlussky et al., 2008, 2009], from the other side. Myrmeciinae could be ascribed to the tropical group as well, for the only extant myrmecine genera *Myrmecia* Fabricius, 1804 and *Nothomyrmecia* Clarck, 1934 are limited to Australia and adjacent islands now.

The above paradox was pointed out by Wheeler [1915] in his monograph on the Baltic amber ants. By now, a far more general meaning of the Wheeler's dilemma [Archibald, Farrell, 2003] is evident, for the above pattern remained characteristic of the European ant faunas at least since the Middle Eocene till Middle Miocene. *Formica* and *Lasius* occur in all strata since Eocene there, whilst *Oecophylla* is recorded in the Middle Eocene (Messel, Eckfels [Dlussky et al., 2008]), Late Eocene (Baltic amber and Bembridge Marls [Wheeler, 1915; Antropov et al., 2014]), Oligocene (Kleinkembs, Haut-Rhin [Théobald, 1937]), Early (Radoboj [Dlussky, Putyatina, 2014]) and Middle Miocene (Stavropol; Perfilieva, 2015, in press). *Gesomyrmex* spp. are described from the Middle Eocene (Messel, Eckfeld [Dlussky et al., 2008]) and recorded in the Late Eocene ambers [Wheeler, 1915; Dlussky et al., 2009] and Early Miocene of Radoboj [Dlussky, Putyatina, 2014] as well. Diverse Myrmeciinae were widespread in the Middle Eocene of Europe, as well as of North and South America and persisted in Europe at least to the Oligocene [Dlussky, Perfilieva, 2003; Archibald et al., 2006; Dlussky, 2012].

Our observations on the nests of *Oecophylla smaragdina* introduced in 1964 from China to the Lazarevsky Insectarium, All-Soviet Institute of Plant Protection, near Sochy in Cis-Caucasus, reveal that the ants become slow at 6 °C and die at below 0 °C [Panshin, 1965]. So occurrence of the tropic ants evidences warm climate unquestionably. It is less clear why the Holarctic genera are absent from tropic communities, for many their species are well known to survive for years in laboratory at the room temperature. The Holarctic *Formica fusca* Linnaeus, 1758 is recorded established at sea level at Dumaguete, on the island of Negros Oriental, Philippines (9°30'N), and the former author has found it in a sample collected by S.I. Golovach in Cuba. This makes evident that some temperate ants are able to survive in the tropics, at least in anthropogene environments. Hence their absence in

the tropic communities is most probably a result of biotic interactions.

As mentioned above, this does not concern the mountain environments within the tropic zone where temperate species well may exist. For instance, a subspecies of the widespread Palearctic *Formica picea* Nylander, 1846 is recorded in mountains in Taiwan [Forel, 1913]. The southernmost record of *Formica fusca* is mountains of Sumatra Island where it lives in pine-tree forests at 4000 feet altitude [Wheeler, 1927]. Wheeler [1927] considered these mountain populations as relict and implying their past distribution much wider than now.

The above considerations agree with the concept of an extinct climate called equable and characteristic of moderately warm summer and mild winter permitting co-occurrence of tropical and temperate taxa now living distant of each other (e.g., Archibald et al. [2010]). Our observations suggest that features of the equable climate are traceable in the past ant assemblages as late as in the Middle Miocene.

More local and yet of some interest are comparatively low number of isolated wing fossils as well as a composition of the ant subassemblages in two fossiliferous beds in the source outcrop of Svetlovodnaya (cf. Material chapter above). The material accumulated is insufficient for a thorough statistical investigation. Yet it permits to pose at least a couple of questions worth to consider at future researches. The first question concerns proportion of the isolated wings which take usually more than half of ant impressions in rock fossil assemblages (58% in Bembridge, 66% in the Middle Miocene of Vishnevaya Balka, Stavropol, the North Caucasus [Dlussky, 1981]). In contrast, the Svetlovodnaya ant assemblage shows only 15% of isolated wing fossils. Similarly, Svetlovodnaya differs from in female fossils being more common than male ones, whilst the majority of other non-amber assemblages show an opposite proportion (except for Shanwang assemblages in Shandong, China, which is additionally similar at least in the lack of strictly dominating taxa [Zhang, 1989; Zhang et al., 1994]). Taken together, differences in these two parameters might infer that unlike the majority of non-amber ant fossil assemblages, the Svetlovodnaya and Shanwang ones have formed possibly in more close biotops (e.g. tight forest) unfavorable for nuptial swarm formation.

Another observation worth considering here is a supposedly different distribution of ant taxa and sexes between the bed 1 and bed 5 is found appreciably different when compared in sufficiently generalized form. Particularly, both subassemblages consist of comparable number of ants supposedly foraging on ground surface and on vegetation (22 and 31 specimens of Formicomorpha + Myrmeciinae in the bed 1 and 5, respectively). However, the number of ants foraging within soil and leaf litter more differs (5 vs. 11, with the ratio 4.4 : 1 vs. 2.8 : 1, respectively). Similarly, bed 1 has yielded 11 ant females and 8 males (1.4 : 1), bed 5 gives 25 and 5, respectively (5 : 1). This numerical discrepancy might indicate considerable differences in the source environments, although it is not easy to say now which particular features of past biocenoses might be responsible for these differences.

Conclusion

The present description of Svetlovodnaya ant assemblage discovers presence of 1 species in 1 genus in the subfamily Aneuretinae, 5 and 3, respectively, in Dolichoderinae, 8 and 3 in Formicinae, 1 and 1 in each Myrmeciinae, Cerapachyinae, Amblyoponinae and Proceratiinae, 2 and 1 in Ponerinae, and 7 and 3 in Myrmicinae. All species and 4 genera are extinct and 8 genera are still living (morphogenera are not considered to be either extinct or living). Of 31 species discriminated, 23 are formally described and named.

The analysis provided reveals features of the ant assemblage of Svetlovodnaya indicative both of evolution of ants and ant communities in Cenozoic, and of the state of environments and climate and their transformation at and near the Green- to Icehouse transition. The most important of these features can be outlined as follows.

1. The Svetlovodnaya ant assemblage differs from all sufficiently known Cenozoic assemblages (which are unfortunately all European and North American, see above) in being polydominant on the generic level. In contrast, all other sufficiently rich and representative European and North American assemblages show one or two, rarely three genera strictly dominating in a particular assemblage. The reason of this speciality is to be explored.

2. A proper consideration of the taphonomic effects on composition of the past ant assemblages makes possible to demonstrate for the first time that all sufficiently well explored Cenozoic assemblages are dominated with the formicomorph ants. Characteristic of these ants are trophobiosis with the plant sucking Homoptera and foraging mainly on and above the ground surface. These features are most probably responsible, jointly or separately, for the evolutionary success of the formicomorphs. In Europe, formicine ants were particularly successful.

3. Within the non-formicomorph ant subassemblage, the present prevailing position of Myrmicinae over Poneromorpha is dated since at least the latest Eocene: Early and Middle Eocene assemblages show myrmicines subordinated to poneromorphs both in Europe and North America.

4. Geographically, the Svetlovodnaya ant assemblage is more similar to the European rather than to its North American counterparts. No specific similarity is found with the supposedly coeval assemblages from the Priabonian ambers of Europe (Baltic and others).

5. The assemblage under consideration well fits the Wheeler's [1915] paradox (coexistence of strictly tropical and temperate taxa) and so support the equable climate concept as applicable to the Late Eocene climate of the Sikhote-Alin area.

6. The assemblage differs from the majority of non-amber ant assemblages (except for the Miocene of Shanwang, China) in male fossils not dominating strictly over female ones, as well as in low proportion of isolated wing fossils: both these features suggest that the source biotopes could be more close there, representing tight forests or the like.

7. Two subassemblages of the Svetlovodnaya ant assemblage which come from the slightly different

sedimentary beds are found differing in their composition (in respect of participation of both male vs. female sexes and formicomorph vs. non-formicomorph taxa). The cause of this difference is left obscure yet.

Acknowledgements

This study was supported by the Russian Foundation for Basic Research, project No. 14-04-00658.

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