



Early Miocene ants (Hymenoptera, Formicidae) from Radoboj, Croatia

Gennady M. Dlussky and Tatyana S. Putyatina

With 18 figures and 2 tables

Abstract: The ant assemblage of Radoboj (Croatia) described by HEER (1849, 1867) is considered the richest known Miocene assemblage of Europe. However, HEER's data can no longer be used for analysis of the palaeontological history of ants, because they are strongly outdated and require a revision. Such a revision was the purpose of our study. We found in collections of three museums of Austria (Universalmuseum Joanneum in Graz, Geologische Bundesanstalt, and Naturhistorisches Museum in Wien) a total of 537 compression fossils of ants from Radoboj, 459 of which were identified earlier by HEER. We designated the holotypes, lectotypes and neotypes for 54 of the 62 species described by HEER, and subsequently compared the other specimens to these types. As a result, we have identified 350 specimens to subfamily and 309 specimens to species. We re-described 23 species originally described by HEER (1849, 1867) and two species described by MAYR (1867). One genus and eight species are described as new; 27 species and varieties described by HEER are synonymized. The taxonomic placement of eight species described by HEER remains unclear. As a result of our revision, the known assemblage of Radoboj includes 33 species of 15 genera and five subfamilies. The assemblage of Radoboj is especially similar at the subfamily level to the assemblage of Bembridge, UK (Late Eocene) and Stavropol, RF (Middle Miocene).

Key words: Formicidae, revision and new taxa, Early Miocene, Radoboj, Croatia.

1. Introduction

The first substantial study of fossil ants was the monograph on insects from the Miocene deposits of Oeningen (Germany) and Radoboj (Croatia) by HEER (1849). Before this monograph, various authors described in 1822–1831 a total of 11 ant species. These were from Baltic amber, and are currently treated as Formicidae *incertae sedis* (DLUSSKY 2008a), or are from deposits (perhaps Miocene) near Bonn (Germany), including *Formica lignitum* GERMAR, 1837. In HEER's monograph, 68 species and varieties of ants were described, including 40 species from Radoboj. In his later studies, HEER (1864, 1867) added 26 new species and varieties to this checklist (22 of them from Radoboj). Two other species were described from Radoboj by MAYR (1867). To date, a total of 64 species and varieties of fossil ants have been described from Radoboj. Beyond this

deposit, a greater number of species have only been described from the Late Eocene ambers of Europe and from Miocene Dominican amber.

However, in the 19th century it was already clear that HEER's data were in need of a serious revision. In 1867 MAYR studied a collection of ants from Radoboj that were identified by HEER and stored in the Kaiserlich-Königliche Geologische Reichsanstalt (Austria). It turned out that in many cases the same species name was attributed to members of different genera and even subfamilies. HEER (1867) commented on MAYR's article in an footnote and suggested that some labels in the collection identified by HEER were probably mixed up. Unfortunately, this suggestion cannot be verified now. Although the majority of specimens in the studied collections have old numbers drawn directly on the rock surface, HEER never indicated the numbers of specimens examined in his publications.

Since MAYR was unable to acquire HEER's type materials for examination, he could not perform a wholesale revision, and restricted himself to identifying the ants to the genus-level. Subsequently, the generic names of ants assigned by HEER were changed in the catalogue of fossil insects prepared by HANDLIRSCH (1907), who used data for the MAYR's results. He himself did not study HEER's collection, but his interpretations were subsequently accepted by other authors (BOLTON 1995, and others).

In his monograph, HEER used a classification of ants that was already outdated by the standards of 1849, and even more so by 1867, after the publication of the study by MAYR (1855) laid the foundations of our modern classification. This is clear from HEER's (1849) descriptions of genera, as well as his notes surrounding the description of new taxa, in which he compared extinct species directly to extant ones. He placed all Formicinae in the genus *Formica* and all Myrmicinae in the genus *Myrmica*, although, at that time, many of the species he included in these two genera already belonged to other genera. He placed all ants from Radoboj in only four genera: *Formica* (waist one-segmented, forewing without a closed mcu cell), *Ponera* (in 1867, *Poneropsis*; waist one-segmented, forewing with closed mcu cell), *Myrmica* (waist two-segmented, forewing with closed mcu cell) and *Attopsis* (waist two-segmented, forewing without closed mcu cell). According to the modern system, HEER's "*Formica*" includes all Formicinae, his "*Poneropsis*" includes the majority of species of Poneromorpha and Dolichoderinae, and his "*Myrmica*" includes the majority of Myrmicinae. As for *Attopsis*, the establishment of this genus was based on an erroneous interpretation of imprints, as will be shown below.

After MAYR's work, no research scientists have revisited HEER's collections, although it was obvious that the material needed a revision. Such a revision was the purpose of our study. With this in mind, we examined ants from the deposits of Radoboj stored in three museums of Austria. The most valuable collection is stored in Universalmuseum Joanneum, Department for Geology & Palaeontology (UMJG&P). It includes 148 imprints from Radoboj, attributed here to 41 species. The 139 specimens bear original labels written by HEER. As many as 39 specimens (28 species) match figures in HEER's monographs (i.e., they are doubtlessly type specimens). The last revision of the collection was performed by students (unfortunately, unqualified for this kind of work) around 1995. After the latter work, the vast majority of specimens were

assigned five-digit catalogue numbers. In the text of this study we provide the numbers of specimens from this catalogue. One caveat should be noted, however. All of the specimens identified by HEER are labelled as holotypes or syntypes and are listed as such in the museum catalogue, but in a number of cases, specimens labelled and listed as holotypes are not the ones depicted by HEER, and the quantity of supposed syntypes is greater than the number given in his descriptions.

We found the greatest number of imprints (246, including 121 with HEER's original labels) in the collection of the Geologische Bundesanstalt, Wien (GBA). The most recent inventory was compiled in 2009. All of the specimens were given continuous numbers. In the text of this article we provide the numbers from this latest inventory. It should be noted, however, that in a number of cases the valid names are written on the new labels and in the catalogue incorrectly, because the original labels were misread. For instance, in some cases *occulta* (the specific epithet of an extant species described from Canada) stands for *occultata*, and *rollari* or *gottari* stand for *kollari*. This collection contains none of HEER's type specimens.

The third collection is stored in the Naturhistorisches Museum, Wien (NHMW). It contains 145 imprints of ants, with only 82 of them identified to species. The majority of specimens have numbers like 1852.XXIX.30, assigned after the compilation of the inventory in 1852. We refer to these numbers in this article. In this collection we found several specimens which, judging by their old numbers, were studied by MAYR.

Our study of the materials immediately confirmed that MAYR was right in most regards: first, most of the species belong to genera other than those to which they were attributed by HEER; second, in HEER's identifications the same name can stand for more than one species. The record-holder in this respect is the name *Formica occultata* – eight different species belonging to five genera and three subfamilies are labelled with this name in the collections observed. On the other hand, one species could often be identified as more than a single species. For instance, specimen GBA no. 2009/016/0515 was identified by HEER as *Formica longaeva*, whereas the counterpart of the same specimen was identified as *Formica occultata*. HEER distinguished between species on the basis of size-related characters and characters that result from fossilization (coloration of impressions, shape of the gaster). In a number of cases, he erected species based on incorrect interpretations of imprints. Therefore, it was impera-

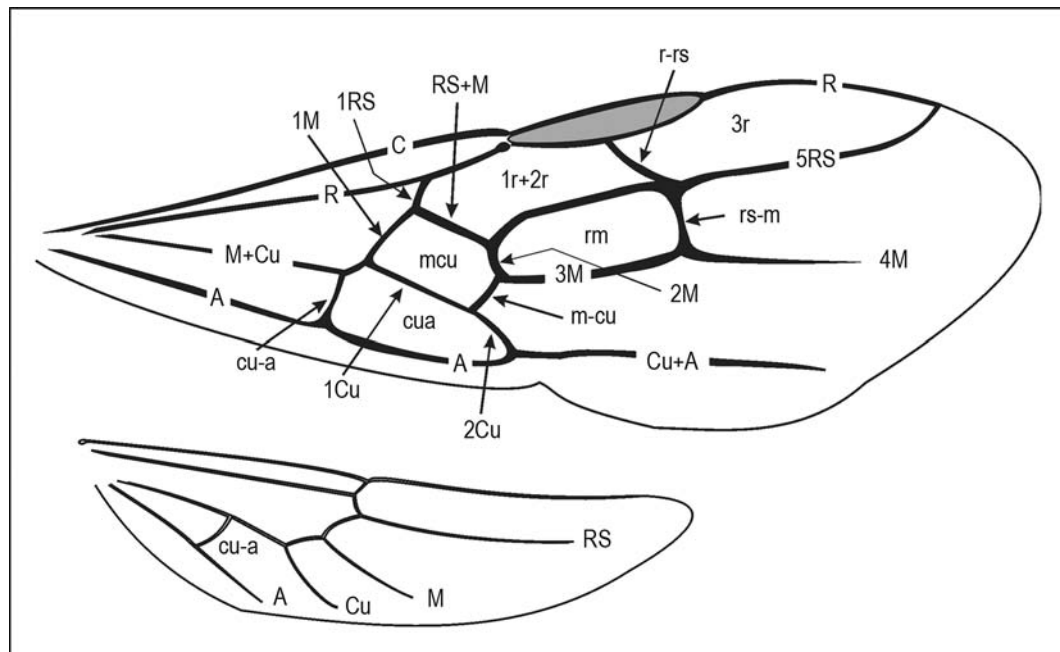


Fig. 1. Wings of gyne of *Gnampptogenys europaea* (MAYR) (Rovno amber). C, R, RS, M, Cu, A – veins; 1RS, RS+M, 2M etc. – vein sections; r-rs, r-m, m-cu etc. – cross veins; 1r+2r, rm, m-cu, cua – cells.

tive to designate type specimens and focus the revision on them.

One more important circumstance should be noted here. HEER believed that the deposits of Oeningen and Radoboj were of the same age, and considered seven species (*Formica lignitum*, *F. obesa*, *F. pinguis*, *F. pinguicola*, *F. macrocephala*, *Poneropsis fuliginosa*, and *Myrmica tertiaria*) common to both sites. However, according to the modern data, the deposits of Radoboj are dated to the Early Miocene, whereas the deposits of Oeningen are dated to the Late Miocene (LUTZ 1997). It is unlikely that any insect species could remain unchanged for several million years.

2. Methods

At the beginning of this study we made color digital photographs of all ant specimens. All subsequent work was performed using these photographs. We then determined the type specimens of all species. In a number of cases, we found specimens conforming to the figures in HEER's works. We designated all such specimens as holotypes or lectotypes. When we failed to find such a specimen, we selected as lectotype one of the specimens stored in UMJG&P, labelled as a syntype and complying with HEER's description and measurements. If no syntype could be found, we design-

ated as neotype the best-preserved specimen that we were certain was identified by HEER and was the best match for his description and measurements. As a result, we determined the types for 54 of the 64 species described by HEER.

Based on the photos, we prepared line drawings of all types and all of the best-preserved specimens. Enlarged prints of the photographs were hand traced by pencil. The resulting draft drawings were scanned and finishing edits were made using the program CorelDraw 15. In the line drawings, full lines indicate visible sclerite boundaries; dashed lines, supposed sclerite boundaries and visible lines other than sclerite boundaries (deformation folds, occasionally superimposed objects, elements of sculpture, etc.); and dotted lines, visible margins of incomplete sclerites. Preserved original sclerites of the impressions are colored in grey, even if these sclerites were chemically modified. Nomenclature of the wing venation (Fig. 1) follows DLUSKY (2009). The other morphological terminology is after BOLTON (1994).

Fossil imprints of ants are considerably deformed. Consequently, the calculated measurements and their ratios are more variable than is typical for three-dimensionally preserved ants. Some measurements are less affected by deformation than others (e.g., length of the mesosoma in comparison to its width and height). The gaster in the imprints is usually strongly deformed; therefore, we did not use measurements of the gaster.

The measurements taken are referred to as follows: AL – mesosoma (alitrunk) length from junction with head to that

with petiole; AH – mesosoma (alitrunk) height; AW – mesosoma (alitrunk) maximum width; BL – total body length; ED – maximum eye diameter; F3L – hind femur length; FWL – forewing length; GL – gaster length; HL – head length without mandibles; HW – maximum head width; HWL – hind wing length; $Icu = [1Cu + (2M+Cu)]/1Cu$; MdL – mandible length; n – number of specimens measured; PtL – petiole length; PtH – maximum petiole height; PtW – maximum petiole width; PptL – postpetiole length; PptW – postpetiole width; ScL – scape length; SctL – scutum length; SctW – scutum width; SctIL – scutellum length; SctIW – scutellum width.

The body length is reported at the beginning of each species description for the following reasons. First, it cannot be measured precisely, because the gaster in the imprints is usually strongly deformed. At the same time, in the process of identification, even an approximate size allows one to immediately exclude a considerably larger or smaller ant species.

3. Geological setting and preservation of imprints

The deposits of Radoboj (Croatia) contain one of the richest and most diverse fossil insect assemblages. Several hundred species of different orders have been described from this site (HEER 1847, 1849, 1853, 1867). The deposits of Radoboj are marine deposits accumulated in a shallow epicontinental sea, possibly in a lagoon. In addition to insects, marine fish and algae have been found in Radoboj. The deposits are dated to the Early Miocene (Burdigalian, 16.0–20.4 Ma) (LUTZ 1997; RASNITSYN & ZHERIKHIN 2002). The insect fossils are represented by imprints on finely laminated micritic limestone.

The imprints are rather poorly preserved. In many specimens, the wing venation has not been preserved or has been preserved only partially. The chitin is strongly modified, so that in most cases the sutures of the mesosoma and details of the morphology of the head are not visible. Tarsi, antennal flagella, and mandibular denticles are rarely preserved. None of the specimens displays fine morphological details, such as spurs or setae. As a result, the imprints are relatively hard to identify.

4. Systematic paleontology

Family Formicidae LATREILLE, 1809
Subfamily Dolichoderinae FOREL, 1878
Genus *Dolichoderus* LUND, 1831

Type species: *Formica attelaboides* LUND, 1831, by monotypy.

Diagnosis (for compression fossils): Gyne. Waist consisting of one segment (petiole); gaster without constriction between first and second gastral (III and IV abdominal) 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. Eyes of moderate size. Antennae 12-segmented. Mandibles triangular, dentate. Propodeum bispinate, bidentate, or distinctly angular in side view, always with concave declivity. Petiole with scale proclined, or triangular in side view. 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.

Species numbers and distribution: The genus *Dolichoderus* comprises 131 species and 20 subspecies in the modern fauna (www.antweb.org, accessed 7 March 2014). The vast majority of these are distributed in the Neotropical, Indo-Australian, and Australian regions. Only nine species are known from the Oriental Region, four from the Nearctic Region and two from the Palaearctic Region, and none have been recorded from the Afrotropical Region. A total of 53 extinct species have been described. The oldest species *D. kohlsi* was recorded from the Middle Eocene Green River Formation, USA (DLUSSKY & RASNITSYN 2002). Nearly half of the fossil species (24) have been described from Late Eocene European ambers (DLUSSKY 2002, 2008b).

Dolichoderus heeri n. sp.
Figs. 2A, 16F

Etymology: The species is named in honour of the palaeoentomologist OSWALD HEER.

Studied material: Holotype UMJG&P no. 77.507a (♀, identified by HEER as *Formica occultata*). Paratypes: UMJG&P nos. 77.568 (♀, identified by HEER as *F. occultata*), 77.569a (♀, identified by HEER as *Formica redtenbacheri*). Other specimens: UMJG&P nos. 77.507b (♂), 77.569b (♂).

Diagnosis: Differs from the other species from Radoboj in the concave declivity of the propodeum.

Description: Gyne. BL 5–5.5 mm. Head nearly 1.2 times as long as wide, with rounded occipital corners and weakly convex occipital margin. Anterior clypeal margin rounded. Eyes displaced backward, making cheek longer than maximum eye diameter. Mesosoma compact, 1.45 times as long as high. Scutum weakly convex in side view. Propodeum angulate in side view, with straight or weakly convex dorsum and concave declivity. Petiole without scale. Gaster oval. Scutum with longitudinal rugae. Forewing with closed cells 1+2r, 3r, rm and mcu. Cell rm triangular, without peduncle, 1.4 times as long as wide. Cross-veins rs-m and 2r-rs coinciding. Cell mcu rhomboidal, a little longer than wide. $Icu = 1.8$.

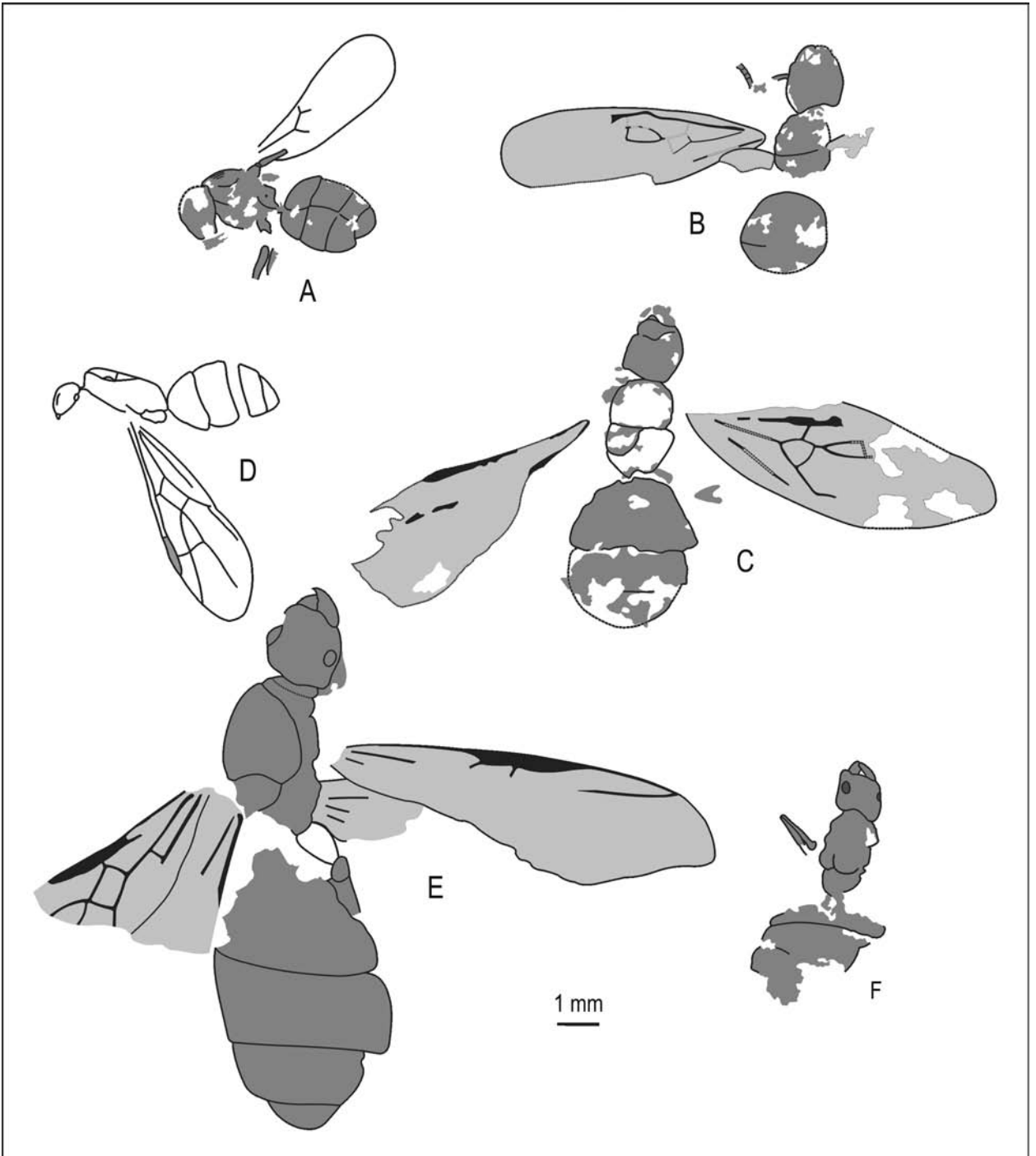


Fig. 2. Species of the subfamily Dolichoderinae. **A** – *Dolichoderus heeri* sp. nov., holotype UMJG&P no. 77.507a (♀); **B** – *Emplastus antiquus* (MAYR, 1867), neotype GBA no. 2009/016/0459 (♀); **C** – *Emplastus dubius* sp. nov., holotype UMJG&P no. 77.527 (♀); **D** – *Emplastus haueri* (MAYR, 1867) (♀, from MAYR, 1867); **E** – *Emplastus miocenicus* sp. nov., holotype NHMW no. 1852.XXIX.32 (♀); **F** – *Emplastus* (?) *ocellus* (HEER, 1849), lectotype of *Formica ocella* HEER, 1849 (♀).

Measurements, in mm: Gynes: UMJG&P no. 77.507a (holotype): BL=5.4, AL=1.8, HL=1.1, FWL=4.7; UMJG&P no. 77.568: BL=5.2, AL=1.7, HL=HW=1.0, FWL=4.8; UMJG&P 77.569a: BL=5.1, AL=1.7. Males: UMJG&P no. 77.507b: BL=4.4, AL=1.25, HW=0.7, FWL=4.4; UMJG&P no. 77.569b: BL=4.4, AL=1.4, HW=0.7, FWL=4.1.

Remarks: Two males are present together with gynes on the same pieces of rock. They are very poorly preserved, so we cannot describe them. However, as their size corresponds to the expected size of *D. heeri* males, we tentatively identified them as males of this species.

Morphogenus *Emplastus* DONISTHORPE, 1920

Type species: *Emplastus emeryi* DONISTHORPE, 1920, by original designation.

Diagnosis: Fossil ants not preserved well enough to fit orthotaxa, and with the following combination of traits: size medium; waist consisting of one segment (petiole); gaster without constriction between first and second gastral (III and IV abdominal) segments; head subrectangular with rounded occipital corners; antennae 12-segmented in gynes and workers and 13-segmented in males; scape of males short; mandibles triangular with denticulate masticatory margin; propodeum rounded in side view, petiole in side view with thick scale (workers and gynes) or triangular (males). Forewing with cells 1+2r, 3r, rm and mcu closed; cell 3r with apex touching wing fore margin, IRS vertical to R or slightly proclined. Icu>1.45.

Species numbers and distribution: Recently, four species from Bembridge, UK (Late Eocene or Early Oligocene marls), were included in this genus (DLUSSKY & PERFILIEVA 2014), however, evidently some fossil species described as *Iridomyrmex*, *Hypoclinea*, *Liometopum*, etc. should also be placed into *Emplastus*.

Remarks: DONISTHORPE (1920) placed this genus into the subfamily Ponerinae and considered it similar to the modern *Myopias* ROGER, 1861. In his opinion, *Emplastus*, as well as *Myopias*, has mandibles without teeth. In fact the holotype of *E. emeryi* has the masticatory margin of its mandibles hidden. Other specimens similar to *E. emeryi* in terms of body proportions and other visible characters have the masticatory margin of the mandibles visible but with blunt teeth. The position of the cross-vein cu-a in the type species (Icu=1.7) differs clearly from that of Ponerinae (DLUSSKY & PERFILIEVA 2014). COCKERELL (1915) and DONISTHORPE (1920) described several species now included in *Emplastus* based on the *Dolichoderus*-like forewing venation (characteristic of several other dolichoderine genera). However, this character is combined with the propodeum being rounded in side view and not angular or bispinate with concave hind contour, as in all living and fossil *Dolichoderus*. Recently, these species were transferred to *Emplastus* (DLUSSKY & PERFILIEVA 2014).

Emplastus antiquus (MAYR, 1867) n. comb.

Figs. 2B, 16B

- 1867 *Liometopum antiquum* MAYR, p. 60, fig. 10 (♀).
 1907 *Liometopum antiquum* MAYR, 1867. – HANDLIRSCH, p. 870.
 1995 *Liometopum antiquum* MAYR, 1867. – BOLTON, p. 247.

Studied material: Neotype (designated here), GBA no. 2009/016/0459 (♀, identified by HEER as *Formica globularis*).

Diagnosis: Differs from all other *Emplastus* species from Radoboj in the concave occipital margin of the head (occipital margin of the other species is weakly convex). *E. britannicus* (COCKERELL, 1915) from Late Eocene deposits of Bembridge has a concave occipital margin, but it is larger (BL 6–8.5 mm); it also has a short (not reaching occipital margin) scape and the forewing nearly as long as the body.

Description: Gyne. BL 5–6 mm. Head 1.08 times as wide as long, with convex sides and concave occipital margin. Scape reaching occipital margin or slightly protruding beyond it. Middle joints of funiculus nearly as long as wide. Mesosoma moderately wide. Forewings longer than body. Cell rm triangular, pedunculate. Gaster roundish.

Measurements of neotype, in mm: BL=5.8, AL=1.9, HL=1.3, HW=1.4, FWL=6.7.

Remarks: MAYR (1867) formally described this species from two specimens as *Formica globularis*. We found no syntypes of MAYR's species in any of the collections studied, but one of the specimens identified by HEER as *Formica globularis* (GBA no. 2009/016/0459, old number 337) proved similar to the description of *Liometopum antiquum*. We designate this specimen as the neotype. The venation of the forewing is only partly preserved, but a triangular cell rm is clearly visible, indicating the placement of this species in Dolichoderinae, rather than Formicinae.

MAYR placed this species in the genus *Liometopum* based on the concave occipital margin of the head, but now species with a convex occipital margin are known also in other genera. Since the imprint displays no other characters unambiguously indicating the placement of this species in *Liometopum*, we suggest transferring it to the form genus (morphogenus) *Emplastus*.

Emplastus dubius n. sp.

Figs. 2C, 16D

Etymology: *Dubius* is the Latin word for uncertain.

Studied material: Holotype UMJG&P no. 77.527 (♀, identified by HEER as *Formica globularis*).

Diagnosis: Differs from the other known species of *Emplastus* in forewing venation. All the other species have a rectangular cell mcu and cell rm without peduncle.

Description: Gyne. BL 7.5 mm. Head a little longer than wide. Mesosoma nearly as wide as head and 1.6 times as long as wide. Scutellum longer than wide. Gaster oval. Forewing venation poorly preserved. Cell *rm* triangular, narrow, pedunculate. Cell *mcu* trapezoidal. Section 1M nearly as long as 2RS.

Measurements of holotype, in mm: AL=2.3, HL=1.4, HW=1.3, FWL=6.8.

Emplastus haueri (MAYR, 1867) n. comb.

Fig. 2D

- 1867 *Hypoclinea haueri* MAYR, p. 60, fig. 11 (♀).
 1893 *Iridomyrmex haueri* (MAYR, 1867). – DALLA TORRE, p. 169.
 1907 *Iridomyrmex haueri* (MAYR, 1867). – HANDLIRSCH, p. 871.
 1992 *Iridomyrmex haueri* (MAYR, 1867). – SHATTUCK, p. 15.
 1995 *Iridomyrmex haueri* (MAYR, 1867). – BOLTON, p. 218.

Diagnosis: Differs from the other described species of *Emplastus* in the elongate metasoma.

Description (from MAYR, 1867): Gyne. BL 5.8 mm (head 1 mm, mesosoma 2 mm, gaster 2.8 mm), forewing 5.4 mm. Head small. Mesosoma very elongate and weakly convex. Gaster oval.

Remarks: MAYR (1867) formally described this species from one specimen identified by HEER as *Formica occultata*. We have found neither the holotype nor specimens similar to it in the studied collections. Judging by the size (AL=2.2, FWL=5.7 mm) and venation of the forewing, the poorly preserved male GBA no. 2009/016/0429 may also belong to this species. Since the diagnostic characters of the genus *Iridomyrmex* are not visible in that specimen, we transfer this species to the form genus *Emplastus*.

Emplastus miocenicus n. sp.

Figs. 2E, 16E

Etymology: Named after the Miocene.

Studied material: Holotype NHMW no. 1852.XXIX.32 (♀, identified by HEER as *Ponera fuliginosa*). Paratype UMJG&P no. 77.485 (♀, identified by HEER as *Formica ungeri*).

Diagnosis: Similar to *E. haueri*, but differs in the larger size.

Description: Gyne. BL 13.5 mm. Head 1.05 times as long as wide, with rounded occipital corners and weakly convex occipital margin. Anterior clypeal margin rounded. Eyes oval, situated at midlength of head sides; gena longer

than maximum eye diameter. Mandibles triangular with dentate masticatory margin. Mesosoma nearly as wide as head. Scutum longer than wide. Gaster oval. Forewing with cell *rm* triangular, comparatively wide, without peduncle. Cell *mcu* rectangular, 1.6 times as long as wide. Section 1M much longer than 1RS. Icu=1.9.

Measurements, in mm: Holotype NHMW no. 1852.XXIX.32: BL=13.5, AL=3.9, HL=1.8, HW=1.7, FWL=10.1; paratype UMJG&P no. 77.485: AL=3.8, FWL=9.0.

Remarks: In the new label (and possibly also in the catalogue) specimen UMJG&P no. 77.485 is marked as the holotype of *Formica ungeri*. This is clearly a mistake. First, *F. ungeri* was described from ten specimens, and HEER designated no holotypes. Second, the specimen is similar to none of the four specimens depicted in HEER's monograph.

Emplastus (?) ocellus (HEER, 1849) n. comb.

Fig. 2F

- 1849 *Formica ocella* HEER, p. 133, pl. 10, fig. 5a, b, pl. 11, fig. 14 a, b (♀♂).
 1849 *Formica ocella* var. *paulo major* HEER, p. 133, pl. 10, fig. 5c, pl. 9, fig. 14c (♂).
 non 1907 *Formica ocella* HEER, 1849. – HANDLIRSCH, p. 864.
 non 1995 *Formica ocella* HEER, 1849. – BOLTON, p. 200.

Studied material: Lectotype of *Formica ocella* UMJG&P no. 77.645a (♀, designated here, figured by HEER 1849: pl. 10, fig. 5a). Paralectotypes of *F. ocella* UMJG&P no. 77.645b (2♂, figured by HEER 1849: pl. 10, fig. 5b). Holotype of *F. ocella* var. *paulo major* UMJG&P no. 77.645c (♂, figured by HEER 1849: pl. 10, fig. 5c)

Diagnosis: Gyne differs from all of the ants known from Radoboj in the shape of the head.

Description: Gyne. BL 6.2 mm. Head longer than wide, with parallel sides, rounded occipital angles and concave occipital margin. Anterior margin of clypeus straight. Eyes oval, situated in front of lateral midlength of head. Gena is nearly as long as maximum eye diameter. Mandibles curved; dentition of masticatory margin not visible. Mesosoma elongate, nearly twice as long as wide. Appendages, petiole and wings not preserved, gaster strongly deformed.

Male. BL 4.9-5.6 mm. Head wider than long. Mesosoma 1.5 times as long as wide and 1.6 times as long as high. Scutum 1.2 times as wide as long. Scutellum 1.3 times as wide as long. Propodeum angulate in side view; with very short dorsal part and straight declivous part. Petiole triangular in side view, 1.3 times as high as long.

Measurements, in mm: UMJG&P no. 77.645a (♀, lectotype): AL=2.1, HL=0.99, HW=1.08; UMJG&P no. 77.645b (♂): AL=1.9, AW=1.25, SctL=0.8, SctW=1.0, SctIL=0.55, SctIW=0.7, F3L=1.5; UMJG&P no. 77.645c (♂): AL=1.9, SctL=0.9, SctIL=0.5.

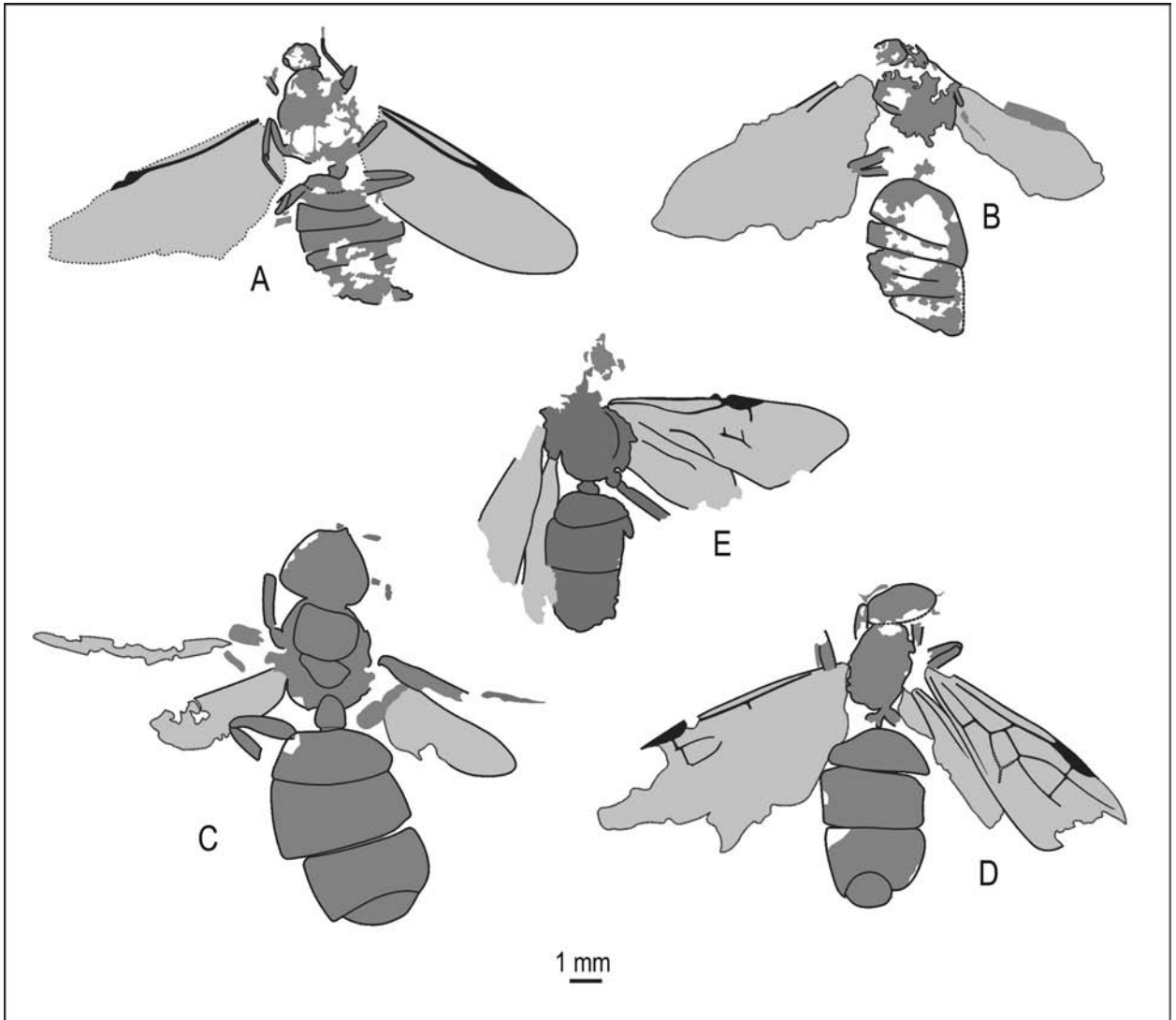


Fig. 3. *Liometopum imhoffii* (HEER, 1849). **A** – Neotype of *Formica imhoffii* HEER, 1849, GBA no. 2009/016/0238 (♂); **B** – lectotype of *Formica schmidtii* HEER, 1849, UMJG&P no. 77.594 (♂); **C** – lectotype of *Ponerula fuliginosa radobojana* HEER, 1849, UMJG&P no. 77.592 (♀); **D** – holotype of *Ponerula affinis* HEER, 1849, UMJG&P no. 77.638 (♀); **E** – neotype of *Poneropsis lugubris* HEER, 1867, NHMW no. 1852.XXIX.35 (♂).

Remarks: HEER described this species from four specimens found in the same piece of rock together with imprints of other ants. He considered them to be two pairs *in copula* at the time of death. We designate as the lectotype specimen UMJG&P no. 77.645a, depicted in pl. 10, fig. 5a. Although the figure is small and very imprecise, it follows from the text that the description of the gyne is based on this specimen (the unusual shape of the mandibles and eyes shifted forward are noted; the size of the specimen also complies with the description). The other gyne has been preserved so poorly that it is impossible to identify it to genus. There is a lateral imprint of a male within the same piece of rock,

described by HEER as *Formica ocella* var. *paulo major*, indicating that it is distinguished by the larger size and more elongate body. However, the difference in size is actually caused by the strongly deformed gaster of this specimen. The length of the mesosoma, which has deformed less strongly in the course of fossilization, is approximately identical in this specimen and in the two males described as *F. ocella*.

MAYR (1867) examined two poorly preserved specimens identified by HEER as *Formica ocella*, and could not determine to which genus they belonged. Therefore, HANDLIRSCH (1907) left this species in the genus *Formica*.

The gyne of this species differs from all of the other ants from Radoboj in the structure of the head so strongly that it is doubtlessly a separate species. At the same time, the specimen is so poorly preserved that it is impossible to determine to which genus it belongs, or to describe a new genus for this species. Based on the similarity of the anterior margin of the clypeus of this ant to those of many members of Dolichoderinae, we have provisionally placed it in the morphogenus *Emplastus*.

Genus *Liometopum* MAYR, 1861
(= *Poneropsis* HEER, 1867)

Type species: *Ponera fuliginosa* HEER, 1867 by subsequent designation of WHEELER 1911, n. syn.

Type species: *Formica microcephala* PANZER, 1798, by monotypy.

Diagnosis (for compression fossils): Size large or medium. Waist consisting of one segment (petiole); gaster without constriction between first and second gastral (III and IV abdominal) segments. Head of gyne 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. Declivitous 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 anterior margin of wing. Icu>1.45

Species numbers and distribution: Seven living species are distributed in temperate and subtopic zones of Eurasia and North America (SHATTUCK 1992). Eight fossil species have been described: *L. oligocenicum* WHEELER, 1915 (Baltic amber, Late Eocene), *L. miocenicum* CARPENTER, 1930, *L. scudderi* CARPENTER, 1930 (Florissant, Oligocene), *L. eremicum* ZHANG, 1989, *L. patamophilum* ZHANG, 1989, *L. lubricum* ZHANG, SUN & ZHANG, 1994 (Shanwang, Miocene), and the two species from Radoboj re-described below.

Remarks: HEER (1867) included all ants that had a one-segmented waist and forewings with closed cells 1+2r, 3r, rm and mcu in the genus *Poneropsis*. Such a diagnosis (later repeated by TAYLOR 1964) fits most genera of Ponerinae and Dolichoderinae. WHEELER (1911) designated *Ponera fuliginosa* HEER as the type species of *Poneropsis*. MAYR (1867) studied three poorly preserved specimens identified by HEER as *P. fuliginosa* (not types) and found that they had a two-segmented waist and were outwardly similar to *Aphaenogaster* (Myrmicinae). We have studied four syntypes of this species and found that three of them undoubtedly belong to the genus *Liometopum* and one is poorly preserved and possibly also belongs to that genus. Therefore, the genus *Poneropsis* HEER, 1867 is junior synonym of *Liometopum* MAYR, 1861.

Liometopum imhoffii (HEER, 1849)

Figs. 3A-E, 16A

- 1849 *Formica imhoffii* HEER, p. 138, pl. 10, fig. 10 (♂).
 1849 *Formica schmidtii* HEER, p. 138, pl. 11, fig. 5b, c (♂).
 1849 *Ponera fuliginosa radobojana* HEER, p. 146, pl. 12, fig. 1a-d (♀), n. syn.
 1849 *Ponera affinis* HEER, p. 147, pl. 12, fig. 2 (♀), n. syn.
 1867 *Poneropsis affinis* (HEER, 1849). – HEER, p. 19, n. syn.
 1867 *Poneropsis fuliginosa* (HEER, 1849). – HEER, p. 19, n. syn.
 1867 *Poneropsis lugubris* HEER, p. 21, pl. 1, fig. 23b, c (♂), n. syn.
 1867 *Poneropsis lugubris* var. *minor* HEER, p. 21, n. syn.
 1867 *Poneropsis imhoffii* (HEER, 1849). – HEER, p. 24, pl. 2, fig. 3.
 1867 *Poneropsis schmidtii* (HEER, 1849). – HEER, p. 24, pl. 2, fig. 4.
 1867 *Poneropsis livida* HEER, p. 25, pl. 2, fig. 5 (♂), n. syn.
 1867 *Poneropsis morio* HEER, p. 26, pl. 2, fig. 6 b (♀), n. syn.
 1867 *Poneropsis morio* var. *pallens* HEER, 1867, p. 26, pl. 2, fig. 6c (♂), n. syn.
 1867 *Aphaenogaster fuliginosa* (HEER, 1849). – MAYR, p. 57, n. syn.
 1867 *Aphaenogaster livida* (HEER, 1867). – MAYR, p. 57, n. syn.
 1867 *Liometopum imhoffii* (HEER, 1849). – MAYR, p. 55.
 1907 *Liometopum imhoffii* (HEER, 1849). – HANDLIRSCH, p. 870.
 1907 *Liometopum schmidtii* (HEER, 1849). – HANDLIRSCH, p. 871.
 1907 (Dolichoderidae) *morio* (HEER, 1867). – HANDLIRSCH, p. 871, n. syn.
 1907 (Dolichoderidae) *lugubris* (HEER, 1867). – HANDLIRSCH, p. 872, n. syn.
 1907 *Aphaenogaster fuliginosa* (HEER, 1849). – HANDLIRSCH, p. 874, n. syn.
 1907 *Aphaenogaster livida* (HEER, 1867). – HANDLIRSCH, p. 874, n. syn.
 1907 (*Poneropsis*) *affinis* (HEER, 1849). – HANDLIRSCH, p. 880, n. syn.
 1907 *Poneropsis lugubris* var. *minor* HEER, 1867. – HANDLIRSCH, p. 880, n. syn.
 1907 *Poneropsis morio* var. *pallens* (HEER, 1867). – HANDLIRSCH, p. 881, n. syn.
 1964 *Poneropsis fuliginosa* (HEER, 1849). – TAYLOR, p. 138, n. syn.
 1994 *Liometopum imhoffii* (HEER, 1849). – SHATTUCK, p. 129.
 1995 *Aphaenogaster livida* (HEER, 1867). – BOLTON, p. 70, n. syn.
 1995 *Liometopum imhoffii* (HEER, 1849). – BOLTON, p. 247.
 1995 *Poneropsis affinis* (HEER, 1849). – BOLTON, p. 363, n. syn.
 1995 *Poneropsis fuliginosa* (HEER, 1849). – BOLTON, p. 363, n. syn.
 1995 *Poneropsis lugubris* HEER, 1867. – BOLTON, p. 363, n. syn.

- 1995 *Poneropsis lugubris* var. *minor* HEER, 1867. – BOLTON, p. 363, n. syn.
 1995 *Poneropsis morio* HEER, 1867. – BOLTON, p. 363, n. syn.
 1995 *Poneropsis pallens*: (HEER, 1867). – BOLTON, p. 363, n. syn.

Studied types: Neotype (designated here) of *Formica imhoffii* GBA no. 2009/016/0238 (♂). Lectotype (designated here) of *Formica schmidtii* UMJG&P no. 77.594 (♂, figured in pl. XI, fig. 5c). Lectotype (designated here) of *Ponera fuliginosa*: UMJG&P nos. *77.592 (♀), *77.593 (♀, counterpart of the same specimen) (labelled as syntypes). Holotype of *Ponera affinis*: UMJG&P no. 77.638 (♀). Neotype (designated here) of *Poneropsis lugubris*: NHMW no. 1852.XXIX.35 (♂).

Other studied material: GBA: 2009/016/0092 (♀), 2009/016/0146 (♀), 2009/016/0552b (♀). UMJG&P: 77.491 (♀), 77.520 (♀), 77.577 (♀), 77.585 (♂), 77.623 (♂), 77.637 (♀). NHMW: 1852.XXIX.37 (?), 1843.XLIX.3 (♂), 1877.XXV.18a (2♀), K.K. Polytechn. Institut, 1868 (♂), Jahr 1868 (♂), ♂ without number.

Diagnosis: Differs from *L. eremicum* and *L. patamophilum* from the Miocene deposits of Shanwang (ZHANG, 1989) in the wing venation: *L. eremicum* with pedunculate cell *rm*, and cell *rm* of *L. patamophilum* more than twice as long as wide (in *L. imhoffii*, cell *rm* is not pedunculate and 1.6 times as long as wide). 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).

Description: Gyne. BL 11.5–13.3 mm. Head 1.2–1.4 times as wide as long, with convex sides and concave occipital margin. Mesosoma wider than head, robust, 1.3–1.6 times as long as wide. Scutum large, 1.3–1.4 times as wide as long. Scutellum transverse. Legs rather short and thick. Petiole with wide scale, oviform in side view, nearly two times as wide as long. Gaster oval. Forewing as in genus. Cell *rm* rather large, triangular, without pedicel, nearly twice as long as wide. Cell *mcu* rectangular, 1.6 times as long as wide. *Icu*=1.6.

Male. BL 8.5–9.5. Mesosoma noticeably wider than head, robust, 1.3–1.5 times as long as wide. Scutum large, wider than long. Scutellum transverse. Legs longer and thinner than in gyne. Petiole triangulate in side view, nearly as long as high, and 1.5 times as long as wide. Gaster oviform. Forewing as in gyne.

Measurements, in mm: Gynes. UMJG&P no. 77.491 (lectotype): AL=3.8, AW=3.0, PtL=0.6, PtW=1.2, FWL=10.7; GBA no. 2009/016/0146: AL=3.5, AW=2.25, SctL=1.4, SctW~1.8, SctL=0.65, SctW=1.4, FWL=8.4; GBA no. 2009/016/0552b: AL=3.2, AW=2.3, PtW=0.8; UMJG&P no. 77.520: AL=3.0; UMJG&P no. 77.577: BL=11.5, AL=3.3; UMJG&P no. 77.592: BL=12.7, AL=3.8, AW=2.9, HL=2.0, HW=2.7, SctL=1.6, SctW=2.0, SctL=1.6, SctW=2.0, F3L=2.4; UMJG&P no. 77.593: BL=12.6, AL=3.8, AW=2.2,

SctL=1.5, SctW=2.1, PtL=0.6, PtW=1.0; UMJG&P no. 77.638: AL=2.7, AW=1.9.

Males: GBA no. 2009/016/0238: BL=8.7, AL=3.1, AW=2.35, FWL=8.7; UMJG&P.77.585: AL=3.5; UMJG&P no. 77.594: AL=3.25, AW=2.7; NHMW no. 1843.XLIX.3: BL=8.4, AL=3.0, AH=2.3; NHMW no. 1852.XXIX.35: AL=3.2, PtL=0.4, PtW=0.6, FWL=7.7; NHMW without number: BL=9.5, AL=3.6, AH=2.4, PtL=PtH=0.6, F3L=2.2.

Remarks: Originally HEER (1849) described two species as *Formica imhoffii* and *F. schmidtii*, but subsequently transferred them to the genus *Poneropsis*. He labelled specimens belonging to these species either as *Formica*, or as *Formica (Ponera)*, or as *Ponera*. The former species was described by HEER from three males. The collection of UMJG&P contains specimen no. 77.491, labelled as syntype, but it cannot be considered a syntype, because it is an imprint of a gyne, rather than a male. We designate here as the neotype the specimen NHMW 2009/016/0238, identified by HEER as *Ponera imhoffii* and complying with the description. *Formica schmidtii* was described from two males. The collection of UMJG&P contains five specimens labelled as syntypes. One of them is a gyne, and one (identified with a question mark) does not even belong to Hymenoptera; therefore, these two can by no means be considered syntypes. The other three specimens are males and one of them (UMJG&P no. 77.594) matches with HEER's figure (1849: pl. 11, fig. 5c). We designate this specimen as the lectotype. MAYR (1867) studied two specimens identified by HEER as *Ponera imhoffii* and six specimens identified as *Ponera schmidtii* and concluded that the two specimens of *P. imhoffii* and the three specimens of *P. schmidtii* are actually males of the same species of the genus *Liometopum*. In accordance with this view, HANDLIRSCH (1907) synonymised these two species and transferred them to the genus *Liometopum*. Having examined the type specimens, we have come to the same conclusion as MAYR did.

HEER (1849) originally described *Ponera fuliginosa* based upon three gynes from Oeningen as *P. fuliginosa oeningensis* (p. 145), and then from four gynes from Radoboj as *P. fuliginosa radobojana* (p. 146). The collection of UMJG&P contains three specimens, two of them labelled as syntypes (nos. 77.593 and 77.637), and one (no. 77.592) as the holotype. Specimen no. 77.593 is the counterpart of no. 77.592. None of the specimens complies with HEER's figures; therefore, we designate specimens nos. 77.592 and 77.593 as the lectotype, since HEER designated no holotypes. The individual impressed in these specimens is similar to HEER's description and figures and doubtlessly represents a gyne of the genus *Liometopum*. MAYR (1867) studied three specimens identified by HEER as *Ponera fuliginosa* and found that they had a two-segmented waist and were outwardly similar to *Aphaenogaster*. Based on these observations, HANDLIRSCH (1907) transferred this species in the genus *Aphaenogaster*. However, the specimens examined by MAYR were not types, and HEER's figures clearly show that this species has a one-segmented waist and wing venation typical of Dolichoderinae.

The single specimen described by HEER as *Ponera affinis* has been preserved (UMJG&P no. 77.638) and we des-

ignite it as the holotype. HEER wrote that this species was very similar to *P. fuliginosa*, from which it differed in the more oval head, more elongate gaster, and shorter wings. In fact, the head of the imprint is strongly deformed, and the gaster became elongate postmortem as a result of pressure, making the wing length smaller relative to the body length. Otherwise, the holotype of this species does not differ in any visible characters from the lectotype of *P. fuliginosa*. In a later study HEER (1867) transferred this species to the genus *Poneropsis*. MAYR failed to find specimens of this species, and therefore HANDLIRSCH (1907) provisionally left it in that genus.

HEER (1867) described *Poneropsis lugubris* from two males, which have not been preserved. We found only one specimen identified by HEER (NHMW no. 1852.XXIX.35), which we designate as the neotype. It is a little smaller than indicated in the description, but similar in general habitus to HEER's figures and displays no difference from *Liometopum* in outward characters. Judging by the figures and description, the specimens described by HEER also belong to this genus, as also suggested by HEER's remark at the end of the description: "Dürfte vielleicht als Männchen zu der *Poneropsis fuliginosa* gehören". On the same page, HEER described *P. lugubris* var. *minor*, which, judging by the description, differs only in the a little smaller size (body length 8.8, rather than 9.9 mm). MAYR (1867) studied five specimens identified by HEER as *P. lugubris* and wrote that judging by wing venation they belong to the subfamily Dolichoderinae. In the catalogue by HANDLIRSCH they are listed as (Dolichoderidae) *lugubris* (p. 872) and *Poneropsis lugubris minor* (p. 880), but BOLTON (1995) left this species in the genus *Poneropsis*.

We found no differences in preserved characters between males of *Liometopum*, described by HEER as *Formica imhoffii*, *F. schmidtii* and *Poneropsis lugubris*, and between gynes of this genus, described by him as *Ponera fuliginosa* and *P. affinis*. HEER noted the similarity between these species and distinguished between them based on size and minor differences in the shape of the head, mesosoma, and gaster. In fact, the differences in size between these species are safely within the limits of intraspecific variation of Recent *Liometopum* (body length of *L. microcephalum* 9–11 mm in gynes and 8–10 mm in males), and the differences in the shape of the mesosoma and gaster revealed by HEER result from deformation in the course of fossilization. The ratios of gyne and male size in *Liometopum* specimens from Radoboj are identical to those found in extant species of the genus. Therefore, we believe that it is reasonable to regard them as members of a single species. In addition, we believe that it is reasonable to regard the two species and one variety – the types of which we have not seen (*Poneropsis livida*, *P. morio* and *P. morio* var. *pallens*) – as junior synonyms of *Liometopum imhoffii*.

HEER (1867) described *Poneropsis livida* from a single specimen, which has not been preserved. He considered it a gyne, but it can be seen from the figure that actually it was a male with a small head and short scape. HEER wrote that this specimen "vielleicht gehört es als solches zu der *Poneropsis schmidtii*", a statement with which we agree, judging by the figure. In the collection of GBA we found ten imprints identified as *P. livida* (three of them identified with certainty

and bearing HEER's labels). One of these imprints represents a male *Formica ungeri*, and the others are so poorly preserved that it makes their identification impossible. MAYR (1867) saw two specimens identified by HEER and suggested that they could represent males of *Aphaenogaster*. Based on this suggestion, HANDLIRSCH (1907) placed this species in the genus *Aphaenogaster*. However, the male depicted in HEER's figure could by no means belong to this genus and doubtlessly represents the genus *Liometopum*.

HEER (1867) described a gyne of *Poneropsis morio* and a male of *P. morio* var. *pallens* from one specimen each. We found in the studied collections two specimens identified by HEER as *P. morio*, but they comply neither with the descriptions nor with the figures provided by HEER and clearly belong to other species. MAYR (1867) examined two specimens identified by HEER as *P. morio* and considered them males of Dolichoderinae, but they were so poorly preserved that he could not identify them to genus. In the catalogue of HANDLIRSCH (1907) these subspecies were listed as a gyne (Dolichoderidae) *morio* (p. 871) and a male *Poneropsis morio pallens* (p. 881). In the catalogue of BOLTON (1995) they were listed as the separate species *P. morio* and *P. pallens*. In our opinion, HEER's figures depict a gyne and a male *Liometopum* indistinguishable by their visible characters from *Liometopum imhoffii*.

Subfamily Formicinae LATREILLE, 1809 Genus *Attopsis* HEER, 1849

Type species: *Attopsis longipennis* HEER, 1849, by subsequent designation of WHEELER 1911: 159.

Diagnosis: Gyne. Waist consisting of one segment (petiole); gaster without constriction between first and second gastral (III and IV abdominal) segments. Pronotum, propodeum and petiole armed with paired spines. First gastral segment nearly as long as second. Forewings long, greatly protruding over gastral tip; cell 3r closed, cell rm and perhaps mcu absent; sections 5RS and 4M with joint start (cross-vein rs-m absent).

Attopsis is similar in the presence of spines on the mesosoma and petiole and in wing venation to *Polyrhachis* F. SMITH, 1857. However, in *Polyrhachis*, the first gastral segment is considerably bigger than the others and makes up almost half of the gaster, whereas in *Attopsis longipennis*, it is subequal to the second segment.

Species included: Type species, known from Radoboj.

Remarks: According to HEER's diagnosis, the genus *Attopsis* is characterized by a two-segmented waist and by forewing venation rare among Myrmicinae: the cells rm and mcu are absent and the distal branches of RS and M diverge from a common point. Among the 18 examined specimens placed by HEER in the genus *Attopsis*, only two had two-segmented waists, but their wing venation differed from that described by HEER. We placed these two specimens in the genus *Paraphaenogaster*. In the other specimens, except the holotype of *A. longipennis*, either a one-segmented waist with an

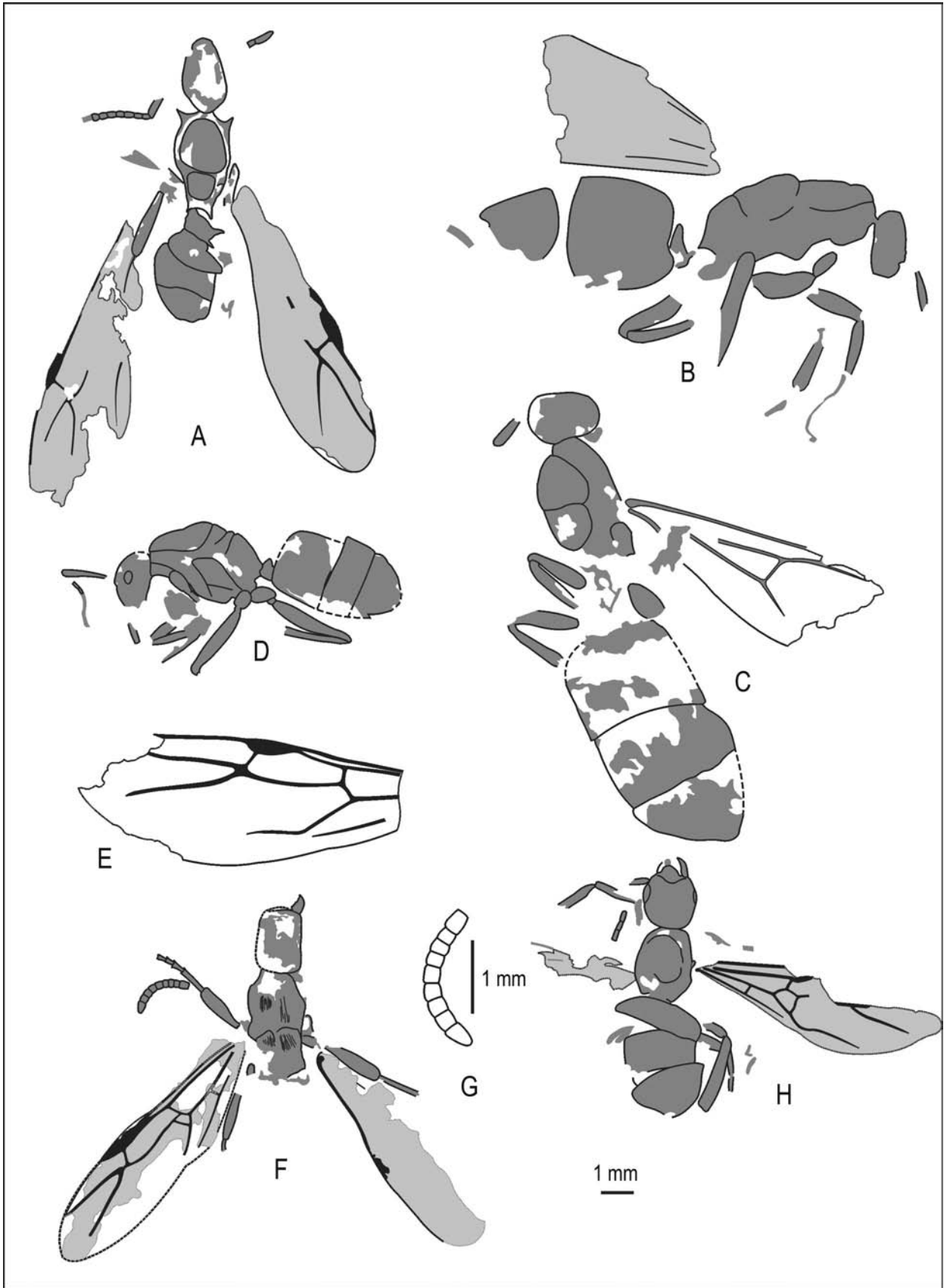


Fig. 4.

elongate petiole is clearly visible, or only fragments of chitin have been preserved in place of the waist. Moreover, the first gastral segment of these specimens is only slightly bigger than the second segment, giving evidence that the waist of these ants was one-segmented. In Myrmicinae, the first gastral segment is always considerably longer than any of the following gastral segments. In our opinion, these ants are males of *Oecophylla obesa* (HEER) (see below).

MAYR (1867) examined three specimens identified by HEER as *Attopsis anthracina* and four specimens identified by HEER as *A. nigra*. Among the latter, he found two gyne Myrmicinae with a wide body, rugose sculpture of the dorsal surface of the mesosoma and petiole, and granulate sculpture of the gaster. The wing venation of these ants had not been preserved. Assuming that the venation was as specified by HEER in the description of the genus *Attopsis*, MAYR concluded that these ants had to be placed in the genus *Cataulacus* F. SMITH. We have not found within the studied collections any specimens complying with MAYR's descriptions. Since those specimens were doubtlessly not types, and since, according to HEER's description, members of the genus *Attopsis* have an elongate mesosoma, these specimens should be placed in other genera.

Attopsis longipennis HEER, 1849

Figs. 4A, 17A

- 1849 *Attopsis longipennis* HEER, p. 155, pl. 12, fig. 11 (♀).
 1893 *Attopsis longipennis* HEER, 1849. – DALLA TORRE, p. 139.
 1907 *Attopsis longipennis* HEER, 1849. – HANDLIRSCH, p. 877.
 1911 *Attopsis longipennis* HEER, 1849. – WHEELER, p. 159.
 1995 *Attopsis longipennis* HEER, 1849. – BOLTON, p. 77.
 2003 *Attopsis longipennis* HEER, 1849. – BOLTON, p. 258.

Studied material: Lectotype UMJG&P no. 210 962, gyne figured by HEER (1849: pl. 12, fig. 11).

Description: Gyne. Body length 8.8 mm. Head oval, elongate, 1.3 times as long as wide. Occipital margin rounded, occipital angles absent. Scape protruding beyond occipital margin of head. Preserved joints of funiculus longer than wide. Mesosoma slightly wider than head, 1.75 times as long as wide. Pronotum with pair of short straight denticles. Scutum relatively small, not overhanging pronotum, slightly longer than wide and twice as long as scutellum. Parapsidal furrows absent. Petiole massive, with pair of slightly curved denticles. Forewings narrow and long. Right wing clearly showing closed cell 3r; vein sections 5RS and 4M with joint

start (cross-vein rs-m absent), indicating absence of closed cell rm. HEER's figure shows that closed cell mcu is absent, but actually the area where the cross-vein m-cu (that could close this cell) should have been was not preserved in this specimen.

Measurements of lectotype, in mm: AL=3.2, AW=1.8, HL=2.5, HW=1.5, FWL~11.

Remarks: HEER described this species from two specimens, one of them (UMJG&P no. 210 962) was figured (1849: pl. 12, fig. 11), and has been preserved, and we designate it as the lectotype.

Genus *Camponotus* MAYR, 1861

Type species: *Formica ligniperda* LATREILLE, 1802, by subsequent designation of BINGHAM (1903).

Diagnosis (for compression fossils): Waist consisting of one segment (petiole); gaster without constriction between first and second gastral (III and IV abdominal) segments. Antennae geniculate in both sexes, 12-segmented in gynes and workers, and 13-segmented in males. Scape attached at some distance from clypeus. Mesosoma and petiole nondentate. First gastral segment slightly longer than second. Petiole with scale. Forewing with closed cells 1+2r, 3r, and without closed rm and mcu; sections 5RS and 4M with joint start (cross-vein rs-m absent).

Species numbers and distribution: 1095 living species and 491 subspecies distributed worldwide. 34 fossil species were described from Late Eocene, Oligocene and Miocene deposits of Europe, Asia and North America (www.antweb.org, accessed 7 March 2014).

Camponotus induratus (HEER, 1849)

Figs. 4B-E, 17D

- 1849 *Formica indurata* HEER, p. 116, pl. 11, fig. 2 (described as ♂).
 1849 *Formica pingucola radobojana* MAYR, 1867. – HEER, p. 118, pl. 9, fig. b, g; pl. 11, figs. 14h, 15c (♂), n. syn.
 1867 *Formica indurata* HEER, 1849. – HEER, p. 9, pl. 1, fig. 6 a, b.
 1867 *Formica pingucola* HEER, 1849. – HEER, p. 10, pl. 1, fig. 8, n. syn.

Fig. 4. Species of the subfamily Formicinae. **A** – *Attopsis longipennis* HEER, 1849, lectotype UMJG&P no. 210 962 (♀); **B-E** – *Camponotus induratus* (HEER, 1849). **B** – Holotype of *Formica indurata* HEER, 1849 UMJG&P no. 77.632, (♀); **C** – specimen NHMW no. 1852.XXIX.4 determined by HEER as *Formica indurata*, studied by MAYR (♀); **D** – lectotype of *Formica pingucola radobojana* HEER, 1849, UMJG&P no. 77.644c (♂); **E** – paralectotype of *F. pingucola radobojana* UMJG&P no. 77.645i (forewing); **F-G** – *Gesomyrmex breinii* (HEER, 1849): **F** – lectotype of *Myrmica breinii* HEER, 1849, UMJG&P no. 77.482 (♀); **G** – funiculus of the same specimen; **H** – *Heeridris croaticus* sp. nov., holotype NHMW no. 1852.I.999 (♀).

- 1867 *Camponotus induratus* (HEER, 1849). – MAYR, p. 52.
 1867 *Camponotus pinguiculus* (HEER, 1849). – MAYR, p. 52, n. syn.
 1907 *Camponotus pinguiculus radobojanus* (HEER, 1849). – HANDLIRSCH, p. 867, n. syn.
 1907 *Camponotus induratus* (HEER, 1849). – HANDLIRSCH, p. 868.
 1995 *Camponotus induratus* (HEER, 1849). – BOLTON, p. 105.
 1995 *Camponotus pinguiculus* (HEER, 1849). – BOLTON, 117, n. syn.

Studied types: Holotype of *Formica indurata* UMJG&P no. 77.632, (♀, figured in pl. 11, fig. 2, HEER, 1849). Lectotype (designated here) of *Formica pinguicola radobojana* UMJG&P no. 77.644c (♂, figured in pl. 11, fig. 15 c). Paralectotypes of *F. pinguicola radobojana* UMJG&P nos. 77.645h (sex unknown, figured in HEER 1849, pl. 11, fig. 14h), 77.645i (wing, figured HEER 1849, pl. 11, fig. 14i), 77.646b (♂, figured in HEER 1849, pl. 10, fig. 9b), 77.646g (sex unknown, figured in HEER 1849, pl. 10, fig. 9g).

Other studied material: GBA: 2009/016/0149 (♀). NHMW: 1852.XXIX.4 (♀, specimen studied by MAYR), 1865.X.1121 (♂), specimen without number (♀).

Diagnosis: All known Miocene species of *Camponotus* (only gynes) were described from Shanwang (China) (ZHANG 1989). *C. induratus* differs from them in the combination of its size and angulate propodeum.

Description: Gyne. BL 13.5–17 mm. Head longer than wide, with parallel sides, rounded occipital angles and weakly concave occipital margin. Eye oval. Scape extending beyond posterior corner of head. Second and third joints of funiculus nearly twice as long as wide. Mesosoma 1.75–2.1 times as long as high. Scutum longer than scutellum, not overhanging pronotum. Propodeum angular in side view, with dorsum and declivity forming rounded obtuse angle; propodeal dorsum shorter than declivity. Petiole with high scale. Gaster oval. Forewing as in genus diagnosis; cell 1+2r twice as long as wide; section 1M longer than IRS.

Male. BL ca. 10 mm. Eye oval, situated slightly behind midlength of head, making gena twice as long as maximum eye diameter. Scape extending beyond posterior corner of head, nearly as long as head. Second and third joints of funiculus nearly three times as long as wide. Mesosoma nearly 1.5 times as long as high. Propodeum gradually rounded in side view. Legs rather long. Petiole triangular in side view. Gaster oviform in side view.

Measurements, in mm: Gynes: UMJG&P no. 77.632 (holotype): AL=5.3, HL=2.3; GBA no. 2009/016/0149: AL=5.6, HL=2.5; NHMW no. 1852.XXIX.4: BL=15.2, AL=5.0, ScL=1.6, SctL=1.4; NHMW without number: BL=14.3, AL=4.8, HL=2.8, HW=2.3. Males: UMJG&P no. 77.644c: BL=9.9, AL=3.6, HL=1.9, ED=0.4, F2L=2.3, F3L=2.6; UMJG&P no. 77.646b: AL=3.8.

Remarks: MAYR (1867) examined two specimens identified by HEER as *Formica indurata* (including NHMW no. 1852.

XXIX.4), and identified them as gynes of *Camponotus*. At the same time, he doubted that the holotype figured by HEER (1849: pl. 11, fig. 2) and described by HEER as male was actually an ant. However, his doubts are explained by the poor quality of the figure. We have studied the holotype and come to the conclusion that it belongs to the same species of *Camponotus*, but it is a gyne, not a male, as HEER believed. MAYR (1867) also studied one specimen identified by HEER as *Formica pinguicola radobojana* and identified it as a male *Camponotus*. We have examined five syntypes of *F. pinguicola radobojana* stored in UMJG&P: specimens UMJG&P nos. 77.644c and 77.646b are doubtlessly males of *Camponotus*; the forewing UMJG&P no. 77.645i is also a typical *Camponotus* wing; specimens UMJG&P nos. 77.645h and 77.646g, labelled as syntypes, are poorly preserved, and we identified them as Formicidae *incertae sedis*. Therefore, we fully agree with MAYR that *F. indurata* and *F. pinguicola radobojana* are actually gynes and males of *Camponotus*. Furthermore, in our opinion, they are gynes and males of the same species, and there is no reason to consider them two different species. *F. pinguicola* was originally described from Oeningen, not from Radoboj, and the actual taxonomic status of *F. pinguicola oeningensis* remains unknown.

Genus *Gesomyrmex* MAYR, 1868

Type species: *Gesomyrmex hoernesii* MAYR, 1868, by monotypy.

Diagnosis (for compression fossils): Gyne. Waist consisting of one segment (petiole); gaster without constriction between first and second gastral (III and IV abdominal) segments. Head longer than wide. Antennae geniculate, 10-segmented, with short scape. Mandible with 5–10 acute teeth. Posterolateral corners of the head and propodeum without spines. Metacoxae closely approximated. Forewings with closed cells 1+2r, 3r and mcu; vein sections 5RS and 4M with joint start (cross-vein rs-m absent).

Species numbers and distribution: Six extant species are known, which are distributed in the Oriental tropics. Five fossil species are known from the Middle Eocene of Germany (Messel, Eckfeld) and one from Late Eocene European ambers (DLUSSKY et al. 2009).

Gesomyrmex breinii (HEER, 1849), n. comb. Figs. 4F–G, 17F

- 1849 *Myrmica breinii* HEER, p. 161, pl. 13, fig. 5 (♂).
 1907 *Myrmica breinii* HEER, 1849. – HANDLIRSCH, p. 875.
 1995 *Myrmica breinii* HEER, 1849. – BOLTON, p. 277.

Studied material: Lectotype (designated here), UMJG&P no. 77.482, ventral imprint of gyne without petiole and gaster.

Diagnosis: The anterior clypeal margin is as in *Gesomyrmex*

flavescens DLUSSKY, WAPPLER & WEDMANN, 2009 (other fossil species have anterior margin projected as rounded lobe), but the head is longer than in *G. flavescens* (1.2 times as long as wide in *G. flavescens* and 1.4 times in *G. breinii*).

Description: Gyne. Judging by the preserved parts, BL ca. 9 mm. Head subrectangular, 1.4 times as long as wide. Anterior clypeal margin weakly convex. Completely preserved funiculus 9-segmented. Scape, although displaced, obviously shorter than head. Mandible triangular with seven teeth. Mesosoma elongate, twice as long as wide. Mesosomal sternites weakly striated. Petiole and gaster not preserved. Forewing long and narrow, with closed cells 1+2r, 3r and mcu; cell mcu small, trapezoid; vein sections 5RS and 4M partly united and forming short vein section RS+M.

Measurements of lectotype, in mm: AL=3.6, AW=1.8, HL=2.0, HW=1.4, FWL=9.3.

Remarks: A single syntype of *Myrmica breinii* has been preserved, and is designated here as the lectotype. The petiole of this specimen has not been preserved, but the combination of characters (head shape, 10-segmented antennae, forewing venation) gives evidence that the species belongs to the genus *Gesomyrmex*. HEER's (1849, pl. 13, fig. 5) figure shows another specimen, in which the head has not been preserved. HEER depicted a two-segmented waist, but judging by the position of the legs and the shape of the mesosoma, the petiolar region depicted in the figure should have been occupied by the propodeum.

Genus *Heeridris* nov.

Type species: *Heeridris croaticus* n. sp.

Ethymology: The genus is named for OSWALD HEER in recognition of his pioneering work on the fossil ants of Radoboj.

Diagnosis: Gyne. Waist consisting of one segment (petiole) with scale; gaster without constriction between first and second gastral (III and IV abdominal) segments. Anterior margin of clypeus rounded. Posterior margin of head gradually rounded, without occipital angles. Eyes large; with head in full-face view the eyes in front of the midlength of the side of the head. Forewing with closed cell mcu, and evidently also 1+2r and 3r; free branches 5RS and 4M leaving cell 1+2r from common expanded point of origin. Icu>1.45.

Remarks: The new genus doubtlessly belongs to the subfamily Formicinae. This is evident from the one-segmented waist and from the wing venation typical of this subfamily. However, this genus has a unique combination of characters, not found in any extant or extinct genus of the subfamily. In those Formicinae that have a closed cell mcu in the forewing (*Formica*, *Lasius*, *Proformica* and others), the eyes are either situated at the midlength of the head or shifted backward, whereas in *Heeridris*, they are strongly shifted forward. The only exception known to us is *Ge-*

somyrmex breviceps (DLUSSKY et al., 2009), in which the eyes are shifted forward, but this species has a subrectangular head with strongly pronounced occipital angles and a concave occipital margin. In the other Formicinae that have the eyes shifted forward (*Plagiolepis*, *Nylanderia* and others) a closed cell mcu in the forewing is absent.

Heeridris croaticus n. sp.

Figs. 4H, 17C

Etymology: The species name is derived from the country of origin (Croatia).

Studied material: Holotype NHMW nos. 1852.I.999 (♀, identified by HEER as *Formica ungeri*), 1852.I.1000 (counterpart of the same specimen). Paratype NHMW, without number (♀).

Description: Gyne. Body length 6-8.5 mm. Head longer than wide, with convex sides and gradually rounded occipital margin. Anterior margin of clypeus protruding as rounded lobe. Eyes large, oval, situated in front of lateral midlength of head. Gena nearly as long as maximum eye diameter. Mesosoma robust, 1.6-1.7 times as long as wide. Scutum not overhanging pronotum. Petiole with scale. Gaster oval. Forewing with closed cell mcu, and evidently also 1+2r and 3r; free branches 5RS and 4M leaving cell 1+2r from common expanded point of origin; 4M faintly curved; cell mcu trapezoid. Icu=2.0.

Measurements, in mm: Holotype: BL=8.2, AL=2.3, AW=1.7, HL=1.9, HW=1.7, ED=0.60, FWL=8.0. Paratype: AL=1.8, HL=1.1, FWL=6.5.

Genus *Oecophylla* F. SMITH, 1860

Type species: *Formica virescens* FABRICIUS, 1775, a junior synonym of *Oecophylla smaragdina* (FABRICIUS, 1775), by subsequent designation of BINGHAM (1903).

Diagnosis (for compression fossils): Waist consisting of one segment (petiole); gaster without constriction between first and second gastral (III and IV abdominal) segments. Size relatively large, head subrectangular with rounded occipital corners; antenna geniculate in both sexes. Scape attached at some distance from clypeus. Mandibles large, triangular, with sharp teeth on the masticatory margin. Petiole elongate, without scale, or nodiform (only in gynes). Forewing with closed cells 1+2r, 3r, with no closed rm and mcu; posterior margin of cell 3r (formed by RS) always concave; vein sections 5RS and 4M with joint start (cross-vein rs-m absent).

Species numbers and distribution: Two extant species of *Oecophylla* are known. *O. longinoda* (LATREILLE, 1802) is widespread in the forested regions of tropical Africa, and *O. smaragdina* (FABRICIUS, 1775) ranges from India across almost all of tropical Asia to the Solomon Islands and

northern Australia. Nine fossil species are known from the Eocene, Oligocene and Miocene deposits of Europe, with one species known from the Miocene deposits of Africa (DLUSSKY et al. 2008).

Oecophylla obesa (HEER, 1849)

Figs. 5A-F, 18A-B, E

- 1849 *Formica obesa* HEER, p. 108, pl. 8, fig. 1 (♀).
 1849 *Formica pinguis* HEER, p. 110, pl. 8, figs. 3, 9a (♀), n. syn.
 1849 *Attopsis anthracina* HEER, p. 156, pl. 12, fig. 12 (♂), n. syn.
 1849 *Attopsis nigra* HEER, p. 157, pl. 12, fig. 13 (♀), n. syn.
 1867 *Attopsis longipes* HEER, p. 29, pl. 2, fig. 15 (♂?), n. syn.
 1867 *Oecophylla obesa* (HEER, 1849). – MAYR, p. 50.
 1867 *Camponotus pinguis* (HEER, 1849). – MAYR, p. 51, n. syn.
 1867 *Cataulacus anthracinus* (HEER, 1849). – MAYR, p. 58, n. syn.
 1893 *Cataulacus anthracinus* (HEER, 1849). – DALLA TORRE, p. 137, n. syn.
 1907 *Oecophylla obesa* (HEER, 1849). – HANDLIRSCH, p. 860.
 1907 *Camponotus pinguis* (HEER, 1849). – HANDLIRSCH, p. 867, n. syn.
 1907 *Cataulacus niger* (HEER, 1849). – HANDLIRSCH, p. 876, n. syn.
 1907 *Cataulacus anthracinus* (HEER, 1849). – HANDLIRSCH, p. 878, n. syn.
 1907 *Attopsis longipes* (HEER, 1867). – HANDLIRSCH, p. 878, n. syn.
 1995 *Attopsis longipes* (HEER, 1867). – BOLTON, p. 77, n. syn.
 1995 *Camponotus pinguis* (HEER, 1849). – BOLTON, p. 117, n. syn.
 1995 *Cataulacus anthracinus* (Heer, 1849). – BOLTON, p. 137, n. syn.
 1995 *Oecophylla obesa* (HEER, 1849). – BOLTON, p. 298.

Studied types: Lectotype of *Formica obesa* UMJG&P no. 77.625 (designated here, ♀, figured in HEER, 1849, pl. 8, fig. 1b). Paralectotype of *Formica obesa* UMJG&P no. 77.546 (♀, figured in HEER, 1849, pl. 8, fig. 1b). Lectotype of *Formica pinguis radobojana* UMJG&P no. 77.646a (designated here, ♀, figured in HEER, 1849, pl. 10, fig. 646a). Neotype of *Attopsis anthracina* GBA no. 2009/016/0634 (designated here, ♂). Neotype of *Attopsis nigra*: GBA no.

2009/016/0118 (designated here, ♂). Lectotype of *Attopsis longipes* UMJG&P no. 77.561 (designated here, ♂).

Other studied material: GBA: 2009/016/0109 (♀), 2009/016/0136 (♂), 2009/016/0306 (wing), 2009/016/0370 (♀), 2009/016/0420 (♂), 2009/016/0430 (♀), 2009/016/0577 (♀). UMJG&P: 77.484 (wing), 77.554 (?♂), 77.583 (wing), 77.629 (♂), 77.633 (♂), 77.636 (♂). NHMW: 1852.I.1001 (♀), 1852.XXIX.3 (wing), 1852.XXIX.38 (♂), PSWH Coll. 2001a (♂).

Diagnosis: Head of *O. obesa* gynes is wider than long and petiole is wider than long, as in both extant species and in the fossil *O. superba* THÉOBALD, 1937 (Kleinkems, Germany; Oligocene), but the scutum of gynes in these species is distinctly wider than long, whereas in *O. obesa* the scutum is nearly as long as wide.

Description: Gyne. BL 15–18 mm, AL 5.2–6.5 mm, FWL 12.5–16.5 mm. Head wider than long, with weakly convex sides and rounded occipital margin. Mesosoma wider than head. Scutum nearly as long as wide, and 2.5 times as long as scutellum, overhanging pronotum in dorsal view. Scutellum wider than long. Legs rather short and thick. Petiole wider than long. Gaster oval. Wing venation typical for *Oecophylla*. Forewing with closed cells 1+2r, 3r, with no closed rm and mcu; pterostigma narrow; vein sections 5RS and 4M with joint start (rs-m lost); cell 3r narrow; 5RS bent into 3r; 1RS and 1M form united transverse vein; 1M longer than 1RS or subequal to it; 1RS inclined, forming acute angle with R; 2r-rs inclined; vein section RS+M (delimiting cell 1+2r from below) bent.

Male. BL 6–7 mm, AL 2.5–3.5 mm, FWL 6–7 mm. Head comparatively small, narrower than mesosoma. Mesosoma twice as long as high and 2.2–2.4 times as long as wide. Legs rather long and thin. Scutum narrow, distinctly longer than wide. Petiole longer than wide and longer than high, narrowed anteriorly. Gaster oviform. Wing venation as in gyne.

Measurements, in mm: Gynes: UMJG&P no. 77.625 (lectotype): AL=6.5, FWL=15.4, HW=2.6; UMJG&P no. 77.646a: AL=5.8, HL=2.1 (2.7 including mandibles); GBA no. 2009/016/0430: AL=5.7, FWL=16.4, HL (including mandibles)=2.6; GBA no. 2009/016/0577: AL=5.2, HL=2.0 (2.6 including mandibles), HW=2.3; NHMW no. 1852.I.1001: AL=6.0, FWL=12.5, HW=2.4. Males: AL 2.4–3.3 (average 3.0, n=7), FWL 6.3–7.9 (average 7.5, n=9).

Remarks: *Formica obesa* was described from four specimens, three of which are stored in UMJG&P. We designate as lectotype the imprint of a gyne, 77.625, figured by HEER

Fig. 5. *Oecophylla obesa* (HEER, 1849). **A** – lectotype of *Formica obesa radobojana* UMJG&P no. 77.625 (♀); **B** – lectotype of *Formica pinguis radobojana* HEER, 1849, UMJG&P no. 77.646a (♀); **C** – neotype of *Attopsis anthracina* HEER, 1849, GBA no. 2009/016/0634 (♂); **D** – neotype of *Attopsis nigra* HEER, 1949, GBA no. 2009/016/0118 (♂); **E** – lectotype of *Attopsis longipes* HEER, 1867, UMJG&P no. 77.561 (♂); **F** – forewing GBA no. 2009/016/0306.

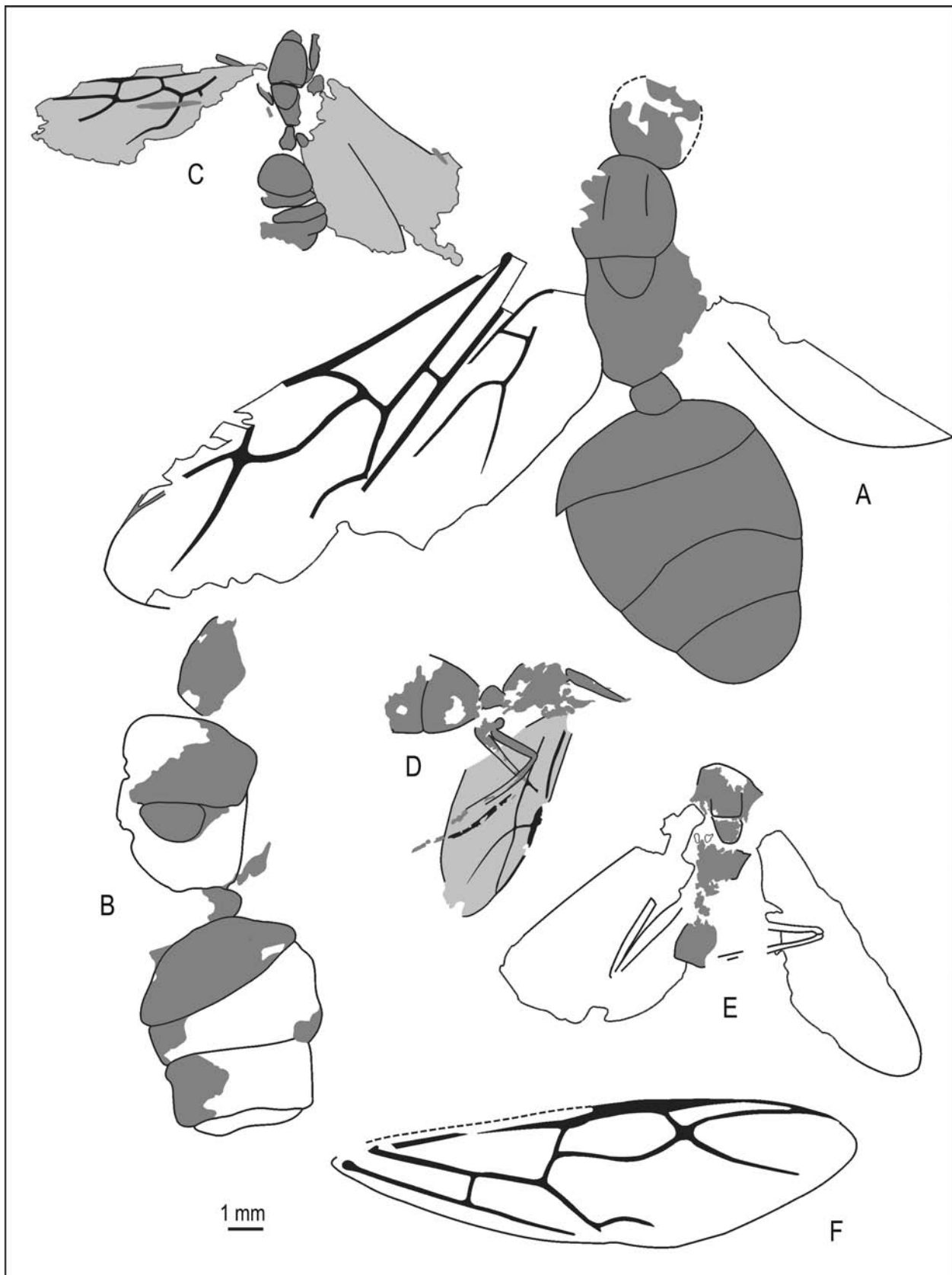


Fig. 5.

(1849: pl. 8, fig. 1b). MAYR (1867), having studied specimens identified by HEER, placed them in the genus *Oecophylla*. We have examined the syntypes and have come to the same conclusion.

Formica pinguis was described from three specimens stored in UMJG&P. We designate as lectotype the imprint of the gyne figured by HEER (1849: pl. 10, fig. 646a). MAYR (1867) examined one specimen identified by HEER, and identified it as belonging to *Camponotus*, but this specimen was not a syntype. The syntypes doubtlessly belong to the genus *Oecophylla*. HEER wrote that *F. pinguis* was very similar to *F. obesa* and differs from it in coloration. We could not find any differences between these species except in coloration. Since the coloration of fossil imprints depends on the specifics of fossilization and cannot be used as a diagnostic character, we believe that *F. pinguis* is a junior synonym of *F. obesa*.

Attopsis antracina and *A. nigra* were described from a single specimen each; neither of these specimens has been preserved. According to HEER's descriptions, the former species was described from a male, and the latter from a gyne, possibly conspecific. However, judging by HEER's figure, the proportions of the holotype of *A. nigra* (shape of the mesosoma, relative wing length) give evidence that it is male. Specimens stored in UMJG&P and listed in the catalogue as syntypes of these species differ from HEER's figures and cannot be considered syntypes. We designate as neotypes the best-preserved specimens most similar to HEER's figures: GBA no. 2009/016/0634 (*A. anthracina*) and GBA no. 2009/016/0118 (*A. nigra*). We found no differences between these species. MAYR (1867) examined three specimens identified by HEER as *Attopsis anthracina* and four specimens identified by HEER as *A. nigra*. Among the latter four, MAYR found two Myrmicinae gynes with wide bodies, rugose dorsal sculpture of the surfaces of the mesosoma and petiole, and granulate sculpture of the gaster. The wing venation of these ants has not been preserved. Assuming that the venation was as characterized by HEER in the description of the genus *Attopsis*, MAYR concluded that the ants had to be placed in the genus *Cataulacus* F. SMITH, 1854. We have failed to find in the studied collections any specimens complying with MAYR's description. Since these specimens were doubtlessly not types, MAYR's synonymization cannot be considered valid. We have examined seven specimens identified by HEER as *A. anthracina* and six specimens identified by HEER as *A. nigra*. Only two of them have two-segmented waists, but their wing venation differs from that described by HEER. We place these specimens in the genus *Paraphaenogaster*. In the other specimens, either a one-segmented waist with an elongate petiole is clearly visible, or only fragments of chitin have been preserved in place of the waist. Furthermore, the first gastral segment of these specimens is only slightly larger than the second, giving evidence of a one-segmented waist. In Myrmicinae the first gastral segment is always considerably longer than the following segments. HEER probably erroneously interpreted the long petiole as a two-segmented waist. The combination of the peculiar wing venation and elongate petiole give evidence that these ants belong to the genus *Oecophylla*.

HEER described *Attopsis longipes* from two specimens. Only specimen UMJG&P no. 77.561 has been preserved,

which differs from HEER's figure and is listed in the catalogue as the holotype. However, it cannot be considered the holotype, and we designate it as lectotype. Judging by the description, this species should differ from the other species of the genus in the longer legs. However, the relative length of the legs in the lectotype of this species is the same as in the neotype of *A. nigra*. The specimen is poorly preserved, but judging by the visible characters (shape of the scutum and scutellum, relative wing length), it is no different from *A. nigra*, and the two species can be synonymized.

In recent and fossil members of the genus known from both males and gynes, gynes are 1.5–2 times as large as males. The size ratio between gynes and males of *Oecophylla* from Radoboj is approximately the same. Since it is unlikely that gynes and males from the same deposit belonged to different species, we believe that the specimens described as *Attopsis antracina*, *A. nigra* and *A. longipes* are males of *Oecophylla obesa*.

Genus *Formica* LINNAEUS, 1758

Type species: *Formica rufa* LINNAEUS, 1758; by subsequent designation by CURTIS 1839: 752.

Diagnosis (for compression fossils): Gyne. Waist consisting of one segment (petiole) with scale; gaster without constriction between first and second gastral (III and IV abdominal) segments. Head usually longer than wide, with rounded occipital angles. Anterior margin of clypeus rounded or angulate. With head in full-face view the eyes distinctly behind the midlength of the side of the head; gena much longer than maximum eye diameter. Mandibles triangular, dentate. Antennae 12-segmented; scape protruding beyond posterior margin of head. Second to fifth joints of funiculus 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 expanded origin; 5RS and 4M curved approximately equally; section 2-3RS often S-shaped. Icu>1.45. Male and gyne size subequal. Gaster oval.

Species numbers and distribution: A total of 175 extant valid species and 25 subspecies of *Formica* distributed in the Palearctic and Nearctic are known to date (www.antweb.org, accessed 7 March 2014). BOLTON's catalogue also included a checklist of 72 extinct species, but he failed to take into account that ten of them had already been synonymised earlier (DLUSSKY 2008a), so that a total of 61 extinct species are included in the genus currently. Nine of them were described from Late Eocene ambers of Europe (DLUSSKY 2008a), eleven from Oligocene deposits of Europe (NOVÁK 1877; MEUNIER 1915, 1917, 1923; THÉOBALD 1837), three from Oligocene deposits of the United States (CARPENTER 1930), four from Miocene deposits of China (ZHANG 1989), and 37 from Miocene deposits of Europe, including 30 from Oeningen and Radoboj (HEER 1849, 1867). However, this number is clearly overestimated, and following modern revisions the assemblages of the Oligocene and Miocene will doubtlessly comprise fewer species. For instance, in

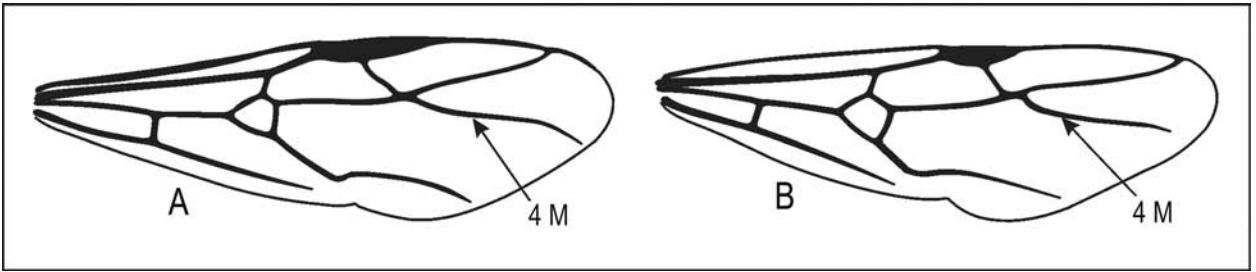


Fig. 6. Forewing venation of Recent *Formica rufa* (A) and *Lasius niger* (B).

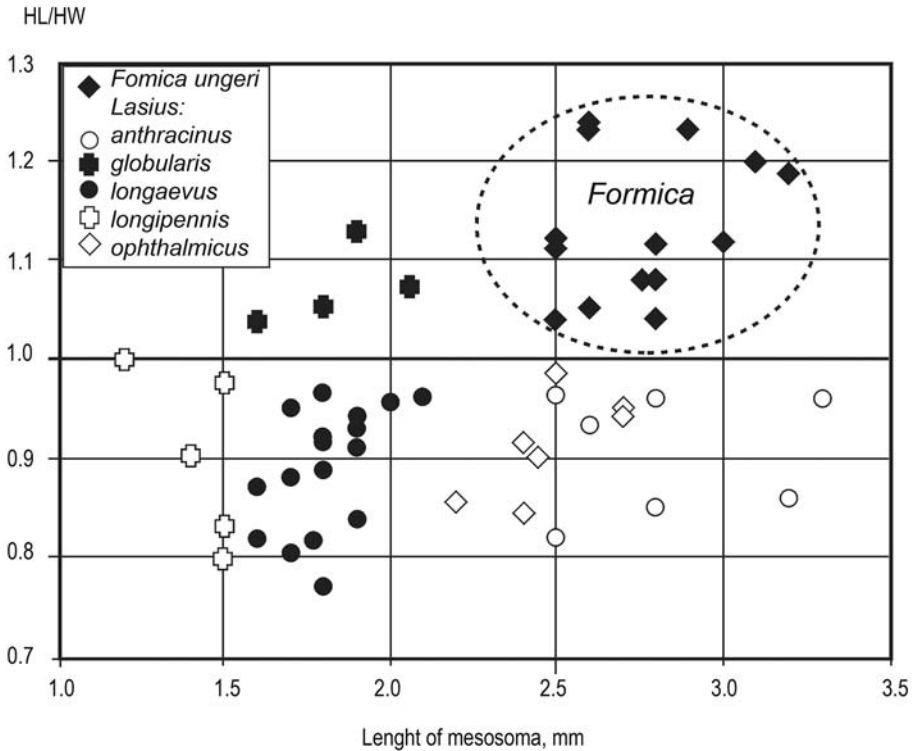


Fig. 7. Relationship between mesosoma length and proportion of head (HL/HW) of gynes of *Formica* and *Lasius* from Radoboj.

this study almost all species of *Formica* from Radoboj are either synonymised or transferred to other genera. A total of three species are currently known from Radoboj, two of them described by HEER and one described here as new.

Up to the present, the oldest record of *Formica* was from the Late Eocene: Baltic amber and compression fossil Bagshot Beds, Great Britain (where *Formica heteroptera* COCKRELL, 1920 was described based on a forewing). However, according to our unpublished data, compression fossils belonging to this genus are present in the deposits of Messel and Eckfeld, Germany, dating to the Middle Eocene.

Remarks: Members of the genera *Formica* and *Lasius* make up 72% of all compression fossils identified to genus.

The division of this set into genera and species was the most difficult part of our work in this revision. The imprints are so poorly preserved that genera can be safely distinguished only by the wing venation (particularly the shape of vein section 4M) (Fig. 6), position of the hind coxae, and the proportions of the joints of the funiculus. But even these characters have been preserved only in some of the specimens. Only two specimens could be reliably identified: the holotype of *Formica obscura* HEER, and the specimen described below as *F. parexsecta*. We identified the other specimens to species based upon biometric characters. Analysis of the whole set of gynes has shown that two large groups can be recognized (Fig. 7). Members of the first group have the head wider than long and mesosoma relatively wide. All

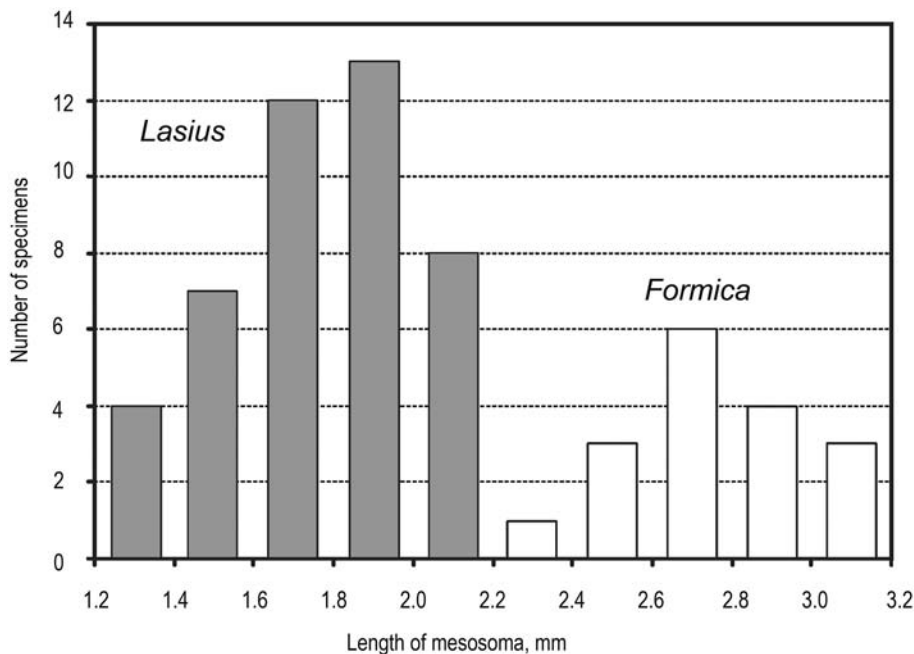


Fig. 8. Frequency distributions of mesosoma length classes among males of *Formica* and *Lasius* from Radoboj.

specimens that have wing venation or antennal funiculus preserved, or hind coxae visible, display characters of the genus *Lasius*. Further division of this group into species will be expounded below. In members of the second group the head is longer than wide and the mesosoma relatively narrow. This group can be divided into two subgroups: smaller individuals (AL=1.5-2.1 mm) and larger individuals (AL=2.3-3.3 mm) (Fig. 8). We provisionally placed the smaller individuals in the genus *Lasius*. The larger individuals that have the wing venation or antennal funiculus preserved display characters of the genus *Formica*. In addition, they have relatively short wings, which are also typical of gynes of the genus *Formica*. Further division of this group proved impossible, and therefore we placed it in one species, *Formica ungeri*. The set of males can be clearly divided by size into two groups separated by a hiatus: smaller (AL=1.2-2.1 mm) and larger (AL=2.3-3.1 mm). All the larger individuals that have wing venation preserved display characters of *Formica*, and all the smaller ones display characters of *Lasius*. We have failed to find characters by which males of *Formica* could be divided into species, and therefore placed them all in the same species.

Formica ungeri HEER, 1849

Fig. 9A-F

1849 *Formica ungeri* HEER, p. 128, pl. 10, fig. 1b-e (♀).

1849 *Formica redtenbacheri* HEER, p. 129, pl. 10, fig. 2b (♀), n. syn.

1849 *Formica acuminata* HEER, p. 142, pl. 11, figs. 13, 14g (♂), n. syn.

1849 *Ponera elongatula* HEER, p. 150, pl. 12, fig. 7 (♀), n. syn.

1867 *Formica redtenbacheri* HEER, 1849. – HEER, p. 13, n. syn.

1867 *Formica oblita* HEER, 1849. – HEER, p. 13, pl. 1, fig. 12 (♀), n. syn.

1867 *Formica kollari* HEER, 1849. – HEER, p. 15, pl. 1, fig. 14 (♀), n. syn.

1867 *Formica aemula* HEER, 1849. – Heer, p. 18, pl. 1, fig. 19 (♂), n. syn.

1867 *Poneropsis elongatula* (HEER, 1849). – HEER, p. 22, n. syn.

1867 *Formica ungeri* HEER, 1849. – MAYR, p. 53.

1867 *Lasius redtenbacheri* (HEER, 1849). – MAYR, p. 54, n. syn.

1907 *Lasius redtenbacheri* (HEER, 1849). – HANDLIRSCH, p. 861, n. syn.

1907 *Formica ungeri* HEER, 1849. – HANDLIRSCH, p. 862.

1907 *Formica acuminata* (HEER, 1849). – HANDLIRSCH, p. 864, n. syn.

1907 *Formica aemula* HEER, 1867. – HANDLIRSCH, p. 864, n. syn.

1907 *Formica kollari* HEER, 1867. – HANDLIRSCH, p. 864, n. syn.

1907 *Formica oblita* HEER, 1867. – HANDLIRSCH, p. 864, n. syn.

1907 *Poneropsis elongatula* (HEER, 1849). – HANDLIRSCH, p. 880, n. syn.

1964 *Formicidae incertae generis*. – TAYLOR, p. 138, n. syn.

- 1995 *Formica acuminata* (HEER, 1849). – BOLTON, p. 190, n. syn.
 1995 *Formica aemula* HEER, 1849. – BOLTON, p. 191, n. syn.
 1995 *Formica kollari* HEER, 1867. – BOLTON, p. 197, n. syn.
 1995 *Formica oblita* HEER, 1867. – BOLTON, p. 200, n. syn.
 1995 *Formica ungeri* HEER, 1867. – BOLTON, p. 205.
 1995 *Lasius redtenbacheri* (HEER, 1849). – BOLTON, p. 225, n. syn.
 1995 *Poneropsis elongatula* (HEER, 1849). – BOLTON, p. 363, n. syn.

Studied types: Lectotype of *F. ungeri* UMJG&P no. 77.566 (designated here, ♀, figured by HEER 1849, pl. 10, fig. 1c); paralectotype of *F. ungeri* UMJG&P no. 77.548 (♀, figured by HEER 1849: pl. 10, fig. 1e); lectotype of *Formica redtenbacheri* UMJG&P no. 77.510 (designated here, ♀, labelled as syntype); lectotype of *Formica acuminata* UMJG&P no. 77.645g (designated here, ♂, figured by HEER 1849: pl. 10, fig. 1c); lectotype of *Formica aemula* UMJG&P no. 77.519 (designated here, ♂, labelled as holotype); neotype of *Ponera elongatula* UMJG&P no. 77.641 (designated here, ♀); holotype of *Formica kollari* UMJG&P no. 77.574 (♀, figured by HEER 1867: pl. 1, fig. 14).

Other studied material: GBA: 2009/016/0012 (♀), 2009/016/0021 (♀), 2009/016/0027 (♀), 2009/016/0075 (♂), 2009/016/0078 (♂), 2009/016/0106 (?), 2009/016/0143 (♀), 2009/016/0161 (♀), 2009/016/0213 (♀), 2009/016/0248 (♀), 2009/016/0258 (♂), 2009/016/0320 (♀), 2009/016/0346 (♀), 2009/016/0350 (♀), 2009/016/0359 (♂), 2009/016/0361 (♀), 2009/016/0365 (♀), 2009/016/0371 (♀), 2009/016/0450 (♀), 2009/016/0468 (♀), 2009/016/0476 (♂), 2009/016/0524 (♂), 2009/016/0550 (♀), 2009/016/0552a (♀), 2009/016/0557 (♂), 2009/016/0665 (♀). UMJG&P: 77.500 (♀), 77.502 (♀), 77.509 (♀), 77.516 (♀, syntype of *F. ophthalmica* figured by HEER 1849: pl. 9, fig. 9b), 77.526 (♀), 77.531 (♂), 77.532 (♀), 77.533 (♂), 77.542 (♀), 77.551 (♂), 211 029 (♀), 211 033 (♀), 211 027 (♂), 211 034 (♂). NHMW: 1852.I.1042 (♀), 1852.I.1045 (♂), 1852.XXIX.10 (♀), 1852.XXIX.17 (♂), 1852.XXIX.21a (♀), 1852.XXIX.27 (♂), 1852.XXIX.28 (♀), 1852.XXIX.30 (♂), 1852.XXIX.5c (♀), 1852.XXIX.6 (♂), D.1185 (Jahr 1884) (♀), PSWH Coll. 2001d (♀), ♂ without number.

Diagnosis: Gynes of *F. ungeri* differ from the other Formicinae species from Radoboj in the following combination of characters: BL 6.1–9.8 mm, AL 2.3–3.3 mm; head longer than wide, with straight or weakly convex occipital margin; mesosoma elongate; forewing of *Formica*-type.

Description: Gyne. BL 6.1–9.8 mm, AL 2.3–3.3 mm, FWL 6.8–8.8 mm. Head longer than wide (HL/HW=1.04–1.23), with rounded occipital angles, and straight or weakly convex occipital margin. Anterior margin of clypeus rounded. Scape a little shorter than head (HL/SL=1.01–1.02). Second to fifth joints of funiculus nearly twice as long as wide. Mesosoma elongate, 1.8–2 times as long as wide. Legs rather long and thin. Forewings nearly as long as body (FWL/BL=0.8–1.1), and 2.3–3.3 times as long as mesosoma. Vein section 1M 1.2–1.8 (average 1.4) times as long as IRS. Cell

mcu trapezoid; vein section ICu 1.4–1.8 (average 1.6) times as long as RS+M.

Male. BL 6.3–9.3 mm, AL 2.3–3.1, FWL 5.2–8.3 mm. Head nearly as long as wide with rounded occipital margin. Scutum in side view weakly convex dorsally and rounded anteriorly. Dorsal and declivous parts of propodeum form rounded obtuse angle in side view; propodeal dorsum much shorter than declivous part. Forewing about as long as body (FWL/BL 0.8–1.1, average 1.0, n=6) and 2.0–2.8 times (average 2.6, n=10) longer than mesosoma. Wing venation as in gynes.

Measurements, in mm: Lectotype UMJG&P no. 77.566 (♀): BL=8.0, HL=1.8, FWL=7.1. Lectotype of *F. acuminata* (♂): BL=8.5, AL=2.9, HL=1.3. Variation: Gynes: BL 7.2–9.8 (average 8.6, n=25), AL 2.4–3.4 (average 2.8, n=23), HL 1.3–2.1 (average 1.7, n=23), HW 1.2–1.8 (average 1.4, n=13), FWL 7.1–9.1 (average 8.1, n=17). Males: BL 6.3–9.3 (average 7.8, n=8), AL 2.3–3.1 (average 2.7, n=17), FWL 5.2–8.3 (average 6.8, n=10).

Remarks: HEER described *Formica ungeri* from ten specimens. The collection of UMJG&P contains nine specimens labelled as syntypes. Two of them, including specimen UMJG&P no. 77.566, designated here as the lectotype, belong to the genus *Formica*, one (77.496) belongs to the genus *Lasius*, one (77.485) is described here as *Emplastus miocenicus* sp.n., and five (77.486, 77.535 77.545, 77.555 and 77.556) are poorly preserved and cannot be reliably identified to any known species. HEER distinguished this species from the other “*Formica*” by the shape of the gaster and pale (brown) coloration of the imprints. Neither of these characters, as mentioned above, can be used as diagnostic characters for compression fossils. MAYR (1867) examined specimens identified by HEER but not belonging to the type series. MAYR identified five of them (4♀, 1♂) as *Lasius*, and three as gynes of *Formica*. HANDLIRSCH (1907) left this species in the genus *Formica*. Subsequently, this status of the species was accepted by BOLTON (1995).

Formica redtenbacheri was described from 12 gynes. The collection of UMJG&P contains 20 specimens labelled as syntypes, but none of them complies with HEER’s figures. Four of them belong to the genus *Formica*, four to the genus *Lasius*, two to the subfamily Dolichoderinae, and six are poorly preserved and cannot be reliably identified to genus. We designate here as lectotype the best-preserved specimen, UMJG&P no. 77.510, which is similar to HEER’s description and figure. MAYR (1867) examined 22 specimens identified by HEER as *F. redtenbacheri* and came to the conclusion that most of them belonged to the genus *Lasius*. Based on this, HANDLIRSCH (1907) transferred this species to the genus *Lasius*. Subsequently, this status of the species was accepted by BOLTON (1995, 2013). HEER mentioned in his description of this species that it was similar to *F. ungeri* and differed from it in the short, thick gaster, dark coloration and longer cell mcu. The first two characters cannot be used as diagnostic characters for compression fossils, and the shape of the cell mcu in the lectotypes of *F. ungeri* and *F. redtenbacheri* is almost identical.

Ponera elongatula was described by HEER from one specimen. In a later study, HEER (1867) transferred this spe-

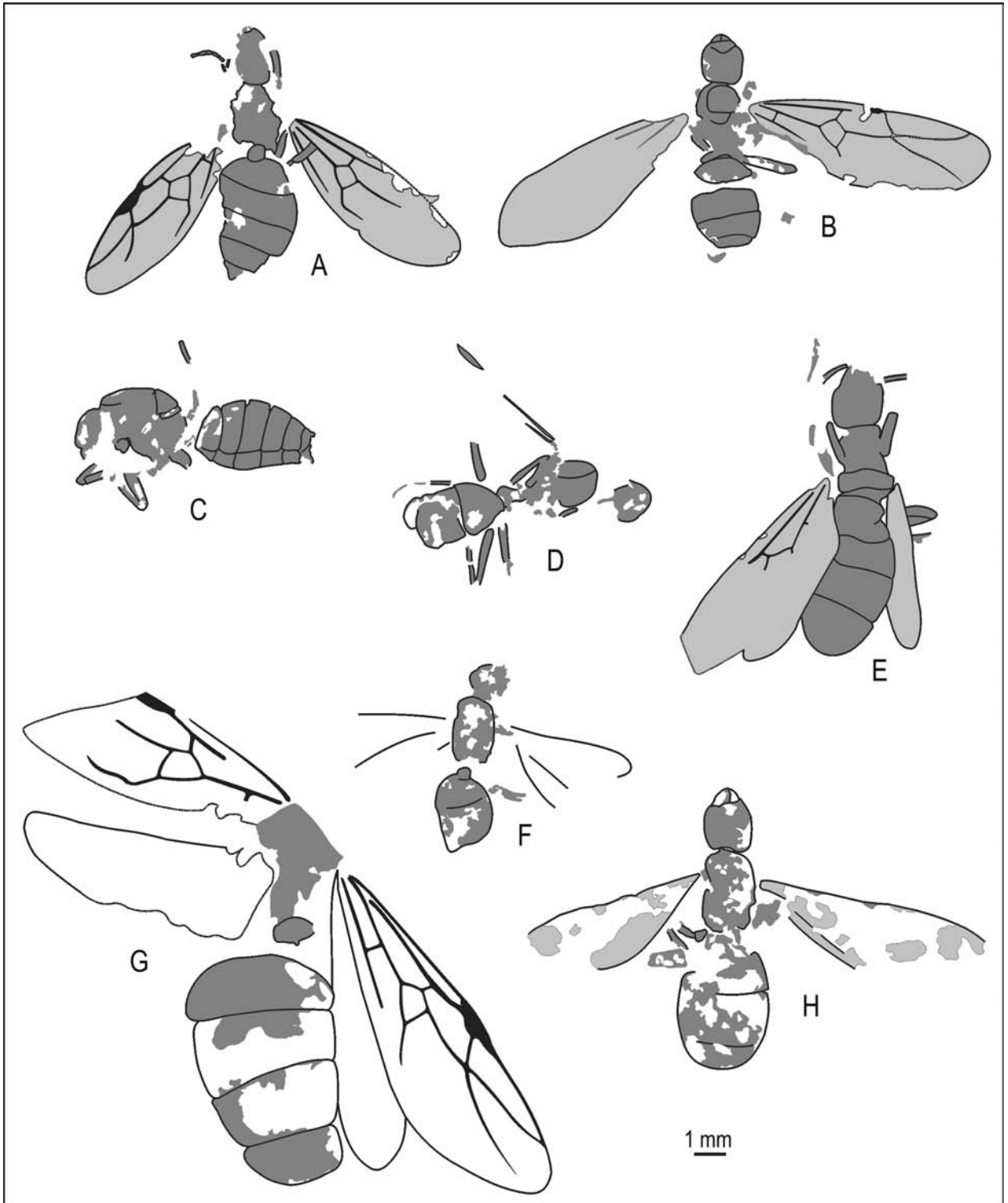


Fig. 9. Species of the genus *Formica*. **A-F** – *F. ungeri* HEER, 1849; **A** – lectotype UMJG&P no. 77.566 (♀); **B** – lectotype of *Formica redtenbacheri* HEER, 1849, UMJG&P no. 77.510 (♀); **C** – lectotype of *Formica acuminata* HEER, 1849, UMJG&P no. 77.645g (♂); **D** – lectotype of *Formica aemula* HEER, 1867, UMJG&P no. 77.519 (♂); **E** – neotype of *Ponerella elongatula* HEER, 1949, UMJG&P no. 77.641 (♀); **F** – holotype of *Formica kollari* HEER, 1867 UMJG&P № 77.574 (♀); **G** – *Formica obscura* HEER, 1849, holotype UMJG&P no. 77.536 (♀); **H** – *Formica parexsecta* sp. nov., holotype GBA no. 2009/016/0355 (♀).

cies to the genus *Poneropsis*. MAYR (1867) examined two specimens identified by HEER, which, in MAYR's opinion, did not belong to this species. However, because they were poorly preserved, he could not identify them. HANDLIRSCH (1907) left this species in the genus *Poneropsis*. TAYLOR (1964) considered HEER's description insufficient for placing this species in the genus *Poneropsis* and treated it as Formicidae incertae generis, but subsequently BOLTON (1995) reinstated the original name. The collection of UMJG&P contains specimen no. 77.641, identified by HEER and labelled as a syntype. However, it cannot be a syntype of this species, because it does not comply with the figure of the only specimen described by HEER. We have designated it as the neotype. This specimen is outwardly similar to HEER's figure, but differs in the larger size (holotype: BL=8.2, AL=2.2; neotype: BL=9.2, AL=2.6). In both the specimen figured by HEER and the neotype, the wing venation has not been preserved and there is no constriction between the first and second gastral segments. Therefore, it is unclear why HEER placed this species within the subfamily Ponerinae. All of its visible characters safely fall within the variation range of *Formica ungeri* gynes.

Formica kollari was described from a single specimen, which has been preserved in UMJG&P. HEER provided only the differences between this species and *F. ocella* and *F. occultata*. However, both these species were described from males, and belong to the genus *Lasius*, whereas the holotype of *F. kollari* is a gyne. Although the specimen is poorly preserved, it is no different in any visible characters (size or proportions of the head and mesosoma) from gynes of *F. ungeri*. MAYR (1867) had not seen this species, and therefore HANDLIRSCH (1907) left it in the genus *Formica*.

As mentioned above, we have failed to find any characters that would allow us to divide *Formica* males into species, and therefore placed them all, including the lectotypes of *F. acuminata* and *F. aemula*, in the same species. Judging from correlation to the extant gynes and males of the genus *Formica*, males of *F. obscura* should have been larger, and males of *F. parexsecta* (which is described below) should have had a concave occipital margin of the head. Since no such specimens had been found, we decided that all of the males found could be placed in *F. ungeri*.

Formica acuminata was described from two specimens. Specimen UMJG&P no. 77.645g, figured by HEER (1849: pl. 11, figs. 13, 14g), has been preserved and we designate it as the lectotype. MAYR (1867) had not seen this species, and therefore HANDLIRSCH, (1907) provisionally left it in the genus *Formica*.

Formica aemula was described from five specimens. According to HEER's description, this species is similar to males of *F. redtenbacheri*, and differs from them in the slightly larger size. Specimen UMJG&P no. 77.519, labelled as holotype, has been preserved. However, it cannot be considered the holotype, because it does not match with the figure in HEER's study. We designate it here as the lectotype. This specimen is poorly preserved, but its visible characters fall within the variation range of *F. ungeri* males. MAYR (1867) saw three of the specimens identified by HEER, but they are so poorly preserved that they could not be identified to genus. Therefore, HANDLIRSCH (1907) provisionally left this species in the genus *Formica*.

HEER described *Formica oblita* from two specimens, which we have failed to find. We have also failed to find in the studied collections any other specimens identified as *F. oblita*. MAYR (1867) examined one specimen identified by HEER, but not one of the syntypes, and came to the conclusion that it is similar to other specimens identified by HEER as *Formica macrocephala*. Judging by HEER's description, measurements, and figure, *F. oblita* does not differ from *F. ungeri*.

F. ungeri differs from extant species of *Formica* in its tendency toward smaller body size. In the extant members of the subgenera *Formica* s. str., *Serviformica* and *Raptiformica*, body length varies from 9 to 11 mm, while in *F. ungeri* it varies from 7.2 to 9.8 mm (average 8.6). However, extinct members of this genus included even smaller species: gynes of *Formica flori* from European ambers (Late Eocene) had a body length of 6.5-7 mm.

Formica obscura HEER, 1849

Fig. 9G

- 1849 *Formica obscura* HEER 1849, p. 119, pl. 9, fig. 2, pl. 11, fig. 15 d (♀).
 1867 *Lasius obscurus* (HEER, 1849). – MAYR, p. 52.
 1907 *Lasius obscurus* (HEER, 1849). – HANDLIRSCH, p. 862.
 1995 *Lasius obscurus* (HEER, 1849). – BOLTON, p. 225.

Studied material: Holotype UMJG&P no. 77.536 (♀, forewing, gaster and fragment of mesosoma, figured by HEER 1849: pl. 9, fig. 2).

Diagnosis: Differs from *F. ungeri* in its larger size.

Description: Forewing of gyne. FWL 12.1 mm. Cell 1+2r 3.1 times as long as wide. Cell 3r 4.9 times as long as wide. Vein section 1M 1.8 times as long as IRS. Cell mcu trapzoidal; vein section 1Cu nearly twice as long as RS+M.

Remarks: HEER described this species from a single, partly preserved specimen. He also identified three isolated gasters found on other pieces of rock as *F. obscura*. We examined one of these imprints (UMJG&P no. 77.644d), and it can belong to a gyne of any species of Formicinae similar in size. Therefore, specimen UMJG&P no. 77.536, figured by HEER, can be considered the holotype. MAYR (1867) examined only one specimen identified by HEER as *F. obscura*, which proved to be a poorly preserved gyne of *Lasius*. Based on this, Handlirsh (1907) transferred this species to the genus *Lasius*. Judging by the forewing venation, the holotype of this species doubtlessly belongs to the genus *Formica*. Assuming that the proportions and variation of this species were the same as in extant species of this genus, and even that the holotype was the largest specimen of this species, the length of the smallest specimens had to be at least 9.9 mm, which is outside the variation range of *F. ungeri*. Judging by their size, three specimens GBA no. 2009/016/0034 (BL=10.0, AL=3.6), GBA no. 2009/016/0043 (BL=9.9) and NHMW no. 1877.XXV.17 (BL=10.7) may also belong to

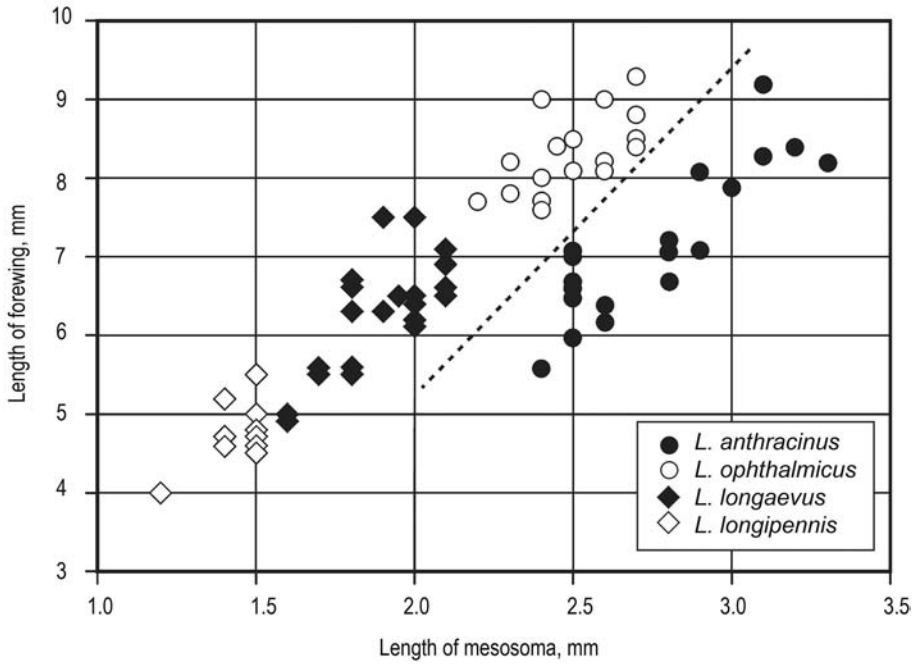


Fig. 10. Relationship between mesosoma length and forewing length of species of *Lasius*.

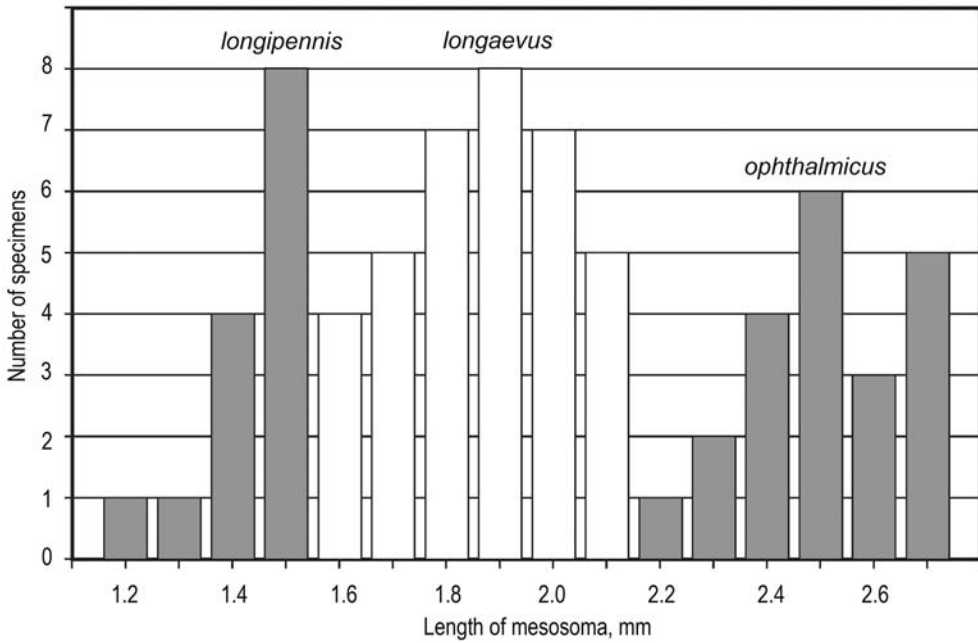


Fig. 11. Frequency distributions of mesosoma length classes among gynes of three species of *Lasius*.

this species. However, as the wing venation had not been preserved, the imprints do not allow identifying them to genus with certainty.

Formica parexsecta n. sp.

Figs. 9H, 17F

Etymology: Name from the Greek *para* (near) and species name *exsecta*.

Studied material: Holotype GBA no. 2009/016/0355 (♀, identified as *Formica redtenbacheri*).

Diagnosis: Differs from all Miocene Formicinae in the elongate head with a concave occipital margin.

Description: Gyne. BL=9 mm. Head longer than wide (HL/HW=1.13), with weakly convex sides, rounded occipital corners, and concave occipital margin. Anterior margin of clypeus rounded. Mesosoma elongate, twice as long as wide. Wing venation not visible.

Measurements of holotype, in mm: AL=3.2, AW=1.6, HL=1.7, HW=1.5.

Remarks: *F. parexsecta* is outwardly similar to Recent species of *Formica exsecta* group (subgenus *Coptoformica*).

Genus *Lasius* FABRICIUS, 1804.

Type species: *Formica nigra* LINNAEUS, 1758; by subsequent designation by BINGHAM 1903, p. 338.

Diagnosis (for compression fossils): Gyne. Waist consisting of one segment (petiole) with scale; gaster without constriction between first and second gastral (III and IV abdominal) segments. Head with rounded occipital angles. Anterior margin of clypeus rounded. With head in full-face view the eyes distinctly behind the midlength of the side of the head; gena much longer than maximum eye diameter. Mandibles triangular, dentate. Antennae 12-segmented; scape protruding beyond posterior margin of head. Second to fifth joints of funiculus 1.0-1.4 times as long as wide (except in subgenus *Dendrolasius*). Antennal insertion near posterior margin of clypeus. Hind coxae broadly separated. Forewing with closed cells 1+2r, 3r, and mcu; free branches 5RS and 4M leaving cell 1+2r from common expanded region; 4M strongly curved basally; section 2-3RS straight or weakly convex. Icu>1.45. Gynes 1.5-2.2 times as large as males (except in subgenus *Austrolasius*).

Species numbers and distribution: A total of 111 extant species and 3 subspecies of *Lasius*, living in the Palearctic and Nearctic, and 25 extinct species and subspecies have been described to date (www.antweb.org, accessed 7 March 2014). Four of the extinct species have been described from Late Eocene ambers of Europe (DLUSSKY 2011), three from Oligocene deposits of France (THÉOBALD 1937), one from

Oligocene deposits of the United States (CARPENTER 1930), four from Miocene deposits of China (ZHANG 1989), and 13 from Miocene deposits of Europe. Ten of the latter 13 taxa were originally described by HEER from Radoboj in the genus *Formica*, but subsequently transferred to the genus *Lasius* (HANDLIRSCH 1907). In this revision some of the extinct species described from Radoboj are synonymised, and some are transferred to this genus from the genus *Formica*. As a result, six species of the genus *Lasius* are known from Radoboj currently.

Remarks: Species of the genus *Lasius* make up about one half of all ants recorded in Radoboj. Their variation is clearly greater than can be observed within one species in extant members of the genus. In any extant species of *Lasius*, the difference in length between the smallest and the largest gynes is 67% to 90%, with an average of 77%, and between the smallest and largest males 67% to 88%, with an average of 79%. In gynes from Radoboj, the length of the mesosoma is 1.2 mm in the smallest and 3.3 mm in the largest. Assuming that the variation was similar to that of extant species, the mesosoma length had to be 1.2-1.55 mm in the smallest species and 2.5-3.3 mm in the largest. It has to be taken into account that the compression fossils are distorted and may differ in size from the actual ants, making the variation greater than in extant species – but even then we clearly have several species. Unfortunately, the material is so poorly preserved that the characters by which extant species and species from Late Eocene ambers of Europe are distinguished are not visible in the imprints. However, we have divided the gynes into five species based on morphometric characters. Two of these species are clearly distinguished by proportions. In *L. globularis* the head is longer than wide, whereas in all other species it is wider than long (Fig. 7). *L. anthracinus* has relatively short wings (Fig. 10). In this species the forewing is 2.3-2.9 times as long as the mesosoma, whereas in the other species it is more than 3 times as long as the mesosoma. The other species have similar proportions, but differ in size (Fig. 11). The frequency distribution of this group by the length of the mesosoma has three maximums: 1.5, 1.9 and 2.5 mm. We found no hiatuses, and therefore provisionally divided this group into three species with the length of the mesosoma 1.2-1.5, 1.6-2.1 and 2.2-2.7 mm, ranges approximately equivalent to the intraspecific variation found in extant species. Unfortunately, we have failed to find any characters that would allow us to divide the males similarly into several species. Therefore, we describe the males of *Lasius* from Radoboj as one form species (morphospecies).

Lasius anthracinus (HEER, 1867) n. comb.

Figs. 12A, 17B

- 1867 *Poneropsis anthracinus* HEER 1867, p. 22, pl. 2, fig. 8 (♂).
 1867 *Hypoclinea anthracina* (HEER, 1867). – MAYR, p. 57.
 1878 *Dolichoderus anthracinus* (HEER, 1867). – FOREL, p. 186.
 1907 *Dolichoderus anthracinus* (HEER, 1867). – HAND-

LIRSCH, p. 870.

- 1964 Formicidae *incertae generis*. – TAYLOR, p. 138.
 1994 *Dolichoderus anthracinus* (HEER, 1867). – SHATTUCK, p. 42.
 1995 *Dolichoderus anthracinus* (HEER, 1867). – BOLTON, p. 172.

Neotype of *Poneropsis anthracinus* GBA no. 2009/016/0074 (♀, designated here).

Other studied material: (♀♀).GBA: 2009/016/0140, 2009/016/0196, 2009/016/0239, 2009/016/0245, 2009/016/0393, 2009/016/0424, 2009/016/0503, 2009/016/0513, 2009/016/0649, 2009/016/9021. UMJG&P: 77.497, 77.506, 77.590. NHMW: 1852.XXIX.34, 1852.XXIX.5a (2), 1852.XXIX.8, 1877.XXV.15, 1877.XXV.16, five specimens without numbers.

Diagnosis: Differs from *L. globularis* in the relatively wide head and large size, and from the other species of *Lasius* from Radoboj in its relatively short wings.

Description: Gyne. BL 5.1-10 mm, AL 1.9-3.3 mm. Head wider than long: HL/HW 0.82-0.96 (average 0.91, n=7). Occipital angles rounded, occipital margin weakly convex. Anterior margin of clypeus rounded. Scape longer than head. Second to fifth joints of funiculus nearly twice as long as wide. Mesosoma 1.4-1.9 times as long as wide. Propodeum angulate in side view; propodeal dorsum much shorter than declivity. Legs moderately short and thick. Petiole nearly twice as high as long. Gaster oval. Forewings usually shorter than body (FWL/BL=0.7-1.0, average 0.9, n=15) and 2.3-3.0 (average 2.6, n=22) times as long as mesosoma. Cell mcu trapezoid; vein section 1Cu 1.6-2.0 times as long as RS+M.

Measurements, in mm: Neotype: BL=9.5, AL=3.0, HL=1.9, FWL=7.9. Variation: BL 5.1-10.0 (average 8.2, n=15), AL 1.9-3.3 (average 2.7, n=24), HL 1.0-1.9 (average 1.5, n=10), HW 1.2-2.0 (average 1.6, n=9), FWL 5.3-9.2 (average 7.0, n=22).

Remarks: This species was described from four specimens, which have all been lost. We found in the collection of GBA two specimens, one of which (2009/016/0074), identified by HEER (which is certain), we designate as the neotype. MAYR (1867) examined one male identified by HEER, and placed it in the genus *Hypoclinea*. Subsequently, FOREL (1878) syno-

nymised the genus *Hypoclinea* MAYR, 1755 (type species *Formica quadripunctata* LINNAEUS, 1771) under the genus *Dolichoderus* LUND, 1831, automatically transferring *H. anthracina* to the latter genus. This status was later accepted for this species by HANDLIRSCH (1907). In his revision of the fossil species of the genus *Ponera*, TAYLOR (1964) treated this species as *Formicidae incertae generis*, but then SHATTUCK (1994) reinstated it in the genus *Dolichoderus*. Actually, the neotype of *Poneropsis anthracinus* doubtlessly belongs to the genus *Lasius*.

Lasius ophthalmicus (HEER, 1849) n. comb.

Fig. 12B-C

- 1849 *Formica ophthalmica* HEER, p. 125, pl. 9, fig. 9, pl. 10. Fig. 9e (♀).
 1849 *Formica macrocephala radobojana* HEER, p. 126, pl. 9, fig. 10a, b. (♀), n. syn.
 1867 *Formica ophthalmica* HEER, 1849 – HEER, p. 11.
 1867 *Formica macrocephala* HEER, 1849 – HEER, p. 12, pl. 1, fig. 11, n. syn.
 1867 *Formica ophthalmica* HEER, 1849 – MAYR, p. 52.
 1867 *Formica macrocephala radobojana* HEER, 1849 – MAYR, p. 53, n. syn.
 1907 *Formica macrocephala radobojana* HEER, 1849 – HANDLIRSCH, p. 864, n. syn.
 1907 *Formica ophthalmica* HEER, 1849 – HANDLIRSCH, p. 865.
 1995 *Formica ophthalmica* HEER, 1849 – BOLTON, p. 200.
 1995 *Formica macrocephala*: HEER, 1849 – BOLTON, p. 198 (as unresolved junior primary homonym of *Formica macrocephala* ERICHSON, 1842), n. syn.

Studied types: Lectotype of *Formica ophthalmica* UMJG&P no. 77.646e (designated here, ♀, figured by HEER 1849: pl. 9, fig. 9, pl. 10, fig. 9e). Neotype of *Formica macrocephala radobojana* UMJG&P no. 77.539 (designated here, ♀, figured by HEER 1867: pl. 1, fig. 11).

Other studied material: (♀♀). GBA: 2009/016/0110, 2009/016/0123, 2009/016/0194, 2009/016/0204, 2009/016/0275, 2009/016/0291, 2009/016/0330, 2009/016/0351, 2009/016/0509, 2009/016/0536, 2009/016/0556, 2009/016/0663. UMJG&P: 77.492, 77.496, 77.508, 77.517, 77.557, 77.588. NHMW: 1852.XXIX.12, 1852.XXIX.13, 1877.XXV.18c, PSWH Coll 2001b (2).

Fig. 12. Species of the genus *Lasius*. **A** – *L. anthracinus* (HEER, 1867), neotype of *Poneropsis anthracinus* HEER, 1867, GBA no. 2009/016/0074 (♀); **B-C** – *L. ophthalmicus* (HEER, 1849); **B** – lectotype of *Formica ophthalmica* HEER, 1849, UMJG&P no. 77.646e (♀); **C** – neotype of *Formica macrocephala radobojana* HEER, 1849, UMJG&P no. 77.539 (♀); **D** – *L. longaevus* (HEER, 1849), lectotype of *Formica longaeva* HEER, 1849, UMJG&P no. 77.580 (♀); **E** – *L. longipennis* (HEER, 1849), lectotype of *Formica longipennis* HEER, 1849, UMJG&P no. 77.503 (♀); **F** – *L. globularis* (HEER, 1849), lectotype of *Formica globularis* HEER, 1849, UMJG&P no. 77.635 (♀); **G-J** – *L. occultatus* (HEER, 1849); **G** – lectotype of *Formica occultata* HEER, 1849, UMJG&P no. 77.499 (♂); **H** – neotype of *Formica minutula* HEER, 1849, UMJG&P no. 77.543 (♂); **I** – lectotype of *Formica pumila* HEER, 1849, UMJG&P no. 77.644b (♂); **J** – neotype of *Formica obliterata* HEER, 1849, UMJG&P no. 77.565 (♂).

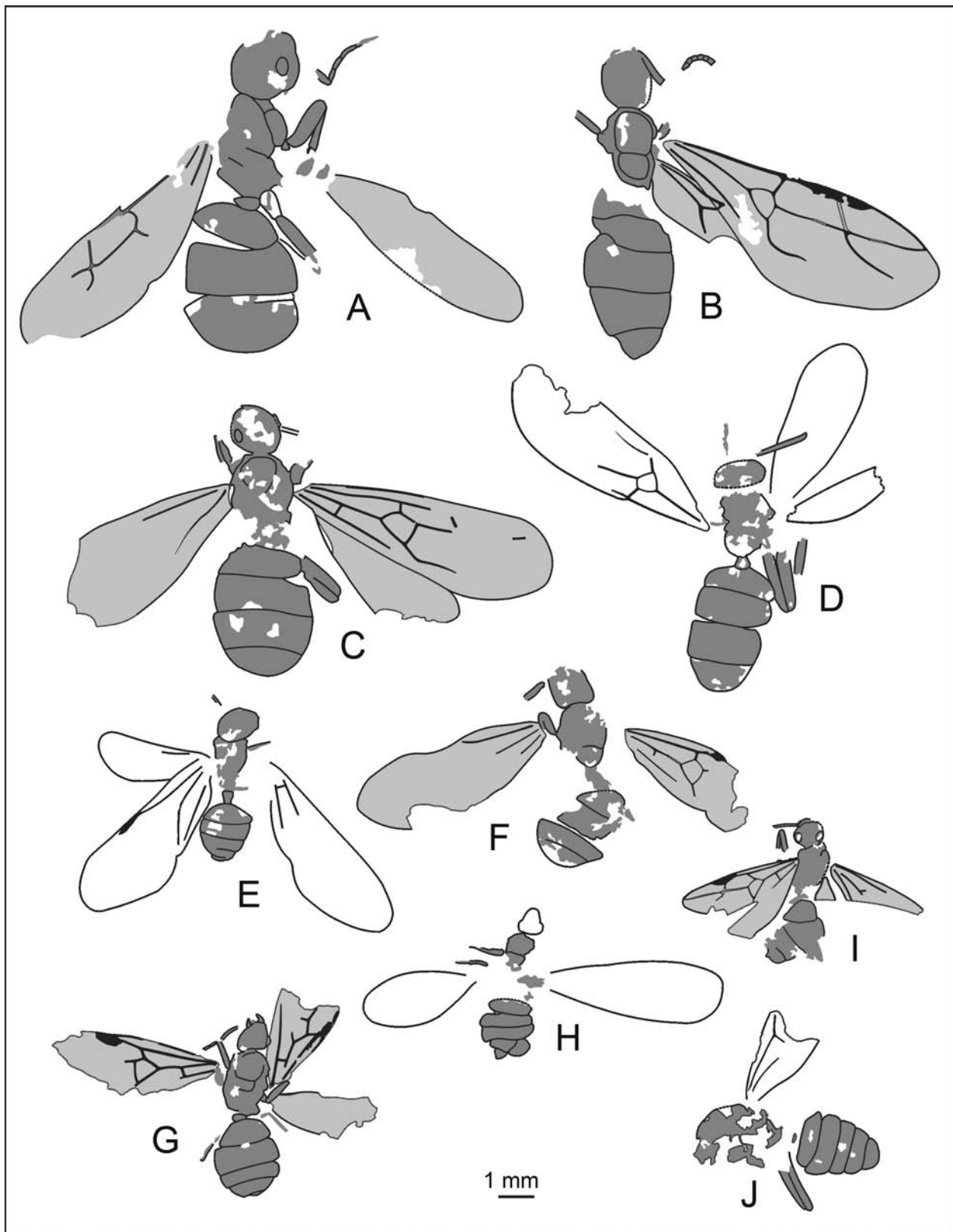


Fig. 12.

Diagnosis: Differs from *L. anthracunus* in the longer forewings and from *L. globularis* in the wider head.

Description: Gyne. BL 6.5-8.8 mm, AL 2.2-2.7 mm. Head wider than long: HL/HW 0.85-0.99 (average 0.91, n=8). Occipital angles rounded, occipital margin straight or weakly convex. Anterior margin of clypeus rounded. Scape a little longer than head. Second to fifth joints of funiculus 1.4-1.5 times as long as wide. Mesosoma 1.2-1.7 (average 1.5, n=16) times as long as wide. Scutum longer than wide. Propodeum rounded in side view. Legs moderately short and thick. Gaster oval. Forewings usually longer than body (FWL/BL=0.9-1.3, average 1.1, n=17) and 3.1-3.8 (average 3.3, n=18) times as long as mesosoma. Cell mcu trapezoid; vein section 1Cu 1.75-2.3 (average 2.0) times as long as RS+M.

Measurements, in mm: Lectotype of *F. ophthalmica* UMJG&P no. 77.646e: BL=8.8, AL=2.7, AW=1.6, HL=1.5, FWL=8.8; neotype of *F. macrocephala radobojana* UMJG&P no. 77.539: BL=7.8, AL=2.4, AW=1.6, HL=1.3, HW=1.4, FWL=8.0. Variation: BL 6.5-8.8 (average 7.55, n=19), AL 2.2-2.7 (average 2.50, n=21), AW=1.4-2.0 (average 1.71, n=16), HL=1.1-1.8 (average 1.41, n=10), HW 1.3-1.8 (average 1.46, n=17), FWL 7.1-9.3 (average 8.25, n=21)

Remarks: HEER described *Formica ophthalmica* from six specimens. The collection of UMJG&P contains five specimens labelled as syntypes. We identified specimens UMJG&P no. 77.502 and 516 as *Formica ungeri*. The second of these was depicted (HEER 1849, pl. 9, fig. 9b), but the interpretation of the imprint is incorrect. HEER took the folds formed on the head as a result of distortion of the imprint for very large oval eyes. It was based on this character that he described this species as new. However, actually this specimen has a clearly visible left eye, which has a shape normal for *Formica*. In all other imprints, the eyes are invisible, and it is unclear why HEER placed those imprints in this species. Three specimens are located on one piece of rock (UMJG&P no. 77.646), but only one of them is sufficiently well-preserved and can be safely identified as *Lasius*. We designate this specimen here as the lectotype. MAYR (1867) examined nine specimens identified by HEER. Seven of them belonged to the genus *Formica*, one to *Lasius*, and one to Myrmicinae. Based on those results, HANDLIRSCH (1907) left the species in the genus *Formica*.

Formica macrocephala was described by HEER (1849) from Oeningen, and he described specimens from Radoboj that he placed in the same species as *Formica macrocephala radobojana*. The collection of UMJG&P contains seven specimens identified by HEER as *F. macrocephala*, but none of them complies with the figures provided in the 1849 publication. However, they include specimen UMJG&P no. 77.539, which was figured in the 1867 publication. It cannot be considered a syntype, and therefore we designate it here as the neotype. MAYR (1867) left this species in the genus *Formica*. According to HEER's description, *F. macrocephala* differs from *F. ophthalmica* in the more rounded scale, but actually the shape of the scale is not visible clearly in any of the imprints. We could not find any principal differences between the types of these species.

Lasius longaevus (HEER, 1849)

Fig. 12D

- 1849 *Formica longaeva* HEER, p. 132, pl. 10, fig. 4 (♀).
 1867 *Formica longaeva* HEER, 1849. – HEER, p. 14.
 1867 *Lasius longaevus* (HEER, 1849). – MAYR, p. 54.
 1907 *Lasius longaevus* (HEER, 1849). – HANDLIRSCH, 861.
 1995 *Lasius longaevus* (HEER, 1849). – BOLTON, p. 223.

Lectotype UMJG&P no. 77.580 (designated here, ♀, figured by HEER 1849: pl. 10, fig. 4).

Other studied material: (♀♀). GBA: 2009/016/0024, 2009/016/0036, 2009/016/0037 (2), 2009/016/0046, 2009/016/0199, 2009/016/0203, 2009/016/0217, 2009/016/0299, 2009/016/0352, 2009/016/0377, 2009/016/0402, 2009/016/0482, 2009/016/0487, 2009/016/0541, 2009/016/0606, 2009/016/0622a, 2009/016/0659, 2009/016/0677. UMJG&P: 77.504, 77.511, 77.570, 77.575, 211 031. NHMW: 1842.I.21, 1852.XXIX.26, 1852.XXIX.7, K.K. Polytech. Institut, 1868, 4 specimens without numbers.

Diagnosis: Similar to *L. ophthalmicus* and differs from it in the smaller size.

Description: Gyne. BL 3.8-6.7 mm, AL 1.6-2.1 mm. Head wider than long: HL/HW 0.77-0.97 (average 0.90, n=16). Occipital angles rounded, occipital margin weakly convex or stright. Anterior margin of clypeus rounded. Scape a little longer than head. Mesosoma 1.2-1.7 (average 1.4, n=23) times as long as wide. Propodeum rounded in side view. Legs moderately short and thick. Gaster oval. Forewings nearly as long as body (FWL/BL=0.9-1.3, average 0.9, n=15) and 3.05-3.9 (average 3.3, n=24) times as long as mesosoma; cell mcu trapezoidal; vein section 1Cu 1.6-1.8 times as long as RS+M.

Measurements, in mm: Lectotype UMJG&P no. 77.580: BL=6.5, AL=2.1, AW=1.3, HW=1.2, FWL=6.9. Variation: BL 3.8-6.7 (average 5.47, n=29), AL 1.6-2.1 (average 1.87, n=35), AW 1.0-1.7 (average 1.33, n=23), HL 0.77-1.5 (average 1.01, n=19), HW 0.82-1.7 (average 1.13, n=21), FWL 4.9-7.5 (average 6.20, n=24).

Remarks: HEER described this species from two specimens, one of which, depicted in pl. 10, fig. 4, has been preserved in the UMJG&P collection, and we designate it as the lectotype. HEER distinguished *Formica longaeva* from other species of Formicinae ("*Formica*") by the shape of the petiole and gaster. However, in the lectotype of this species, the petiole is deformed, and the shape of the gaster can never really be used as a diagnostic character for compression fossils. MAYR (1867) examined six specimens and identified four of them as *Lasius*, and two as Myrmicinae of unclear generic placement. Following these identifications, HANDLIRSCH (1907) placed this species in the genus *Lasius*.

Lasius longipennis (HEER, 1849)

Fig. 12E

- 1849 *Formica longipennis* HEER, p. 136, pl. 10, fig. 7 (♀).
 1867 *Lasius longipennis* (HEER, 1849). – MAYR, p. 55.
 1907 *Lasius longaevus* (HEER, 1849). – HANDLIRSCH, 864.
 1995 *Lasius longaevus* (HEER, 1849). – BOLTON, p. 223.

Lectotype: UMJG&P no. 77.503 (designated here, ♀, figured by HEER, 1849: pl. 10, fig. 7).

Other studied material: (♀♀). GBA: 2009/016/0098, 2009/016/0141, 2009/016/0151, 2009/016/0274, 2009/016/0344, 2009/016/0404, 2009/016/0566. UMJG&P: 77.644a (syntype of *Formica pumila* figured by HEER, 1849: pl. 11, fig. 15a), 77.646h (syntype of *Formica pumila* figured by HEER, 1849: pl. 10, fig. 9h). NHMW: 1852.I.1048, 1902.III.217, Jahr 1868, ♀ without number.

Diagnosis: Similar to *L. ophthalmicus* L. and *L. longaevus* and differs from them in its significantly smaller size.

Description: Gyne. BL 3.6–6.1 mm, AL 1.2–1.5 mm. Head usually slightly wider than long: HL/HW 0.8–1.0 (average 0.90, n=5). Occipital angles rounded, occipital margin weakly convex. Anterior margin of clypeus rounded. Scape longer than head. Mesosoma 1.2–1.5 (average 1.35, n=5) times as long as wide. Propodeum rounded in side view. Legs moderately short and thick. Gaster oval. Forewings nearly as long as body (FWL/BL=0.9–1.3, average 1.1, n=11), and 3.0–3.7 (average 3.3, n=11) times as long as mesosoma; cell mcu trapezoidal.

Measurements, in mm: Lectotype: BL=4.2, AL=1.5, FWL=5.5. Variation: BL 3.6–6.1 (average 4.40, n=14), AL 1.2–1.5 (average 1.43, n=14), AW 0.9–1.3 (average 1.05, n=5), HL 0.7–1.0 (average 0.83, n=7), HW 0.8–1.1 (average 0.91, n=5), FWL 4.0–5.5 (average 4.75, n=11).

Remarks: HEER (1849) described this species from two specimens, one of which, depicted in pl. 10, fig. 7, has been preserved, and we designate it as the lectotype. According to the original description, this species differs from the other “*Formica*” in its longer wings. However, some specimens that HEER identified as other species (including the lectotypes of *F. globularis* and *F. ophthalmica*), have wings that are just as long. MAYR (1867) examined two specimens identified by HEER, one of which was a male *Lasius*, and the other was not an ant. Based on this, HANDLIRSCH (1907) placed this species in the genus *Lasius*.

Lasius globularis (HEER, 1849)

Fig. 12F

- 1849 *Formica globularis* HEER, p. 131, pl. 10, fig. 3 (♀).
 1867 *Formica globularis* HEER, 1849. – HEER, p. 14.
 1867 *Formica capito* HEER, p. 14, pl. 1, fig. 13 (♀), n. syn.
 1867 *Lasius globularis* (HEER, 1849). – MAYR, p. 54.
 1907 *Lasius globularis* (HEER, 1849). – HANDLIRSCH, p. 862
 1907 *Formica capito* HEER, 1867. – HANDLIRSCH, 863, n. syn.
 1995 *Formica capito* HEER, 1867. – BOLTON, p. 162, n. syn.
 1995 *Lasius globularis* (HEER, 1849). – BOLTON, p. 223.

Lectotype: UMJG&P no. 77.635 (designated here, ♀, figured by HEER, 1849: pl. 10, fig. 3).

Other studied material: (♀♀). GBA: 2009/016/0182, 2009/016/0394, 2009/016/0624. UMJG&P: 77.552, 77.567. NHMW: 1852.XXIX.14.

Diagnosis: Differs from the other species of *Lasius* from Radoboj based on its longer head. Differs from *Formica ungeri* in its smaller size.

Description: Gyne. BL 4.4–7.0 mm, AL 1.6–2.1 mm. Head longer than wide: HL/HW 1.02–1.33 (average 1.1, n=6). Occipital angles rounded, occipital margin weakly convex. Anterior margin of clypeus rounded. Scape longer than head. Mesosoma 1.5–1.9 (average 1.6, n=4) times as long as wide. Scutum nearly as long as wide. Propodeum rounded in side view. Gaster oval. Forewings nearly usually shorter than body (FWL/BL=0.8–1.05, average 1.0, n=7) and 2.8–3.2 (average 3.0, n=6) times as long as mesosoma. Cell mcu trapezoid.

Measurements, in mm: Lectotype: BL=6.0, AL=2.1, AW=1.2, HL=1.2, HW=1.1, FWL=6.3. Variation: BL 4.4–7.0 (average 5.75, n=9), AL 1.6–2.1 (average 1.87, n=8), AW 1.0–1.3 (average 1.14, n=4), HL 0.7–1.4 (average 1.13, n=8), HW 0.7–1.2 (average 0.98, n=7), FWL 5.0–6.6 (average 5.72, n=7).

Remarks: We designate as the lectotype specimen UMJG&P no. 77.635, depicted by HEER in pl. 10, fig. 7. MAYR (1867) identified most of the specimens he had examined as *Lasius*, but one of them proved to be a male *Formica*, and one was described by MAYR as *Liometopum antiquum*. Based on this, HANDLIRSCH (1907) placed this species in the genus *Lasius*.

HEER described *Formica capito* from a single specimen, which has not been preserved. MAYR (1867) had not seen this species. We have also failed to find it in the studied collections. Judging by the figure and description, this species is most likely a junior synonym of *Lasius globularis*. Apparently, the poorly preserved specimens GBA no. 2009/016/0134, UMJG&P no. 77.522, NHMW no. 1852.I.1035, and three specimens without numbers (one of them this label “Jahr, 1868”) also belong to this species.

Lasius occultatus (HEER, 1849)

Fig. 12G–J

- 1849 *Formica occultata* HEER, p. 134, pl. 10, fig. 6, pl. 11, fig. 11 (♀♂).
 1849 *Formica occultata* var. *major* HEER, p. 135 (♂), n. syn.
 1849 *Formica minutula* HEER, p. 136, pl. 10, fig. 8 (♀), n. syn.
 1849 *Formica pumila* HEER, p. 137, pl. 10, fig. 9g, h, pl. 11, figs. 14d, e, 15a, b (♀♂), n. syn.
 1849 *Formica oblitterata* HEER, p. 144, pl. 11, figs. 11c, 12 b (♂), n. syn.

- 1867 *Formica occultata* HEER, 1849. – HEER, p. 15.
 1867 *Formica minutula* HEER, 1849. – HEER, p. 16, pl. 1, fig. 15, n. syn.
 1867 *Formica obliterata* HEER, 1849. – HEER, p. 18, n. syn.
 1867 *Lasius occultatus* (HEER, 1849). – MAYR, p. 54.
 1867 *Lasius minutulus* (HEER, 1849). – MAYR, p. 55, n. syn.
 1867 *Lasius obliteratus* (HEER, 1849). – MAYR, p. 55, n. syn.
 1907 *Lasius occultatus* (HEER, 1849). – HANDLIRSCH, p. 860.
 1907 *Lasius minutulus* (HEER, 1849). – HANDLIRSCH, p. 861, n. syn.
 1907 *Lasius obliteratus* (HEER, 1849). – HANDLIRSCH, p. 861, n. syn.
 1907 *Formica pumila* HEER, 1849. – HANDLIRSCH, p. 865, n. syn.
 1995 *Formica pumila* HEER, 1849. – BOLTON, p. 202, n. syn.
 1995 *Lasius minutulus* (HEER, 1849). – BOLTON, p. 224, n. syn.
 1995 *Lasius obliteratus* (HEER, 1849). – BOLTON, p. 225, n. syn.
 1995 *Lasius occultatus* (HEER, 1849). – BOLTON, p. 225.

Studied types: Lectotype of *Formica occultata* UMJG&P no. 77.499 (designated here, ♂). Neotype of *Formica minutula* UMJG&P no. 77.543 (designated here, ♂). Lectotype of *Formica pumila* UMJG&P no. 77.644b, (designated here, ♂, figured by HEER, 1849: pl. 11, fig. 15b). Neotype of *Formica obliterata* UMJG&P no. 77.565 (designated here, ♂).

Other studied material: (♂♂). GBA: 2009/016/0015, 2009/016/0025, 2009/016/0072 (2), 2009/016/0167, 2009/016/0172, 2009/016/0276, 2009/016/0302, 2009/016/0312, 2009/016/0323, 2009/016/0329, 2009/016/0348, 2009/016/0366, 2009/016/0426, 2009/016/0444, 2009/016/0457, 2009/016/0484, 2009/016/0506, 2009/016/0511, 2009/016/0520, 2009/016/0529, 2009/016/0588, 2009/016/0589, 2009/016/0604, 2009/016/0619, 2009/016/0622b, 2009/016/0626, 2009/016/0628. UMJG&P: 77.505, 77.512, 77.514, 77.529, 77.579, 77.587, 211 030. NHMW: 1852.I.1032, 1852.I.1047, 1852.I.1049, 1852.XXIX.18, 1852.XXIX.20, 1852.XXIX.21b, 1852.XXIX.22.

Diagnosis: We provisionally place in this species males of several species of the genus *Lasius* that cannot be distinguished when preserved as compression fossils. The males are readily distinguishable from gynes, because they have five visible gastral segments (rather than four, as in gynes). They differ from males of the genus *Formica* in the smaller size and forewing venation (see diagnoses of the respective genera), but lack diagnostic features of their own.

Description: Male. BL 3.7-5.9 mm, AL 1.2-2.1 mm. Head wider than long: HL/HW 0.83-0.90. Eyes large. Scape longer than head. Mesosoma 1.3-1.6 (average 1.43, n=16) times as long as wide and 1.4-1.8 (average 1.61, n=7) times as long as high. Scutum weakly convex in side view and wider than long. Propodeum rounded in side view. Petiole triangulate

in side view and nearly as long as wide. Forewing 0.85-1.3 (average 1.05, n=18) times as long as body and 2.3-3.7 (average 2.84, n=34) times as long as mesosoma.

Measurements, in mm: Lectotype of *F. occultata* UMJG&P no. 77.499: BL=5.2, AL=1.9, HL=0.74, hw=0.87, FWL=4.4. Neotype of *F. minutula* UMJG&P no. 77.543: BL=4.5, AL=1.6, FWL=4.9. Lectotype of *F. pumila* UMJG&P no. 77.644b: BL=4.2, AL=1.4, HL=0.7, HW=0.8, FWL=3.7. Neotype of *F. obliterata* UMJG&P no. 77.565: BL=5.9, AL=2.1, FWL=5.6. Variation: BL 3.7-5.9 (average 4.72, n=22), AL 1.2-2.1 (average 1.71, n=44), HL 0.70-0.93 (average 0.82, n=7), HW 0.78-1.03 (average 0.92, n=4), FWL 3.4-6.8 (average 4.88, n=35).

Remarks: As noted above, males of *Formica* and *Lasius* are readily distinguishable by size (Fig. 8). Although the set of *Lasius* males, which includes the types of four species described by HEER, obviously consists of several species, we could find no characters by which these species could be distinguished. As can be seen from the figure, the frequency distribution of these males by size is unimodal. Therefore, we place all males of this genus in one form species.

HEER (1849) described *Formica occultata* from 63 specimens and identified a total of 594 specimens of this species (HEER, 1867). We examined 117 specimens identified by HEER; 59 of them are so poorly preserved that could not be placed in any species. The others proved to represent nine species of five genera and three subfamilies. The collection of UMJG&P contains 17 specimens labelled as syntypes, but none of them complies with HEER's figures. We designate as the lectotype the best-preserved male specimen, UMJG&P no. 77.499. According to MAYR (1867), the majority of specimens identified by HEER as *Formica occultata* belong to the genus *Lasius*, but one specimen was described by MAYR as *Hypoclinea haueri*. Based on this, HANDLIRSCH (1907) transferred this species to *Lasius*.

The variety *Formica occultata* var. *major* was described from a single imprint of a male without a head. According to the HEER's description, it is similar to *Formica occultata* and differs from it only in the slightly larger size. This specimen has not been preserved.

HEER (1849) described *Formica minutula* from a single whole gyne and two fragments. We have examined 17 specimens identified by HEER; six of them proved to be males of the genus *Lasius*, one proved to be a gyne of *L. longipennis*, and the others are poorly preserved and cannot be identified to genus. None of these specimens complies with HEER's figure. Male specimen UMJG&P no. 77.543 is labelled as a syntype, but it cannot be considered a syntype of this species, because it does not comply with HEER's figure. Therefore, we designate it as neotype. MAYR (1867) examined two specimens, which he identified as males of *Lasius*. Based on this, HANDLIRSCH (1907) transferred this species to the genus *Lasius*.

HEER (1849) described *Formica pumila* from six imprints found in three large pieces of rock, UMJG&P nos. 77.644, 77.645 and 77.646, together with imprints of other insects, mostly ants. We designate as the lectotype the best-preserved male specimen UMJG&P no. 77.644b, depicted by HEER in pl. 11, fig. 15b. MAYR (1867) examined three

specimens identified by HEER as *F. pumila* and wrote that they could belong to three different species and even genera, but could not be identified because of the poorly preserved imprints. Based on this, HANDLIRSCH (1907) left this species in the genus *Formica*.

HEER (1849) described *Formica obliterated* from two males, which had no wings preserved. He also noted that the species was very similar to *F. occultata* and differed from it in the slightly larger size. Neither of these specimens has been preserved. The collection of UMJG&P contains six specimens labelled as syntypes, but they cannot be considered syntypes, because they do not comply with HEER's figures. Two of them are males of *F. ungeri*, one is a *F. globularis* gyne, one is poorly preserved and cannot be identified, and two are males of the genus *Lasius*. We designate one of these males (UMJG&P no. 77.565) as the lectotype. MAYR (1867) examined four specimens identified by HEER and, although he could not discern the wing venation, suggested that they were probably males of the genus *Lasius*. Based on this, HANDLIRSCH (1907) transferred this species to the genus *Lasius*.

Subfamily Amblyoponinae FOREL, 1893

Morphogenus *Casaleia* PAGLIANO & SCARAMOZZINO, 1990

Type species: *Protamblyopone inversa* DLUSSKY, 1981, by original designation.

Diagnosis (for compression fossils): Gyne. Petiole essentially sessile, with steep, broad anterior face, but without distinctly descending posterior face, and markedly broadly attached to first gastral (III abdominal) segment. Helcium protruding from very high on anterior face of first gastral segment; first gastral segment above helcium without free anterior face. Mandible triangular. Eyes rather large, usually situated nearly at midlength of head's lateral surface. Antenna 12-segmented. Petiole trapezoidal in dorsal view, broadly attached to first gastral segment, nearly 40% as wide as first 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), and *C. eocenica* DLUSSKY & WEDMANN, 2012 (Messel, Germany, Middle Eocene).

Casaleia longiventris (HEER, 1849), n. comb.

Fig. 13A

1849 *Formica longiventris* HEER, 1849, p. 123, pl. 9, fig. 6a-c (♀).

1907 *Formica longiventris* HEER, 1849. – HANDLIRSCH, p. 864.

1995 *Formica longiventris* HEER, 1849. – BOLTON, p. 197.

Studied material: Lectotype of *Formica longiventris* UMJG&P no. 77.584 (designated here, ♀).

Diagnosis: *C. longiventris* differs from *C. inversa* and *C. eocenica* in its size (body length is 6.5 mm in *C. inversa*, and 4.9 mm in *C. eocenica*), and in its more elongate mesosoma.

Description: Gyne. BL 10 mm. Head longer than wide. Eyes oval. With head in full-face view the eyes at the midlength of the side of the head. Mesosoma elongate, nearly as wide as head, and 1.8 times as long as wide. Scutum 1.3 times as wide as long. Scutellum 1.6 times as wide as long. Petiole twice as wide as long, broadly attached to first gastral tergite. First gastral tergite 1.5 times as long as second and nearly as wide as second. Constriction between first and second gastral segments distinct.

Measurements of holotype, in mm: AL=2.9, AW=1.6, HL=1.6, HW=1.5, SctL=1.1, SctW=1.4, SctIL=0.6, SctIW=1.0, PtL=0.5, PtW=1.0, HWL=6.4, GL=5.2.

Remarks: HEER (1849) described *Formica longiventris* from seven specimens. According to his description, this species differs from all of the other species of *Formica* in its long and narrow gaster. We found in the collection of UMJG&P two specimens of this species that were identified by HEER and labelled as syntypes. Specimen UMJG&P no. 77.584, which we designate as the lectotype, is similar to the description in size and proportions (BL=9.9, HL=2.2, HW=1.9, AL=3.0, AW=2.2, GL=5.5, FWL=8.8). The elongate gaster with a distinct constriction between the first and second gastral segments and the petiole broadly attached to the gaster give evidence that this ant belongs to the subfamily Amblyoponinae, and the position of the eyes and shape of the petiole give evidence that it belongs to the genus *Casaleia*. The second specimen (UMJG&P no. 77.500) cannot be placed in this species, because it has a compact, short oval gaster (GL=3.8).

Subfamily Ponerinae LEPELETIER DE SAINT-FARDEAU, 1835

Morphogenus *Ponerites* DLUSSKY & RASNITSYN, 2002.

Type species: *Ponerites eocenicus* DLUSSKY & RASNITSYN, 2002, by original designation.

Diagnosis: Fossil ants not well enough preserved to fit orthotaxa, with the following combination of traits: Waist consisting of one segment (petiole) of various shape, narrowly attached to first gastral (III abdominal) segment. Gaster usually with constriction between first and second gastral (III and IV abdominal) segments; second gastral (IV abdominal) tergite and sternite subequal, gastral apex not directed downward; sting well developed. Gyne and worker antennae geniculate; male antennae with short scape, often filiform. Gyne and worker mandibles triangular with denticulate masticatory margin. Denticles or spines on head, mesosoma and waist absent. Forewing with closed cells 1+2r, 3r, rm and mcu. Icu<1.45.

Species included: *Ponerites eocenicus*, *P. coloradensis*

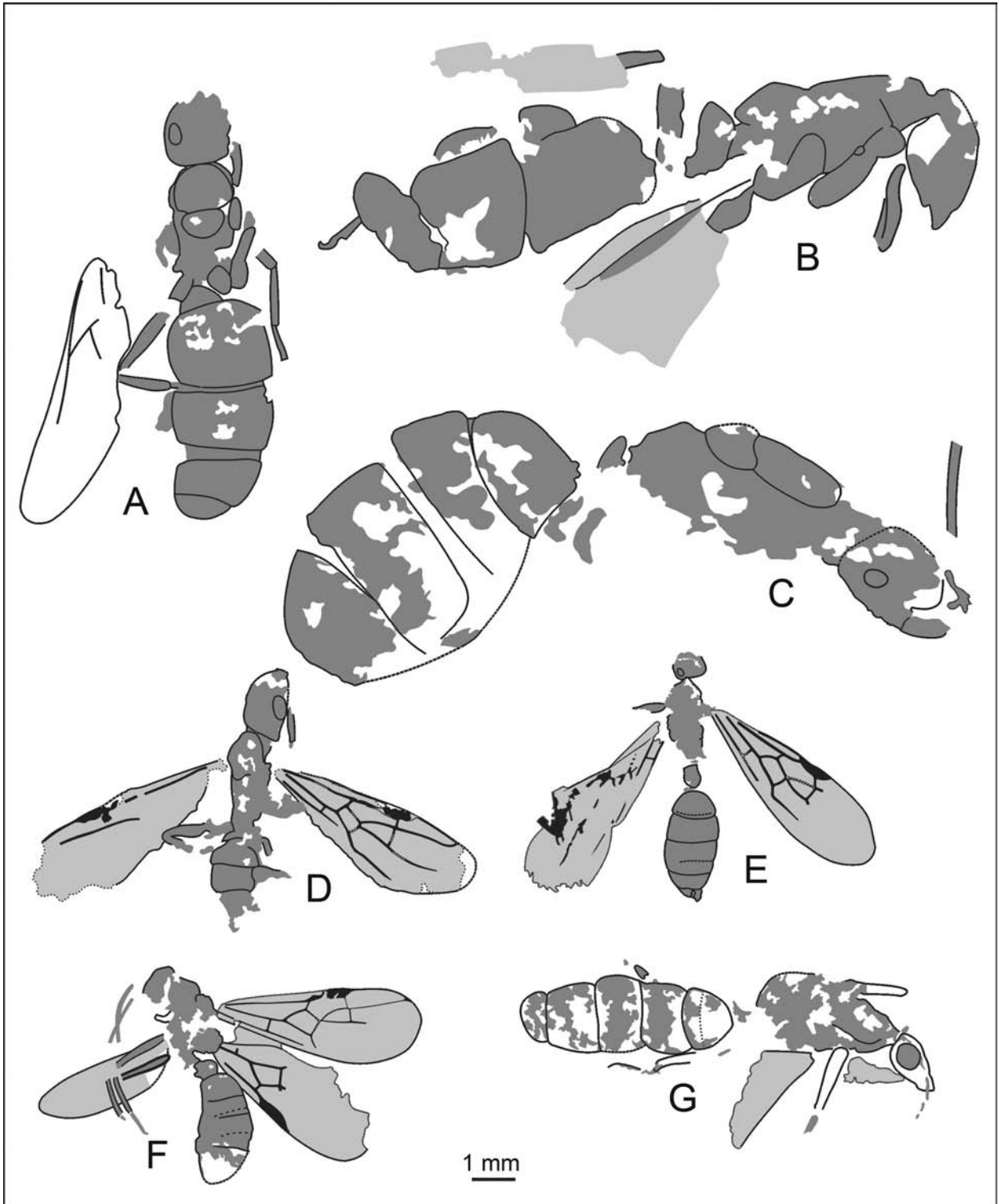


Fig. 13. Species of poneromorph subfamilies. **A** – *Casaleia longiventris* (HEER, 1849), lectotype of *Formica longiventris* HEER, 1849, UMJG&P no. 77.584 (♀); **B** – *Ponerites elongatus* (HEER, 1867), lectotype of *Poneropsis elongata* HEER, 1867 NHMW no. 1852.XXIX.33 (♀); **C** – *Ponerites gracilior* nom. nov., lectotype of *Formica gracilis* HEER, 1867, UMJG&P no. 77.544 (♀); **D** – *Ponerites oblongiceps* sp. nov., holotype GBA no. 2009/016/0515 (♀); **E** – *Ponerites atavinus* (HEER, 1849), holotype of *Formica atavina* HEER, 1849, UMJG&P no. 77.582 (♂); **F** – *Ponerites tenuis* (HEER, 1867), lectotype of *Poneropsis tenuis* HEER, 1867, UMJG&P no. 77.589 (♂); **G** – *Ponerites nitidus* (HEER, 1849). Neotype of *Ponera nitida* HEER, 1849, UMJG&P no. 77.622 (♂).

and *P. hypoponeroides* (DLUSSKY & RASNITSYN, 2002) from the Middle Eocene of the Green River Formation; *P. umbrus* (POPOV, 1932) from the Middle Miocene of the North Caucasus; and six species described below. Evidently, some European Miocene and Oligocene ants described as *Ponera* also belong to this morphogenus.

Ponerites elongatus (HEER, 1867), n. comb.

Fig. 13B

- 1867 *Poneropsis elongata* HEER, p. 19, pl. 1, fig. 21 (♀).
 1907 *Poneropsis elongata* HEER, 1867. – HANDLIRSCH, p. 881.
 1964 Formicidae *incertae generis*. – TAYLOR, p. 138.
 1995 *Poneropsis elongata* HEER, 1867. – BOLTON, p. 363.

Studied material: Lectotype NHMW no. 1852.XXIX.33 (♀)

Diagnosis: Differs from all known species of the genus in its larger size (in the other species, body length is smaller than 10 mm). Differs from *P. gracilior* (described below) in its long first gastral segment and triangular shape of the petiole.

Description: Gyne. BL 16.1 mm. Mesosoma elongate. Scutum weakly convex in lateral view. Propodeum angulate in side view; propodeal dorsum shorter than declivity. Petiole with node, triangular in side view, nearly as long as high. First gastral segment longer than second. Constriction between first and second gastral segments present.

Measurements of lectotype, in mm: AL=4.55, HL=2.8, PtL=PtH=1.5.

Remarks: HEER (1867) described *Poneropsis elongata* from five specimens, of which only one has been preserved; we designate this specimen as the lectotype. It is not very similar to HEER's figure, but doubtlessly belongs to the subfamily Ponerinae and is similar in size to the measurements provided by HEER (BL=15.0, HL=2.7). Since no diagnostic characters distinguishing the genera of this subfamily are visible in the compression fossil, we place this specimen in the formal genus *Ponerites*.

Ponerites gracilior n. nom.

Fig. 13C

- 1867 *Formica gracilis* HEER, p. 7, pl. 1, fig. 3a, b (♀), junior homonym of *Formica gracilis* FABRICIUS 1804, p. 405.
 1907 *Formica gracilis* HEER, 1867. – HANDLIRSCH, p. 864.
 1995 *Formica gracilis* HEER, 1867. – BOLTON, p. 196.

Studied material: Lectotype of *Formica gracilis* HEER UMJG&P no. 77.544 (designated here, ♀, figured in HEER, 1867, pl. 1, fig. 3b).

Diagnosis: Differs from the majority of known species of the genus in its larger size, and shape of the anterior margin of the clypeus. Differs from *P. elongatus* (described above), which is also large, in its short first gastral segment and in the petiole shape.

Description: Gyne. BL 17 mm. Head longer than wide, with parallel sides, rounded occipital corners, and straight occipital margin. Anterior clypeal margin very convex. Eyes oval; with head in full-face view the eyes slightly behind the midlength of the side of the head. Gena length greater than maximum eye diameter. Scape protruding beyond occipital margin. Mandibular bases set far apart. Mesosoma elongate. Scutum slightly convex in lateral view, not overhanging pronotum. Propodeum angulate in lateral view, propodeal dorsum shorter than declivity. Petiole with thick scale. Helcium protruding from very low down on the anterior face of first gastral segment. First gastral segment longer than second. Constriction between first and second gastral segments weak, but distinct.

Measurements of lectotype, in mm: AL=6.2, HL=2.3, HW~2.0, ED=0.55.

Remarks: HEER (1867) described this species from two specimens, one of which, depicted in pl. 1, fig. 3b, has been preserved, and we designate it as the lectotype. *Formica gracilis* HEER, 1867 is a junior homonym of *Formica gracilis* FABRICIUS, 1804 (= *Pseudomyrmex gracilis*). Therefore, we replace the specific epithet with *gracilior*.

The presence of a constriction between the first and second gastral segments, the position of the helcium, and the general habitus of this ant give evidence that it doubtlessly belongs to the subfamily Ponerinae. It is outwardly similar to some members of the genus *Leptogenys* Roger, but key characters that would allow placement of this species in any of the known genera are not visible in the impression. Therefore, we place it in the formal morphogenus *Ponerites*.

Ponerites oblongiceps n. sp.

Figs. 13D, 16C

Etymology: *Oblongiceps* is the Latin word for "oblong-headed".

Studied material: Holotype GBA nos. 2009/016/0515 (♀, identified as *Formica longaeva*) and 2009/016/0543 (counterpart of the same specimen, identified as *Formica occulta*). Paratype GBA no. 2009/016/0672 (♀).

Diagnosis: Differs from all known species of the genus in the elongate head with a concave occipital margin and large oval eyes.

Description: Gyne. BL 6-7 mm. Head longer than wide, with parallel sides, distinct occipital corners, and concave occipital margin. Eyes oval, large; with head in full-face view the eyes in front of the midlength of the side of the head. Genae shorter than maximum eye diameter. Scape reaching occipital margin. Middle joints of funiculus wider

than long. Mesosoma elongate, nearly as wide as head. Scutum weakly convex in lateral view, not overhanging pronotum. Propodeum gradually rounded. Petiole with high scale. Legs rather short and thick. First gastral tergite nearly as long as second. Helcium protruding from very low down on anterior face of first gastral segment, the latter with a high vertical anterior face above the helcium. Constriction between first and second gastral segments distinct. Forewing with closed cells 1+2r, 3r, rm and mcu; cell rm quadrangular, 1.8 times as long as wide; cell mcu pentagonal, nearly twice as long as wide; vein section 1M a little longer than IRS. Icu=1.45.

Measurements, in mm: Holotype: AL=2.4, HL=1.3, HW=1.0, ED=0.6, FWL=5.3. Paratype: BL=6.4, AL=2.3, HL=1.3.

Remarks: The relatively ventral position of the helcium, constriction between the first and second gastral segments, and forewing venation clearly show that this species belongs to the subfamily Ponerinae. Since diagnostic characters used to distinguish between the genera of this subfamily are not visible in the imprint, we place this species in the form genus *Ponerites*.

Ponerites atavinus (HEER, 1849) n. comb.

Fig. 13E

- 1849 *Formica atavina* HEER, p. 143, pl. 11, fig. 10 (♂).
 1867 *Formica atavina* HEER, 1849. – HEER, p. 18.
 1907 *Formica atavina* HEER, 1849. – HANDLIRSCH, p. 864.
 1995 *Formica atavina* HEER, 1849. – BOLTON, p. 191.

Studied material: Holotype UMJG&P no. 77.582 (♂, figured by HEER, 1849: pl 11, fig. 10).

Diagnosis: Males of *Ponerites* have not been described previously. *P. atavinus* differs from *P. nitidus* (described below) in its smaller size and relatively small eyes, and from *P. tenuis* in its elongate petiole and large cell mcu in the forewing.

Description: Male. Body length 5.6 mm. Head small, with rounded occipital angles and straight occipital margin. Eyes rather small, oval; with head in full-face view the eyes behind the midlength of the side of the head. Mesosoma elongate. Petiole nodiform, 1.5 times as long as wide. Gaster elongate, with distinct constriction between first and second gastral segments. Forewing with closed cells 1+2r, rm, mcu, and evidently 3r; cell rm triangular; cell mcu quadrangular, large, nearly twice as long as wide; vein section 1M about 2.5 times as long as IRS. Icu=1.35.

Measurements of holotype, in mm: AL=1.8, HW=0.7, PtL=0.55, PtW=0.37, FWL=5.2.

Remarks: HEER described this species from a single specimen, which has been preserved in the UMJG&P collection. MAYR (1867) examined two specimens identified by HEER,

and placed them, judging by habitus, in the subfamily Myrmicinae. However, HANDLIRSCH (1907) provisionally left this species in the genus *Formica*. The position of the cross-vein cu-a in the forewing and presence of a constriction between the first and second gastral segments clearly indicate that the holotype of this species belongs to the subfamily Ponerinae. Since diagnostic characters used to distinguish between the genera of this subfamily are not visible in the compression fossil, we place this species in the form genus *Ponerites*.

Ponerites tenuis (HEER, 1867), n. comb.

Fig. 13F

- 1867 *Poneropsis tenuis* HEER, p. 22, pl. 2, fig. 1 (♂).
 1867 *Ponera ? tenuis* (HEER, 1867). – MAYR, p. 57.
 1907 *Ponera ? tenuis* (HEER, 1867). – HANDLIRSCH, p. 880.
 1995 *Poneropsis tenuis* HEER, 1867. – BOLTON, p. 363.

Studied material: Lectotype of *Poneropsis tenuis* UMJG&P no. 77.589 (designated here, ♂, figured by HEER, 1867, pl. 2, fig. 1). Other specimens identified by HEER as *Ponera tenuis*: NHMW no. 1852.XXIX.36 (2♂).

Diagnosis: Differs from the male *P. atavinus* (described above) in its short petiole and trapezoid cell mcu in the forewing, and from the male *P. nitidus* (described below) in its smaller size.

Description: Male. BL 6-7 mm. Antennae long, filiform. Mesosoma elongate. Scutum weakly convex in lateral view. Petiole nodiform, shorter than high, with ventral lobe and node rounded in lateral view. Helcium protruding from ventral position on anterior face of first gastral segment, the latter rounded in side view. Legs rather long. Gaster with constriction between first and second segments. Forewing with closed cells 1+2r, 3r, rm and mcu; cell rm triangular, without peduncle, twice as long as wide; cell mcu trapezoidal; vein section 1Cu 1.7 times as long as RS+M; section 1M about 2.5 times as long as IRS. Icu=1.4.

Measurements, in mm: UMJG&P no. 77.589 (lectotype): AL=2.2, FWL=5.0, PtL=0.4, PtH=0.5; NHMW no. 1852.XXIX.36a: AL=2.4, FWL=5.8; NHMW no. 1852.XXIX.36b: AL=2.8, FWL=5.8.

Remarks: HEER (1867) described this species from seven specimens, one of which (depicted by HEER) has been preserved, and we designate it as the lectotype. Two other specimens identified by HEER, preserved closely within the same piece of rock, probably do not belong to the type series. They are on the whole similar to the lectotype, but are a little larger. MAYR (1867) examined three specimens identified by HEER, and came to the conclusion that two of them belong to the subfamily Ponerinae, but differ in venation from each other and from HEER's description, and provisionally placed them in the genus *Ponera*. We have failed to find these specimens in the studied collections.

The lectotype of *P. tenuis* is doubtlessly a male belonging to Ponerinae. Since diagnostic characters used to distin-

guish between the genera of this subfamily are not visible in the compression fossil, we place this species in the form genus *Ponerites*.

Ponerites nitidus (HEER, 1849), n. comb.

Fig. 13G

- 1849 *Ponera nitida* HEER, p. 149, pl. 12, fig. 4 (♂, described as ♀).
 1867 *Poneropsis nitida* (HEER, 1849). – HEER, p. 20.
 1867 *Hypoclinea nitida* (HEER, 1849). – MAYR, p. 57.
 1878 *Dolichoderus nitidus* (HEER, 1849). – FOREL, p. 386.
 1907 *Dolichoderus nitidus* (HEER, 1849). – HANDLIRSCH, p. 870.
 1964 *Poneropsis nitida* (HEER, 1849). – TAYLOR, 1964, p. 138.
 1994 *Dolichoderus nitidus* (HEER, 1849). – SHATTUCK, p. 59.
 1995 *Dolichoderus nitidus* (HEER, 1849). – BOLTON, p. 175.

Studied material: Neotype of *Ponera nitida* UMJG&P no. 77.622 (designated here, ♂).

Diagnosis: Differs from the males of *P. atavinus* and *P. tenuis* (described above) in its larger size.

Description: Male. BL 9.8 mm. Head elongate with large, round eyes. Mesosoma elongate. Propodeum rounded in lateral view. Petiole not preserved. Gaster with constriction between first and second segments. First gastral tergite a little longer and narrower than second. Wing venation not preserved.

Measurements of neotype, in mm: AL=3.4, HL=1.2, ED=0.6.

Remarks: HEER (1849) described this species from one specimen, which has not been preserved. He described it as a gyne, but judging by the number of gastral segments shown in the figure, the specimen was a male, rather than a gyne. Subsequently, he found another specimen, which has been preserved in the UMJG&P collection (HEER 1867). This specimen is labelled as a syntype, but formally it cannot be considered a syntype, and we designate it as the neotype. MAYR (1867) examined one specimen identified by HEER and identified it as a male of *Hypoclinea*. This specimen has not been preserved. FOREL (1878) did not see this specimen, but placed it in the genus *Dolichoderus* (a senior synonym of *Hypoclinea*).

Although the neotype is poorly preserved, the general habitus and presence of a constriction between the first and second gastral segments allow placement in the subfamily Ponerinae and the form genus *Ponerites*.

Subfamily Myrmicinae LEPELETIER DE SAINT-FARGEAU, 1835

Morphogenus *Paraphaenogaster* DLUSSKY, 1981

Type species: *Paraphaenogaster microphthalma* DLUSSKY, 1981, by original designation.

Diagnosis (for compression fossils): Waist with two segments (petiole and postpetiole). Forewing with closed cells 1+2r and mcu, and rm; cell 3r open at apex; apical sections of veins RS and M leaving cell 1+2r+rm separately.

Species included: Type species from Vishnevaya balka, Stavropol, Russia; Middle Miocene. We found forewings with such venation in Bembridge, UK (Late Eocene or Early Oligocene), Bol'shaya Svetlovidnaja, Maritime Province, Russia (Early Oligocene), Rott, Germany (Late Oligocene), Enspel, Germany (Late Oligocene), and Willershausen, Germany (Pliocene), however, these species remain undescribed. *Myrmica aemula* HEER, 1849 from Parschlug, Austria (Miocene), *Myrmica macrocephala* HEER, 1849, *M. rugiceps* HEER, 1849, *M. tertiaria* HEER, 1849 from Oeningen, Germany (Middle Miocene), *Carebara bohemica* (NOVÁK, 1877) from Krottensee, Czechia (Miocene), *Aphaenogaster shanwangensis* (HONG, 1984), *A. lapidescens* ZHANG, 1989 and *A. paludosa* ZHANG, 1989 from Shanwang, China (Middle Miocene) are similar in venation and might also belong to this morphogenus.

Remarks: Similar venation is characteristic of some Myrmicinae: Pheidolini (part of *Aphaenogaster* MAYR) and Solenopsidini (*Solenopsis* Westwood, *Carebara* Westwood).

Paraphaenogaster tertiaria (HEER, 1849), n. comb.

Figs. 14A-B, 18D

- 1849 *Myrmica tertiaria radobojana* HEER, p. 159, pl. 13, fig. 1 (♀).
 1867 *Myrmica tertiaria* HEER, 1849 – HEER, p. 30.
 1867 *Myrmica bicolor* HEER, p. 31, pl. 2, fig. 11 (♀) (syn. by MAYR, 1867).
 1867 (*Myrmicinae*) *tertiaria* (HEER, 1849). – MAYR, p. 58.
 1893 *Myrmica tertiaria* HEER, 1849. – DALLA TORRE, p. 117.
 1907 (*Myrmicidae*) *tertiaria radobojana* (HEER, 1849). – HANDLIRSCH, p. 878.
 1995 *Myrmica tertiaria* HEER, 1849. – BOLTON, p. 284.

Studied material: Holotype of *Myrmica bicolor* UMJG&P no. 77.624 (♀); Specimen GBA no. 2009/016/0603 (?♀) identified by HEER as *Attopsis nigra*.

Diagnosis: Gynes of *Paraphaenogaster* have not been described previously. *P. tertiaria* differs from *P. jurinei* (described below) in its larger size and head shape (head 1.25 times longer than wide in *P. tertiaria*, and 2 times in *P. jurinei*).

Description: Gyne. BL 10-13 mm. Head 1.25 times as long as wide, with parallel sides and rounded occipital margin, without occipital angles. Anterior clypeal margin notched medially. Eyes oval, with head in full-face view the eyes distinctly behind the midlength of the side of the head; ge-

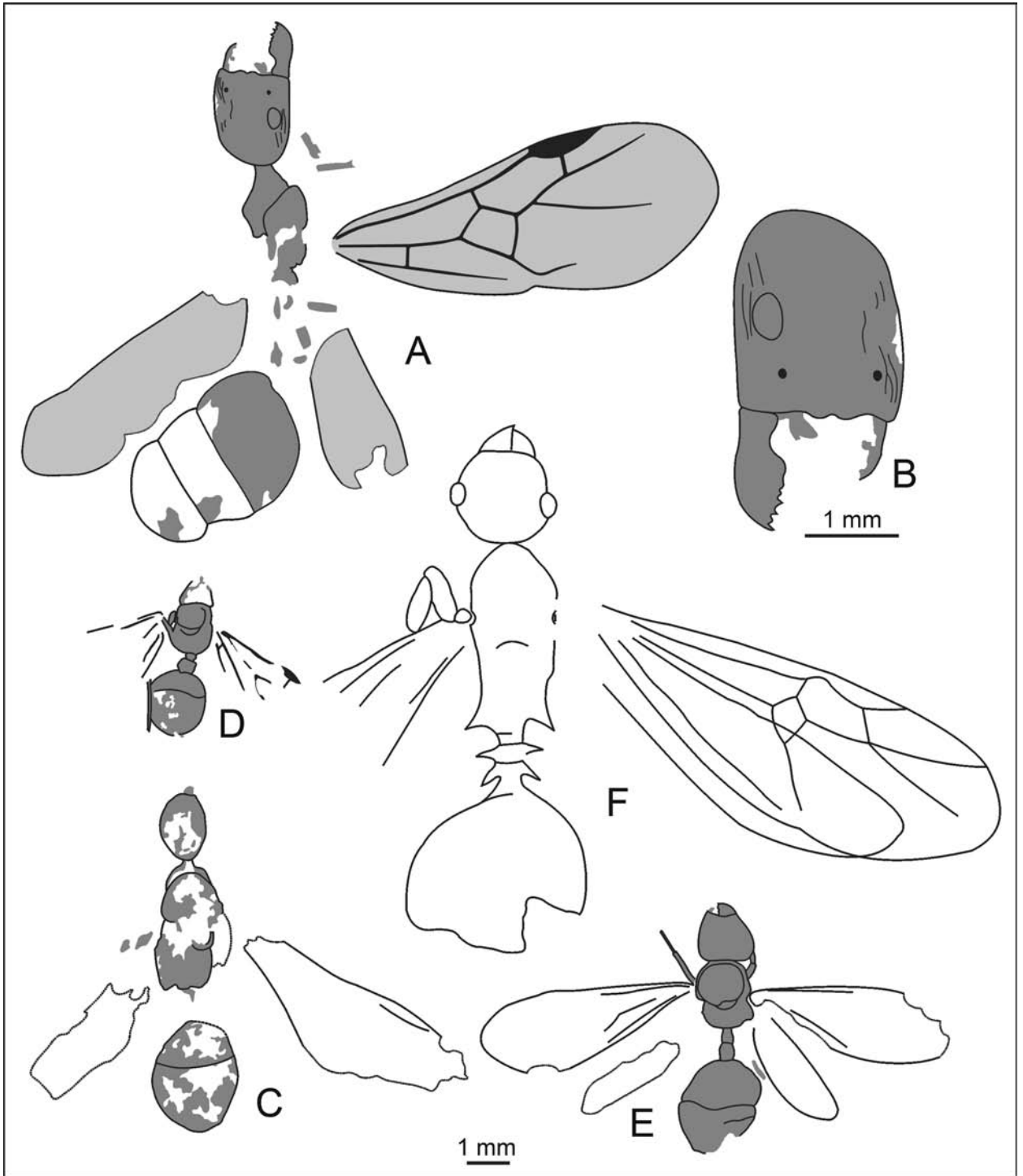


Fig. 14. Species of the subfamily Myrmicinae. **A-B** – *Paraphaenogaster tertiaria* (HEER, 1849); **A** – holotype of *Myrmica bicolor* HEER, 1867, UMJG&P no. 77.624 (♀); **B** – head of the same specimen; **C** – *Paraphaenogaster jurinei* (HEER, 1849), neotype of *Myrmica jurinei* HEER, 1849, UMJG&P no. 211 032 (♀); **D** – *Myrmecites pusillus* (HEER, 1849), neotype of *Myrmica pusilla* HEER, 1849, NHMW no. 1852.XXIX.41 (♀); **E** – *Myrmecites latus*, sp. nov., holotype NHMW no. 2014/0130/0001 (♀); **F** – *Lonchomyrmex freyeri* (HEER, 1867) (♀, from MAYR 1867).

nal length greater than maximum eye diameter. Mandible triangular, with six acute teeth. Mesosoma elongate, narrower than head. Scutum longer than wide. Posterior margin of propodeum and waist not preserved. Gaster oval. Head with longitudinal rugae. Forewing as in genus. Cell *mcu* trapezoid. Section 1M about twice as long as 1RS. *Icu*=2.0.

Measurements, in mm: UMJG&P no. 77.624: *AL*=3.7, *HL*=2.25, *HW*=1.8, *ED*=0.5, *FWL*=9.3; GBA no. 2009/016/0603: *AL*=3.6, *FWL*>7.9.

Remarks: MAYR (1867) examined two specimens identified by HEER as *Myrmica tertiarica*, and one specimen identified by HEER as *M. bicolor*, and came to the conclusion that they were conspecific. We have failed to find in the studied collections any specimens identified by HEER as *M. tertiarica*, but have found the holotype of *M. bicolor*. HEER considered the two-colour pattern of the gaster (black first tergite and pale subsequent tergites) a distinguishing character of *M. bicolor*, but the preserved coloration of compression fossils cannot be considered a diagnostic character. Moreover, it is clearly visible in the imprint of the holotype of *M. bicolor* that on the first gastral tergite carbonised chitin has been preserved, whereas on the other tergites no chitin has been preserved, which explains the two-color pattern of the gaster. Since the size, proportions, and wing venation of *M. tertiarica* and *M. bicolor* (judging by HEER's descriptions and figures) are similar, we believe that it is reasonable to follow MAYR's synonymisation. The holotype of *M. bicolor* is outwardly very similar to a gyne of *Aphaenogaster*, but since the diagnostic characters of this genus are not visible in the compression fossil, we prefer to place it in the form genus *Paraphaenogaster*. Comparison with *P. microphthalma*, the only known species of this genus, is impossible, because that species was described from a male.

Paraphaenogaster jurinei (HEER, 1849), n. comb.
Fig. 14C

- 1849 *Myrmica jurinei* HEER, p. 163, pl. 13, fig. 8 (♀).
1867 *Myrmica concinna* HEER, p. 32, pl. 2, fig. 13 (♀), n. syn.
1867? *Myrmica jurinei* HEER, 1849. – MAYR, p. 59.
1907 *Myrmica concinna* HEER, 1867. – HANDLIRSCH, p. 875, n. syn.
1907? *Myrmica jurinei* HEER, 1849. – HANDLIRSCH, p. 875.
1995 *Myrmica concinna* HEER, 1867. – BOLTON, p. 278, n. syn.
1995 *Myrmica jurinei* HEER, 1849. – BOLTON, p. 280.

Studied material: Neotype of *Myrmica jurinei* UMJG&P no. 211 032 (♀, identified by HEER as *Attopsis anthracina*). Specimen NHMW no. 1852.XXIX.40 (♀, identified by HEER as *Myrmica jurinei*).

Diagnosis: Differs from *M. tertiarica* in its smaller size and head shape (head 1.25 times longer than wide in *P. tertiarica*, and 2 times in *P. jurinei*).

Description: Gyne. BL 7.3–8.3. Head nearly twice as long as wide, with convex sides and rounded occipital margin, without occipital corners. Mesosoma wider than head, elongate, nearly twice as long as wide. Scutum wider than long. Propodeum without spines or teeth. Postpetiole longer than high. Gaster oval.

Measurements, in mm: Neotype: BL=8.3, AL=3.1, AW=1.5, HL=1.5, HW=1.1, FWL=7.1; NHMW no. 1852.XXIX.40: BL~7.3, AL=2.6, FWL=7.5.

Remarks: HEER (1849) described *M. jurinei* from a single specimen. He considered this specimen to be a male, since he believed he had found five gastral segments. However, judging by the general habitus and shape of the gaster, the specimen shown in the figure was most probably a gyne. MAYR (1867) examined three specimens identified by HEER as *M. jurinei*. One of them was outwardly similar to *Myrmica*, but its wing venation has not been preserved. The two others clearly belonged to other species. We have failed to find in the studied collections the holotype of this species, but found two specimens of identical size and body shape. Specimen NHMW no. 1852.XXIX.40, identified by HEER as *M. jurinei*, is poorly preserved, but its waist is clearly two-segmented. The second specimen (which we designate as the neotype), identified by HEER as *Attopsis anthracina*, cannot be placed in this species, because it is considerably larger (AL=3.1, whereas in *A. anthracina*, according to the description, AL=1.6). The waist of this specimen has not been preserved, but the position of the gaster and the longer first gastral tergite give evidence that the waist was two-segmented. Unfortunately, the wing venation has not been preserved in any of these two specimens. Judging by HEER's description and figure, *M. jurinei* had wing venation typical of *Paraphaenogaster*.

HEER described *Myrmica concinna* from two specimens, which, as well as any other specimens identified as *M. concinna*, we have failed to find in the studied collections. MAYR (1867) examined two specimens of this species identified by HEER, but they were poorly preserved, and he could not place them in any genus. Judging by HEER's figure and description, this species belongs to the form genus *Paraphaenogaster* and is a junior synonym of *Myrmica jurinei*.

Morphogenus *Myrmecites* DLUSSKY & RASNITSYN,
2003

Type species: *Myrmecites rotundiceps* DLUSSKY & RASNITSYN, 2003, by original designation.

Diagnosis: Ant compression fossils with two-segmented and short waist (less than half as long as gaster and less than one third as long as mesosoma), petiole sessile, and postpetiole narrowly attached to gaster, which cannot be identified more precisely.

Species included: Type species described from the Green River Formation (Middle Eocene), and species re-described below.

Myrmecites pusillus (HEER, 1849), n. comb.

Fig. 14D

- 1849 *Myrmica pusilla* HEER, p. 164, pl. 13, fig. 9 (described as ♂).
 1867 *Myrmicapusilla* HEER, 1849. – HEER, p. 32, pl. 2, fig. 14.
 1867 *Cremastogaster pusilla* (HEER, 1849). – MAYR, p. 59.
 1907 *Cremastogaster pusilla* (HEER, 1849). – HANDLIRSCH, p. 873.
 1995 *Crematogaster pusilla* (HEER, 1849). – BOLTON, p. 160.

Studied material: Neotype NHMW no. 1852.XXIX.41 (♀, designated here).

Diagnosis: Similar in the structure of the waist to *M. rotundiceps*, and differs from latter in its shorter and wider mesosoma (in *M. rotundiceps* the mesosoma is twice as long as wide).

Description: Gyne. BL 3.8 mm. Head nearly as wide as mesosoma. Mesosoma 1.4 times as long as wide. Propodeum without spines or teeth. Petiole sessile, 1.4 times as wide as long. Postpetiole 1.6 times as wide as petiole and 1.25 times as wide as long. Gaster rounded. Wing venation not preserved.

Measurements of neotype, in mm: AL=1.2, AW=0.85, PtL=0.18, PtW=0.25, PptL=0.32, PptW=0.40.

Remarks: HEER (1849) described *Myrmica pusilla* from a single specimen, which is probably lost. We have found in the studied collections only one specimen identified by HEER, which we designate as the neotype. The measurements of this specimen are similar to those provided by HEER in his description (BL=3.8, AL=1.1, AW~0.8). This specimen is probably different from the one identified by MAYR (1867) as *Crematogaster*. The specimen examined by MAYR had an identifier number 92, whereas the specimen examined by us has an old identifier number 93. Since this specimen has a two-segmented waist, it doubtlessly belongs to the subfamily Myrmicinae. However, the impression is poorly preserved, and diagnostic characters used to distinguish between the genera of this subfamily cannot be discerned; therefore, we place it in the form genus *Myrmecites*.

Myrmecites latus n. sp.

Figs. 14E, 18C

Etymology: *Latus* is the Latin word for “wide”.

Studied material: Holotype NHMW no. 2014/0130/0001, with label “Jahr d. Acq. 1890. Formicidae (HANDL.). Mio-caen. Radoboj. Dr. KATHOLICZKY did.” (♀). Paratype NHMW no. 1852.I.1012 (♀).

Diagnosis: The new species is similar to *M. pusillus*, but clearly differs from it in size, with a shorter mesosoma, and elongate segments of the waist.

Description: Gyne. BL ca. 6 mm. Head 1.2 times as wide as long, with convex sides, rounded occipital corners and weakly concave occipital margin. Anterior margin of clypeus concave. Mandibles triangular. Mesosoma nearly as wide as head, 1.2 times as long as wide. Scutum large, 1.2 times as wide as long. Dorsum of mesosoma convex in side view. Propodeum without spines or teeth, angular in side view. Petiole 1.3 times as long as wide, broader posteriorly than anteriorly. Postpetiole 1.3 times as wide as petiole and 1.3 times as long as wide. Gaster oval. Wing venation not preserved.

Measurements, in mm: Holotype: BL=6.1, AL=1.7, AW=1.3, HL=1.2, HW=1.35, SctL=0.9, SctW=1.1, PtL=0.35, PtW=0.27, PptL=0.44, PptW=0.34, FWL=5.6. Paratype: BL=6.2, AL=2.0, FWL=6.3

Remarks: The specimen we designate as the holotype was identified as *Formica demersa*, but the identification is clearly not HEER's, since the material was received by the museum in 1890, and HEER died in 1883. *F. demersa* was described from Oeningen, but it has never been reported from Radoboj.

Genus *Lonchomyrmex* MAYR, 1867

Type species: *Formica freyeri* HEER, 1867, by monotypy.

Diagnosis (modified from MAYR 1867, terminology corrected): Gyne. Mandibles depressed, not wide, with masticatory margin oblique and dentate and apical tooth strongly protruding. Head rounded, wider than long (excluding mandibles). Eyes rather small, convex, situated approximately at midlength of lateral surface of head. Mesosoma twice as long as wide; propodeum likely with pair of spines set far apart. Waist two-segmented; petiole with pair of long lateral spines directed laterally; postpetiole with pair of short lateral spines slightly directed posterad. Gaster rounded. Forewing with closed cells 1+2r, 3r and mcu; cell rm absent; free branches 5RS and 4M leave cell 1+2r from common expanded junction.

Lonchomyrmex freyeri (HEER, 1867)

Fig. 14F

- 1867 *Formica freyeri* HEER, p. 10, pl. 1, fig. 9 (♀).
 1867 *Lonchomyrmex freyeri* (HEER, 1867). – MAYR, p. 61, fig. 12.
 1907 *Lonchomyrmex freyeri* (HEER, 1867). – HANDLIRSCH, p. 878.
 1995 *Lonchomyrmex freyeri* (HEER, 1867). – BOLTON, p. 248.

Description (from MAYR 1867): Gyne. With characters of genus. Body length 12.5 mm, forewing length 11.5 mm.

Remarks: HEER described this species from a single specimen. MAYR found two specimens identified as *Formica*

freyeri, one of which, judging by the similarity between the figures of HEER and MAYR, was the holotype. MAYR found that this ant actually belonged to the subfamily Myrmicinae and described a new genus. We have failed to find this species in the studied collections.

Species of unclear status and placement

Formicidae *incertae generis*

(Formicidae) *oculata* HEER, 1849 n. comb.

Fig. 15A

- 1849 *Formica oculata* HEER, p. 143, pl. 10, fig. 9d (♂).
 1867 *Formica oculata* HEER, 1849. – HEER, p. 17, pl. fig. 18 (♂).
 1907 *Formica oculata* HEER, 1849. – HANDLIRSCH, p. 865.
 1995 *Formica oculata* HEER, 1849. – BOLTON, p. 200.

Holotype: UMJG&P no. 77.646d (♀).

Remark: HEER described this species from a single specimen, which he considered to be male. Actually, it is a poorly-preserved compression fossil of a gyne. The imprint of the holotype is so poorly preserved that we cannot place it in any known species or describe as a valid species. Therefore, we suggest treating *Formica oculata* as Formicidae *incertae generis*.

(Formicidae) *obtecta* HEER, 1849 n. comb.

Fig. 15B

- 1849 *Formica oblecta* HEER, p. 123, pl. 9, fig. 7, pl. 10, fig. 9c, pl. 11, fig. 14f (♀).
 1907 *Formica oblecta* HEER, 1849. – HANDLIRSCH, p. 865.
 1995 *Formica oblecta* HEER, 1849. – BOLTON, p. 200.

Holotype: UMJG&P no. 77.646c (designated here, ♀, figured by HEER, 1849: pl. 9, fig. 7, pl. 10, fig. 9c)

Remarks: HEER mentions in his description two specimens: a wingless gyne (designated here as the holotype) and a gaster. Apparently, the gyne should be considered the holotype, since the imprint of the gyne is strongly distorted, and ants cannot be identified by gaster alone. Therefore we cannot place this species in any known species or describe as a valid species, and suggest treating *Formica oblecta* as Formicidae *incertae generis*.

The collection of UMJG&P contains specimen no. 77.577, labelled as a syntype of *Formica oblecta*. Actually, it is a gyne of *Liometopum imhoffi*, which cannot be considered a syntype, because it differs from the figures of both specimens from which this species was originally described.

(Formicinae) *fragilis* (HEER, 1849) n. comb.

Fig. 15C

- 1867 *Formica fragilis* HEER, p. 8, pl. 1, figs. 4, 5a, b (♀, ♂). Unresolved junior homonym of *Formica fragilis* F. SMITH, 1859 (= *Leptomymex fragilis*).
 1867 *Plagiolepis fragilis* (HEER, 1867). – MAYR, p. 56.
 1891 *Lasius fragilis* (HEER, 1867) – SCUDDER, p. 713.
 1907 *Plagiolepis fragilis* (HEER, 1867). – HANDLIRSCH, p. 859.
 1995 *Formica fragilis* HEER, 1849. – BOLTON, p. 195.

Studied material: Lectotype of *Formica fragilis* UMJG&P no. 77.541 (designated here, ♀, figured by HEER, 1867: pl. 1, fig. 4b). Other specimens identified by HEER as *F. fragilis*: GBA no. 2009/016/0169 (♀); NHMW no. 1852.XXIX.31 (2♀).

Remarks: HEER (1867) described this species from 12 males and one gyne. The gyne, depicted by HEER in pl. 1, fig. 4b, has been preserved (specimen UMJG&P no. 77.541); we designate this specimen as lectotype. The compression fossil includes the wings and fragments of the gaster. In addition, we have found three other specimens identified by HEER as *F. fragilis*. Specimen GBA no. 2009/016/0169 also includes only the wings and fragments of the gaster. The wing venations of this specimen and of the lectotype are slightly different, but principally similar and characteristic of *Plagiolepis*. However, such venation is also found in small members of other genera of Formicinae, such as *Pre-nolepis* MAYR and *Nylanderia* EMERY. Therefore, we cannot be completely sure that this species actually belongs to the genus *Plagiolepis*. In two other specimens preserved in the same piece of rock (NHMW no. 1852.XXIX.31), the wing venation has not been preserved, and the preservation quality of the fossils does not allow their identification to genus with certainty.

MAYR (1867) examined four specimens identified by HEER and identified two of them as males of *Lasius* and two, without full certainty, as gyness of *Plagiolepis*. Based on this, SCUDDER (1891) transferred this species to *Lasius*, and HANDLIRSCH (1907) transferred it to *Plagiolepis*. In our opinion, *Formica fragilis* HEER should be treated as Formicinae *incertae generis*.

(Formicidae) *obvoluta* HEER, 1849 n. comb.

Fig. 15D

- 1849 *Formica obvoluta* HEER, p. 141, pl. 10, fig. 9f (described as ♂).
 1867 *Formica obvoluta* HEER, 1849. – HEER, p. 16.
 1867 *Formica obvoluta* HEER, 1849. – MAYR, p. 56.
 1907 *Formica obvoluta* HEER, 1849. – HANDLIRSCH, p. 864.
 1995 *Formica obvoluta* HEER, 1849. – BOLTON, p. 200.

Studied material: Holotype UMJG&P no. 77.646f (?worker, designated by HEER, 1849: pl. 10, fig. 9f). Other specimen identified by HEER as *F. obvoluta*: GBA no. 2009/016/0565 (?♂).

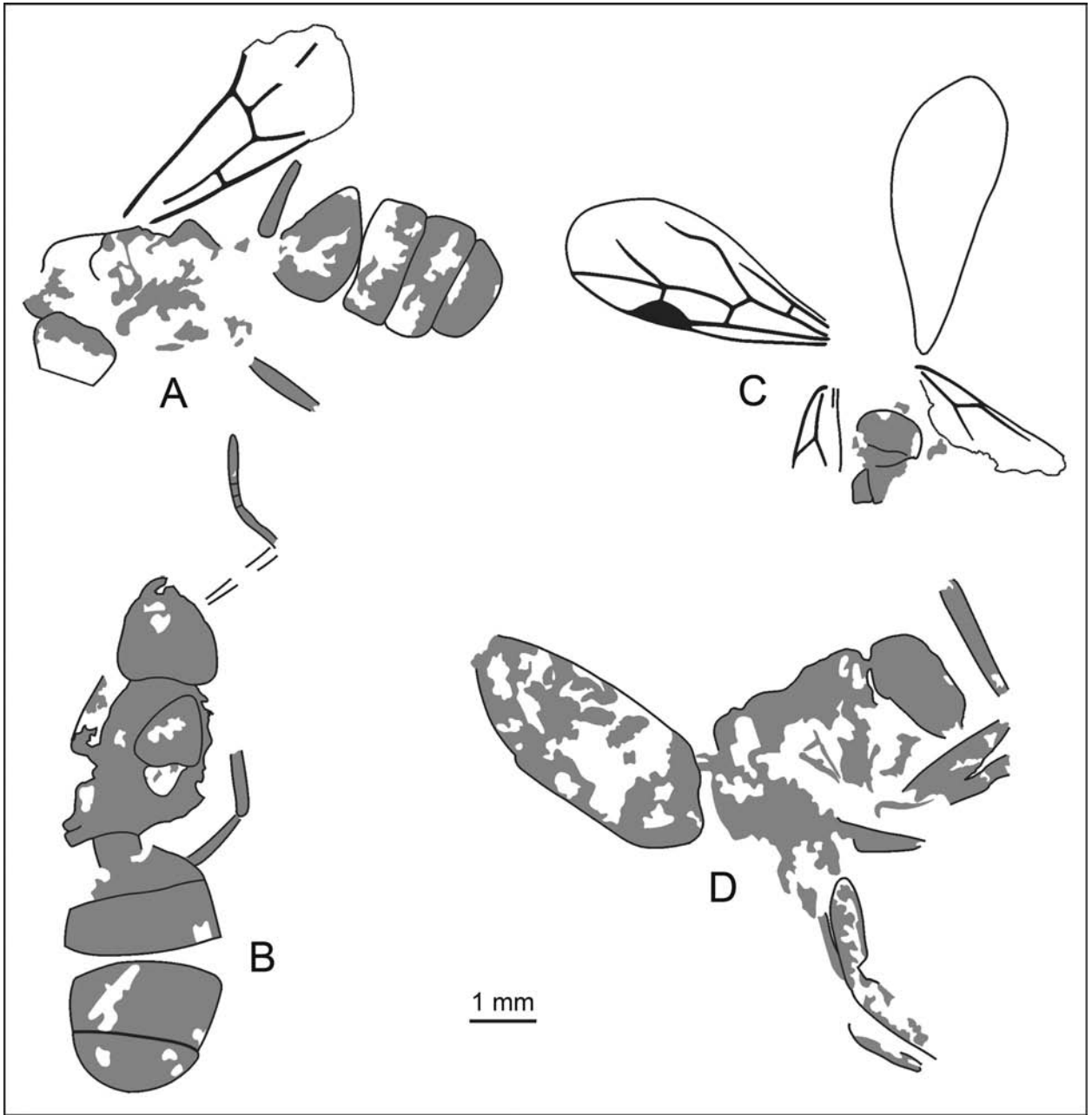


Fig. 15. Formicidae *incertae generis*. **A** – holotype of *Formica oculata* HEER, 1849, UMJG&P no. 77.646d (♀); **B** – holotype of *Formica obtecta* HEER, 1849, UMJG&P no. 77.646c (♀); **C** – lectotype of *Formica fragilis* HEER, 1849, UMJG&P no. 77.541 (♀); **D** – holotype of *Formica obvoluta* HEER, 1849, UMJG&P no. 77.646f (? worker).

Remarks: HEER described this species from a single specimen preserved in the same piece of rock as other ants. This specimen has been preserved in the UMJG&P collection. HEER stated in his description that the gaster of this ant con-

sists of six distinct segments, and therefore, considered this specimen male. Actually, the segmentation of the gaster is not visible in the compression fossil, and the shape of the mesosoma and gaster give evidence that it is most likely a

worker. Specimen GBA no. 2009/016/0565, identified by HEER, is a very poorly-preserved male, which cannot be identified to genus. MAYR (1867) examined two specimens identified by HEER as *F. obvoluta*, and identified one of them as a male of *Formica*. Based on this, HANDLIRSCH (1907) left this species in the genus *Formica*. Judging by the one-segmented waist and absence of a constriction between the first and second gastral segments, the holotype of *F. obvoluta* belongs to Formicinae or Dolichoderinae. However, the specimen is so poorly-preserved that we cannot place it in any known species, or describe as a valid species. Therefore, we suggest treating *Formica obvoluta* as Formicidae *incertae generis*.

Formicidae taxa unavailable for study

Ponera croatica HEER, 1849

- 1849 *Ponera croatica* HEER, p. 148, pl. 12, fig. 3 (♀).
 1964 *Poneropsis croatica* (HEER, 1849). – TAYLOR, p. 138.
 1995 *Poneropsis croatica* (HEER, 1849). – BOLTON, p. 363.

HEER described this species from two specimens, which we have failed to find. We have also failed to find in the studied collections any other specimens identified as *P. croatica*. MAYR (1867) examined one specimen identified by HEER (but not one of the syntypes), and tentatively identified it as a gyne of the subfamily Ponerinae. However, the specimen figured by HEER lacks a constriction between the first and second gastral segments, and the closed cell *rm* in the forewing; therefore, there is no reason to place this species in the subfamily Ponerinae.

Poneropsis pallida HEER, 1867

- 1867 *Poneropsis pallida* HEER, p. 23, pl. 2, fig. 2 (♀).
 1907 *Poneropsis pallida* HEER, 1867. – HANDLIRSCH, p. 880.
 1995 *Poneropsis pallida* HEER, 1867. – BOLTON, p. 363.

HEER described this species from a single specimen, which we have failed to find. MAYR (1867) did not see this species. We have also failed to find in the studied collections any other specimens identified as *P. pallida*. Judging by the figure and description, this species may belong to the subfamily Ponerinae, but this can be determined only if the holotype is found.

Poneropsis brunascens HEER, 1867

- 1867 *Poneropsis brunascens* HEER, p. 27, pl. 2, fig. 7 (♂).
 1907 *Poneropsis brunascens* HEER, 1867. – HANDLIRSCH, p. 881.
 1995 *Poneropsis brunascens* HEER, 1867. – BOLTON, p. 363.

HEER described this species from a single specimen, which we have failed to find. MAYR (1867) did not see this species

either. We have also failed to find in the studied collections any other specimens identified as *P. brunascens*. Judging by HEER's description and figure, the holotype of this species is most probably a male *Liometopum*, but this can be determined with certainty only if the holotype is found.

Myrmica venusta HEER, 1867

- 1867 *Myrmica venusta* HEER, p. 31, pl. 2, fig. 12 (♀). Unresolved junior primary homonym of *Myrmica venusta* F. SMITH, 1858 (= *Monomorium*).
 1867 *Solenopsis venusta* (HEER, 1867). – MAYR, p. 60.
 1907 *Solenopsis venusta* (HEER, 1867). – HANDLIRSCH, p. 873.
 1995 *Myrmica venusta* HEER, 1867. – BOLTON, p. 284.

HEER described this species from a single specimen, which, as well as any other specimens identified as *M. venusta*, we have failed to find in the studied collections. MAYR (1867) examined two specimens of this species identified by HEER (a gyne and a male preserved in one piece of rock) and tentatively identified them as *Solenopsis*. However, judging by HEER's figure, the holotype of this species cannot belong to the subfamily Myrmicinae. The waist and wing venation were not preserved, and it can be seen in the figure that the shape and segmentation of the gaster were characteristic of Formicinae or Dolichoderinae.

5. Conclusions

We found in collections of three museums of Austria a total of 539 compression fossils of ants from Radoboj, 307 of them with original Heer's labels. We designated the holotypes, lectotypes and neotypes for 54 of the 62 species described by HEER, and subsequently compared the other specimens to these types. As a result, we have identified 350 specimens to subfamily and 311 specimens to species. We re-described 23 species originally described by HEER (1849, 1867) and two species described by MAYR (1867). One genus and eight species are described as new; 27 species and varieties described by HEER are synonymized. The taxonomic placement of eight species originally described by HEER remains unclear.

As a result of our revision, the known assemblage of Radoboj includes 33 species of 15 genera and five subfamilies (Tab. 1). These results make it possible to compare this assemblage with other Cenozoic ant assemblages.

Although the ants have been described from many deposits of various ages, the data from the majority of studies cannot be used for comparison, because they contain descriptions of particular species, but no complete data on the assemblage. The ant assemblages

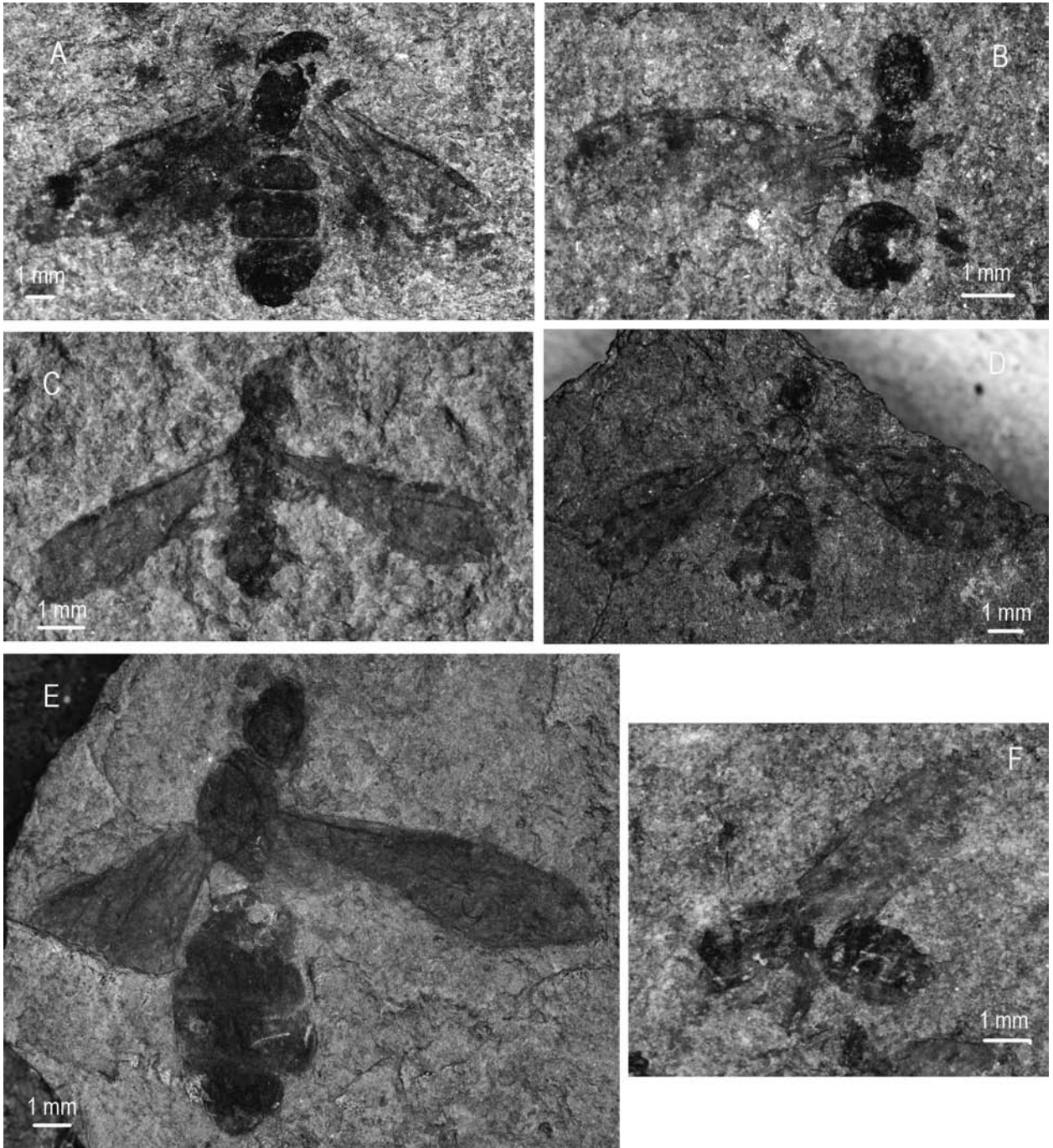


Fig. 16. Photographs of fossils of the subfamily Dolichoderinae and poneromorph subfamilies. **A** – *Liometopum inhoffii* (HEER, 1849), holotype of *Ponera affinis* HEER, 1849, UMJG&P no. 77.638 (♀); **B** – *Emplastus antiquus* (MAYR, 1867), neotype GBA no. 2009/016/0459 (♀); **C** – *Ponerites oblongiceps* sp. nov., holotype GBA no. 2009/016/0515 (♀); **D** – *Emplastus dubius* sp. nov., holotype UMJG&P no. 77.527 (♀); **E** – *Emplastus miocenicus* sp. nov., holotype NHMW no. 1852.XXIX.32 (♀); **F** – *Dolichoderus heeri* sp. nov., holotype UMJG&P no. 77.507a (♀).

Fig. 17. Photographs of fossils of the subfamily Formicinae. **A** – *Attopsis longipennis* HEER, 1849, lectotype UMJG&P no. 210 962 (♀); **B** – *L. anthracinus* (HEER, 1867), neotype of *Poneropsis anthracinus* HEER, 1867, GBA no. 2009/016/0074 (♀); **C** – *Heeridris croaticus* sp. nov., holotype NHMW no. 1852.I.999 (♀); **D** – *Camponotus induratus* (HEER, 1849), specimen NHMW no. 1852.XXIX.4 determined by HEER as *Formica indurata*, studied by MAYR (♀); **E** – *Gesomyrmex breinii* (HEER, 1849), lectotype of *Myrmica breinii* HEER, 1849, UMJG&P no. 77.482 (♀); **F** – *Formica parexsecta* sp. nov., holotype GBA no. 2009/016/0355 (♀).

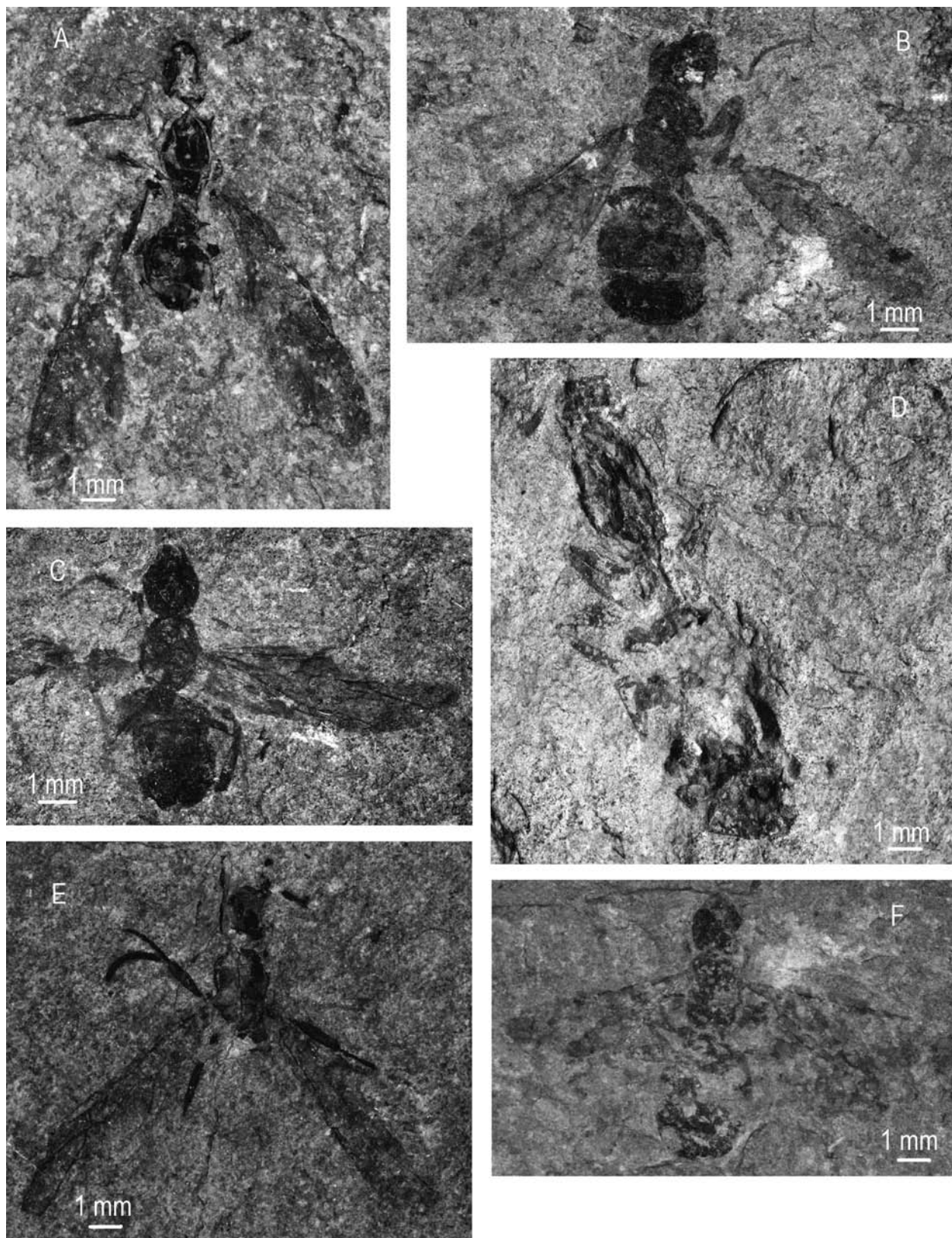


Fig. 17.

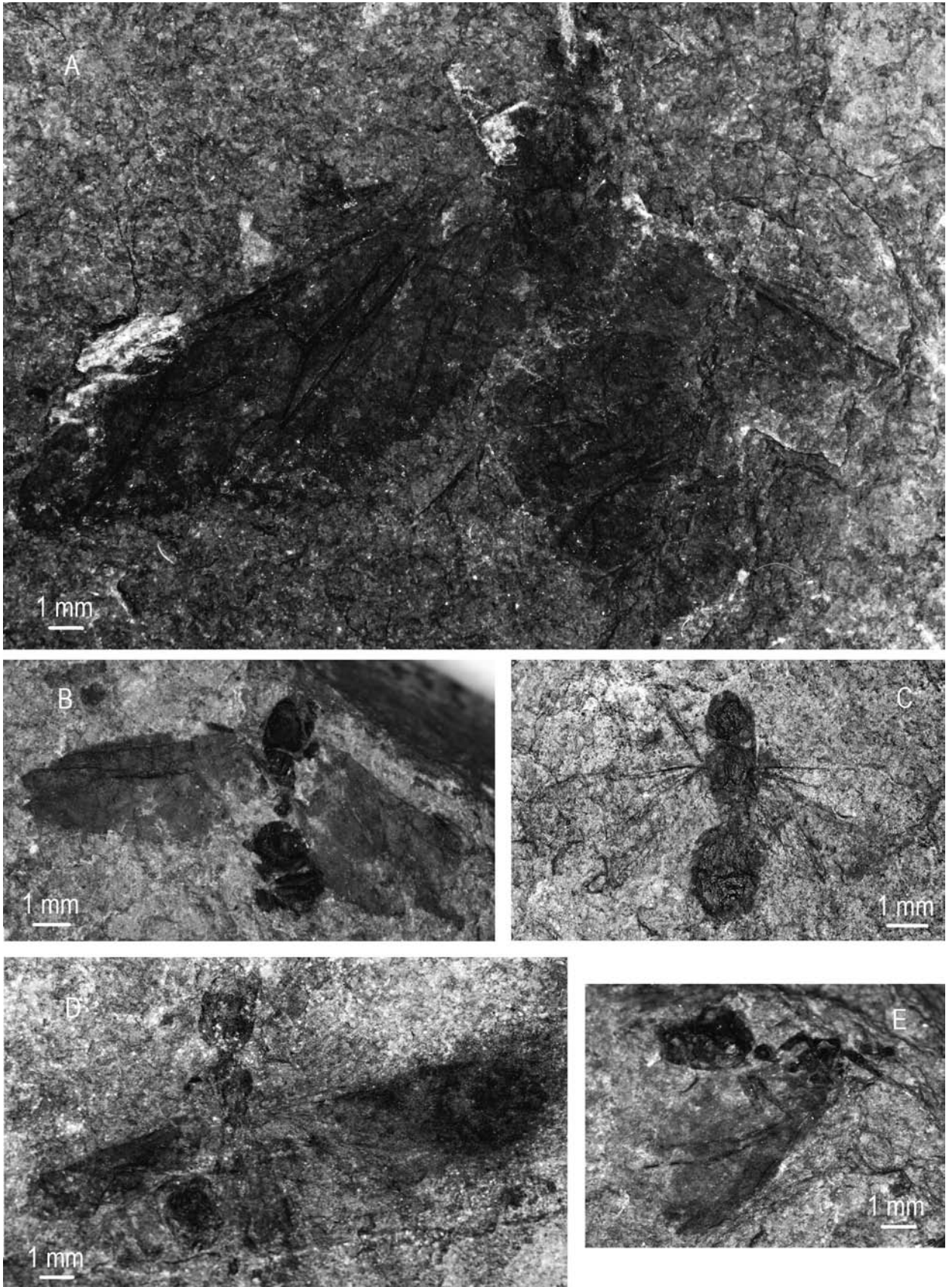


Fig. 18.

Table 1. Composition and proportions of ant species in Radoboj.

Species	Number	Proportion [%]
AMBLYOPONINAE		
* <i>Casaleia longiventris</i> (HEER)	1	0.3
DOLICHODERINAE		
<i>Dolichoderus heeri</i> n. sp.	5	1.6
* <i>Emplastus antiquus</i> (MAYR)	1	0.3
* <i>Emplastus dubius</i> n. sp.	1	0.3
* <i>Emplastus haueri</i> (MAYR)	1	0.3
* <i>Emplastus miocenicus</i> n. sp.	2	0.6
* <i>Emplastus ? ocellus</i> (HEER)	4	1.3
<i>Liometopum imhoffii</i> (HEER)	22	7.1
FORMICINAE		
<i>Attopsis longipennis</i> HEER	1	0.3
<i>Camponotus induratus</i> (HEER)	10	3.2
<i>Formica obscura</i> HEER	4	1.3
<i>Formica parexsecta</i> n. sp.	1	0.3
<i>Formica ungeri</i> HEER	60	19.3
<i>Gesomyrmex breinii</i> (HEER)	1	0.3
<i>Heeridris croaticus</i> n. sp.	2	0.6
<i>Lasius anthracinus</i> (HEER)	24	7.7
<i>Lasius globularis</i> (HEER)	13	4.2
<i>Lasius longaevis</i> (HEER)	33	10.6
<i>Lasius longipennis</i> (HEER)	14	4.5
<i>Lasius occultatus</i> (HEER)	46	14.8
<i>Lasius ophthalmicus</i> (HEER)	25	8.0
<i>Oecophylla obesa</i> (HEER)	23	7.4
MYRMICINAE		
<i>Lonchomyrmex freyeri</i> (HEER)	+	+
* <i>Myrmecites pusillus</i> (HEER)	1	0.3
* <i>Myrmecites latus</i> n. sp.	2	0.6
* <i>Paraphaenogaster jurinei</i> (HEER)	2	0.6
* <i>Paraphaenogaster tertiaria</i> (HEER)	2	0.6
PONERINAE		
* <i>Ponerites atavinus</i> (HEER)	1	0.3
* <i>Ponerites elongatus</i> (HEER)	1	0.3
* <i>Ponerites gracilior</i> n. sp.	1	0.3
* <i>Ponerites nitidus</i> (HEER)	1	0.3
* <i>Ponerites oblongiceps</i> n. sp.	3	1.0
* <i>Ponerites tenuis</i> (HEER)	3	1.0
TOTAL	311	

* species of form genera

described to date (at a modern level) are those of the following fossil sites: Green River Formation, USA, Eocene, Middle Ypresian to Earliest Lutetian, 53.5–48.5 Ma (DLUSSKY & RASNITSYN, 2003); European Baltic, Bitterfeldian, Rovno and Scandinavian ambers, Late Eocene, Priabonian, ca. 37 Ma (review: DLUSSKY & RASNITSYN 2009); Bembridge, Isle of Wight, UK, Late Eocene, Priabonian, ca. 35 Ma (DLUSSKY & PERFILIEVA 2014); Florissant, Colorado, USA, Eocene/Oligocene boundary, ca. 34 Ma (CARPENTER 1930); Stavropol, southern Russia, Middle Miocene, Burdigalian, ca. 16.0–20.4 Ma (DLUSSKY 1981). The rich deposits of the Middle Eocene of Germany from Grube Messel (ca. 47 Ma) and Eckfeld Maar (ca. 44 Ma) have been described only in part (LUTZ 1986; DLUSSKY et al. 2008, 2009; DLUSSKY & WEDMANN 2012). The assemblages described earlier from Oeningen, Austria, Late Miocene (HEER 1849, 1867), Aix-en-Provence, France, Oligocene (THÉOBALD 1937) and Fushun amber, China, Middle Eocene (HONG 2002) require complete revision and cannot be used for comparison at this time.

As shown by earlier studies (DLUSSKY & RASNITSYN 2009), the most adequate results for the comparison of assemblages are the results on the frequency spectra of the subfamilies. Data on the proportions of members of different ant subfamilies in different fossil sites are given in Table 2. We used for comparison Shorygin's index (SHORYGIN 1939), also known as Schoener's overlap index (SCHOENER 1974). It is calculated as the sum of the minimum values of relative abundance across all the species represented in both compared habitats, expressed in percents:

$$PS = \sum \min |P_{ki}, P_{kj}|,$$

where P_{ki} is the proportion of the subfamily k in the total number of specimens in the sample i , P_{kj} is its proportion in the sample j , and $\min |P_{ki}, P_{kj}|$ is the minimum of the two values P .

The assemblage of Radoboj is especially similar at the subfamily level to the assemblage of Bembridge (PS = 0.95). In both Radoboj and Bembridge, Formicinae are dominant (over 80%), the proportion of Dolichoderinae is considerably smaller (9.4% and 13.8%, respectively), and the proportion of Myrmicinae is at most 2%. Strong similarity between these assemblages

Fig. 18. Photographs of fossils of the subfamily Myrmicinae and *Oecophylla obesa* (HEER, 1849). **A, B, E** – *Oecophylla obesa* (HEER, 1849). **A** – lectotype of *Formica obesa radobojana* UMJG&P no. 77.625 (♀); **B** – neotype of *Attopsis anthracina* HEER, 1849, GBA no. 2009/016/0634 (♂); **E** – lectotype of *Attopsis longipes* HEER, 1867, UMJG&P no. 77.561 (♂); **C** – *Myrmecites latus*, sp. nov., holotype NHMW no. 2014/0130/0001 (♀); **D** – *Paraphaenogaster tertiaria* (HEER, 1849), holotype of *Myrmica bicolor* HEER, 1867, UMJG&P no. 77.624 (♀).

Table 2. Proportions of members of different subfamilies of ants in fossil assemblages.

Subfamily	Europa						N. America	
	Baltic amber	Bitterfeld amber	Rovno amber	Bembridge	Radoboj	Stavropol	Green River	Florissant
Amblyoponinae	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Aneuretinae	0.3	0.1	0.0	0.2	0.0	0.0	2.9	0.0
Cerapachyinae	0.1	0.3	0.2	0.0	0.0	0.0	0.0	0.0
Dolichoderinae	63.4	53.9	52.7	13.8	9.4	3.9	71.6	62.6
Ectatomminae	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.0
Formicinae	33.1	37.0	39.5	81.3	84.9	52.6	2.9	32.5
Myrmeciinae	0.1	0.1	0.0	0.0	0.0	0.0	10.8	0.0
Myrmicinae	2.0	5.9	4.7	0.5	2.0	40.8	2.0	4.8
Ponerinae	0.6	0.4	1.0	4.3	3.4	2.6	9.8	0.0
Proceratinae	0.1	0.3	0.3	0.0	0.0	0.0	0.0	0.0
Pseudomyrmecinae	0.3	1.5	1.5	0.0	0.0	0.0	0.0	0.0
Number of specimens examined	11579	679	1155	630	350	76	102	5592

is also found at the generic level. At both sites, members of the genera *Camponotus*, *Dolichoderus* and *Oecophylla*, and form genera *Paraphaenogaster* and *Ponerites* have been recorded, and the majority of ants from Bembridge included in the morphogenus *Leucotaphus* most probably belong to the genus *Lasius*. The principal difference between these assemblages at the generic level is that in Bembridge members of the genus *Oecophylla* are markedly dominant (over 60%, in contrast to 7.4% in Radoboj), and members of the genus *Formica* are absent, while in Radoboj they make up 21.4% of all ant fossils.

The similarity is rather high (PS = 0.61) between the assemblages of Radoboj and Stavropol. At both sites, members of Formicinae are dominant (84.9 and 52.6%, respectively), and members of Dolichoderinae are rare (9.4% and 3.9%, respectively). However, imprints of Myrmicinae make up about 40.8% in Stavropol, in contrast to only 2% in Radoboj. The two assemblages are similar also at the generic level: at both sites fossils of the genera *Camponotus*, *Lasius*, *Liometopum*, and form genera *Paraphaenogaster* and *Ponerites* have been recorded.

The structure of the assemblages of the Late Eocene ambers of Europe considerably differs from those of Bembridge, Radoboj and Stavropol. In these ambers, members of the subfamily Dolichoderinae are dominant (52.7-63.4%), and the proportion of Formicinae is only 33.1-39.5%, determining the relatively low similarity between the assemblages of these ambers

and the assemblage of Radoboj (PS = 0.45 - 0.52). At the same time, these assemblages show signs of continuity. The majority of the genera found in Radoboj are also present in the Late Eocene ambers. It should also be noted that the proportion of extinct genera in the ambers (25 of the 56 recorded genera, or 45%) is markedly higher than in Radoboj, where four of the 15 recorded genera are doubtlessly extinct.

The difference of the assemblage of Radoboj from those of the Middle Eocene deposits of Messel and Eckfeld is even greater. Almost half of the ant fossils known from these deposits are giant members of the genus *Titanomyrma* ARCHIBALD, JOHNSON, MATHEWE & GREENWOOD, 2011, which belongs to the extinct subfamily Formiciinae. Messel is also characterized by a greater diversity and relatively high abundance of poneromorph subfamilies (Amblyoponinae, Ectatomminae and Ponerinae). But, in this case, continuity between the assemblages at the generic level is also clear. Fossil ants found both in the Middle Eocene deposits of Europe and in Radoboj include members of the genera *Casaleia*, *Oecophylla* and *Gesomyrmex*, never recorded in deposits from North America. The similarity of the fossil assemblage of Radoboj with fossil assemblages of North America at the subfamily level is also rather low: PS = 0.44 with Florissant and PS = 0.18 with Green River.

Finally, another peculiar feature of the assemblage of Radoboj should be noted, making it similar to the assemblages of the Late Eocene ambers of Europe and

the assemblage of Bembridge: the simultaneous presence of Palaearctic and tropical elements. In Radoboj, members of the genera *Formica* and *Lasius* are dominant. In the Recent fauna, members of these genera live only in the Palaearctic and Nearctic. At the same time, extant species of the genera *Oecophylla* and *Gesomyrmex* occur exclusively in the tropics. Fossil members of the genus *Oecophylla* were found earlier in Messel, Eckfeld, the Baltic and Bitterfeld ambers, Bembridge, and various Oligocene and Miocene deposits of the Old World (DLUSSKY et al. 2008). Extinct members of *Gesomyrmex* were known earlier from Messel, Eckfeld and the Baltic, Bitterfeld and Rovno ambers (DLUSSKY et al. 2009). Extant members of *Oecophylla* do not survive subzero temperatures; therefore, the records of fossil members of the genus give evidence of a warm climate.

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Addresses of the authors:

GENNADY M. DLUSSKY, Department of Evolution, Biological Faculty, M.V. Lomonosov Moscow State University, Vorobjevy gory, 119992 Moscow, Russia;
e-mail: dlussky@mail.ru

TATYANA S. PUTYATINA, Department of Evolutionary Biology, Biological Faculty, Lomonosov Moscow State University, Vorobjevy gory 1/12, Moscow 119991, Russia;
e-mail: tsergput@gmail.com