



Fossil ants of the genus *Gesomyrmex* Mayr (Hymenoptera, Formicidae) from the Eocene of Europe and remarks on the evolution of arboreal ant communities

GENNADY M. DLUSSKY¹, TORSTEN WAPPLER² & SONJA WEDMANN³

¹Department of Evolution, Biological Faculty, M.V. Lomonosov Moscow State University, Vorobjovy gory, 119992, Moscow, Russia.
E-mail: dlusky@gmail.ru

²Steinmann Institut für Geologie, Mineralogie, Paläontologie, Universität Bonn, Nussallee 8, D-53115 Bonn, Germany.
E-mail: twappler@uni-bonn.de

³Forschungsstation Grube Messel, Forschungsinstitut Senckenberg, Markstraße 35, D-64409 Messel, Germany.
E-mail: sonja.wedmann@senckenberg.de

Abstract

The formicid genus *Gesomyrmex* is reviewed and several new species are described from the middle Eocene (about 47 Ma) of Grube Messel, Germany, and from the middle Eocene (about 43 Ma) of Eckfeld maar, Germany. The new taxa are *Gesomyrmex curiosus* n. sp., *Gesomyrmex breviceps* n. sp., and *Gesomyrmex pulcher* n. sp. from Messel, and *Gesomyrmex flavescens* n. sp., and *Gesomyrmex germanicus* n. sp. from Eckfeld maar. Two previously described Oligocene species must be excluded from *Gesomyrmex*. Former *G. expectans* Théobald, 1937 is transferred to *Eoformica expectans* (Théobald, 1937) (**comb. nov.**), and former *G. miegi* Théobald, 1937 has to be considered as Formicidae incertae sedis (**comb. nov.**). A key to the living and fossil reproductive female caste (gyne) of the genus *Gesomyrmex* is provided. Given the fossil records of *Gesomyrmex hoernesii* Mayr, 1868 from different European amber deposits the presence of this genus in Europe during the Eocene is well established. Both extant and fossil *Gesomyrmex* species have an arboreal mode of life. The comparison of arboreal ant faunas from Eocene to Recent times shows that their community structure apparently changed considerably during this period. We infer that *Gesomyrmex*, along with other genera, was most prosperous during the middle Eocene of Europe, and today has a relict distribution in southern Asia.

Key words: Formicidae, *Gesomyrmex*, Tertiary, Eocene, arboreal ants, community structure

Introduction

Ants (Formicidae, Hymenoptera) are highly eusocial vespoid insects. At present there are recorded 11477 extant and 594 extinct valid species, which have been described in 408 genera (121 extinct) and 28 subfamilies (5 extinct) (Bolton *et al.* 2006). Ants are ecologically important because they play a major role at many levels in an ecosystem, such as predators, scavengers and seed dispersers (Beattie & Hughes 2002; Hölldobler & Wilson 1990).

Gesomyrmex ants are often overlooked arboreal elements of the tropical Asian myrmecofauna. These small, polymorphic formicine ants are native to a variety of forests and montane habitats in the Oriental tropics. *Gesomyrmex* contains six valid extant species, about which little is known. The native range of extant *Gesomyrmex* extends from the highlands of southern Borneo north into western India (Fig. 1). The genus is in the tribe Gesomyrmecini as defined by Bolton (2003) and its closest and only living related genus is *Santschiella* Forel, 1916 from Africa (Congo) with a single known species, *S. kohli* Forel, 1916. The relationships of the Gesomyrmecini with other formicine tribes are far from clear. The oldest literature contains intuitive suggestions about their possible relationship to the subfamily Camponotini, tribe Oecophyllii (Emery 1895, p. 772) or the genus *Santschiella* (Emery 1925, p. 48). The genus *Gesomyrmex* was established by Mayr (1868, p. 50) for a single species obtained from Baltic amber. Extant species were

discovered about 25 years later by André (1892).

The present work is the first comprehensive taxonomic revision of *Gesomyrmex* ants. We rediagnose the genus, clarify species boundaries, describe several new species, and provide descriptions, diagnoses, illustrations, and a key for the gyne caste. The scant information on the arboreal mode of life of *Gesomyrmex* ants is presented and the changing community structure of arboreal ants during the Tertiary is discussed.

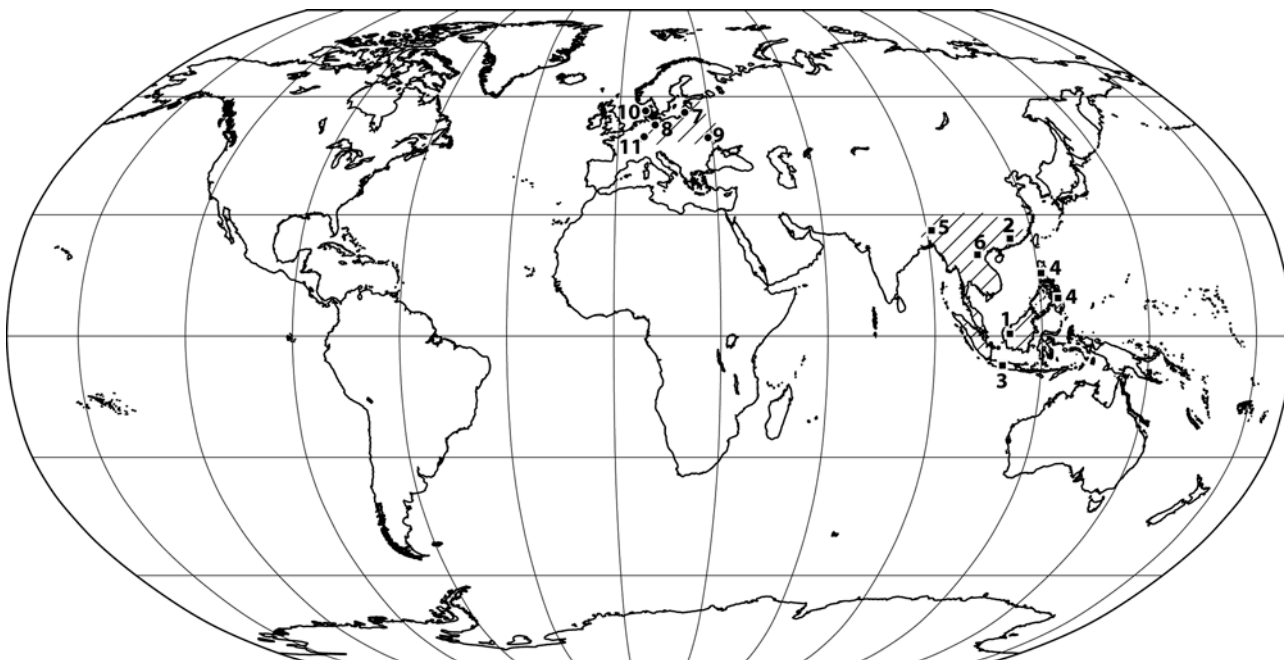


FIGURE 1. Distribution of extant and fossil species of *Gesomyrmex*. 1–6 extant species: 1—*G. chaperi* André, 2—*G. howardi* Wheeler, 3—*G. kalshoveni* Wheeler, 4—*G. luzonensis* (Wheeler), 5—*G. spatulatus* Cole, 6—*G. tobiassi* Dubovikoff; 7–11 fossil species: 7–10—*G. hoernesii* Mayr (7—Baltic amber, 8—Bitterfeldian amber, 9—Rovno amber, 10—Scandinavian amber), 11—Messel and Eckfeld.

Institutional abbreviations

SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany.
GMUG.BST	Amber Collection, Geowissenschaftliches Zentrum der Georg-August-Universität Göttingen, Germany.
PMHU	Humboldt Museum, Berlin, Germany.
MZPW	Museum Ziemi PAN, Warsaw, Poland.
BMNH	Natural History Museum, London, United Kingdom.
NHMM	Naturhistorisches Museum Mainz, Germany.
NMW	Naturhistorisches Museum in Wien, Austria.
PIN	Paleontological institute RAS, Moscow, Russia.
SIZK	Schmalhausen Institute of Zoology, Kiev, Ukraine.
ZMUC	Zoological Museum of University Copenhagen, Denmark.
CGC	personal collection of Mr. Carsten Gröhn, Glinde, Germany.
MKC	personal collection of Mr. Manfred Kutscher, Sassnitz, Rügen, Germany.

Material and methods

The fossil ants from Messel are housed in the collection of the Messelforschung department of the SMF. The ants from Eckfeld are deposited at the Landessammlung für Naturkunde Rheinland-Pfalz in the NHMM. The

slabs with the fossils are stored permanently in glycerin to prevent damage by desiccation.

The fossil specimens were photographed using a digital camera, and enlarged prints were hand traced by pen. The resultant drawing was scanned and improved using standard graphics software. In the line drawings, full lines indicate visible sclerite boundaries, dashed lines indicate supposed sclerite boundaries, and dotted lines indicate visible margins of incomplete sclerites. The preserved, even if chemically modified, original sclerites of impressions are marked grey.

Usually, natural coloration of fossil insects is changed both in impressions and amber inclusions. In the deposits of Grube Messel and Eckfeld insect coloration often reflects the former colour pattern. That is why we describe the coloration of the ants from these deposits.

Ant impression fossils are significantly deformed. Consequentially, the calculated measurements and their ratios are more variable than what is typical for three-dimensionally preserved ants. Some measurements are less affected by deformation than the others, e.g., the length of the mesosoma in comparison to its width and height.

The measurements are referred to as follows:

AL	mesosoma (alitrunk) length from junction with head to that with petiole;
AW	mesosoma (alitrunk) width;
BL	total body length;
ED	maximum eye diameter;
FWL	fore wing length;
HL	head length without mandibles;
HW	maximum head width without eyes;
MdL	mandible length;
PtL	petiole length;
PtW	maximum petiole width;
SL	scape length.

Nomenclature of the wing venation follows Dlussky & Rasnitsyn (2003). Other terminology of ant morphology is after Bolton (1994).

Geological setting. The investigated material originates from very different types of deposits. On the one hand there are the Messel Pit and the Eckfeld maar, which both are sedimentary deposits which originated in former maar lakes. On the other hand there are inclusions from different European amber deposits.

Lacustrine deposits. The Fossilagerstätte Grube Messel is located near the town of Darmstadt in Hesse, Germany. It is a former maar lake that was created by explosive volcanic activity (Schulz *et al.* 2002; Felder & Harms 2004) at approximately 47 Ma (Mertz *et al.* 2004; Mertz & Renne 2005) in the middle Eocene. The Messel Pit fossil site is famous for the extraordinary preservation of its fossils (e.g. Schaal & Ziegler 1992; Koenigswald & Storch 1998). Ongoing excavations have yielded a multitude of insect fossils which allow unique insights into the highly diverse palaeoecosystem of Messel and which comprise a very diverse fauna (e.g. Lutz 1990; Tröster 1991, 1993; Richter & Baszio 2001; Richter & Wedmann 2005; Wappler & Engel 2003, 2006; Wedmann 2005; Wedmann *et al.* 2007; Wedmann & Yeates 2008).

The Eckfeld Maar is located at the lower reaches of the Pellenbach, approximately 2 km NW of Eckfeld near Manderscheid (Eifel, Germany). This former volcanic crater was filled by a freshwater lake with an original diameter of 900 m and a depth exceeding 110 m (Pirrung *et al.* 2001). $^{40}\text{Ar}/^{39}\text{Ar}$ dating of basalt from the diatreme breccia underlying the lake sediments indicates an age of 44.3 ± 0.4 Ma for Eckfeld (Mertz *et al.* 2000). Up to now more than 30,000 macrofossils have been excavated from the Eckfeld maar, documenting a highly diverse terrestrial flora and fauna (e.g., Neuffer *et al.* 1996; Lutz *et al.* 1998; Lutz & Neuffer 2000; Wappler 2003; Wappler & Andersen 2004; Wappler & Engel 2003, 2006, Wappler *et al.* 2004; Wappler & Ben-Dov 2008; Wilde & Frankenhäuser 1998). These fossils, accurately recovered with their precise stratigraphic position, permit a correlation between facies and the composition of their fossil contents (e.g.

Lutz & Kaulfuß 2006; Wappler 2003). With respect to the insect taphocoenosis it must be mentioned that approximately 84% of all specimens recovered are beetles (Coleoptera) (e.g. Lutz 1993; Wappler 2003).

Amber deposits. Baltic amber with its famous insect inclusions originated mainly from Yantarny (former Samland) in the Kaliningrad region of Russia. The former Baltic amber forest presumably was located in Fennoscandia and adjacent regions. Rivers transported large amounts of resin to the Baltic coast where the marine clay deposit with its high content of amber was formed, the so-called Blue Earth (e.g. Weitschat & Wichard 1998). During the Pleistocene parts of the Blue Earth were incorporated into glacial boulder clay, and the result is that nowadays amber can be found mainly on the coastline of both the Baltic Sea and the North Sea (Weitschat & Wichard 1998). So-called Scandinavian amber, which was found on the shore line of Scandinavia, is also part of this same deposit. The sediments containing the majority of Baltic amber in the Kaliningrad region have been dated as 47 to 38 Ma, that is, middle to late Eocene (Ritzkowski 1997).

The Bitterfeld (or Saxonian) amber was found near the small town Bitterfeld, Saxony-Anhalt, Germany. Presently there is a discussion on both origin and age of the Bitterfeld amber. Bitterfeld amber may be, in essence, Baltic amber, which was eroded and redeposited in younger sediments (e.g. Weitschat 1997; Röschmann 1997; Hoffeins & Hoffeins 2003). On the other hand some authors emphasize the independent origin of the Bitterfeld amber (e.g. Barthel & Hetzer 1982; Knuth *et al.* 2002; Fuhrmann 2005). In this study we follow the former assumption that Bitterfeld and Baltic amber are contemporaneous.

Rovno amber was collected in the north of the Rovno and Zhitomir regions in the Ukraine. The amber is chemically identical to Baltic amber (Perkovsky *et al.* 2003). It was found in deposits whose age ranges from late middle Eocene to the Oligocene, with abundant occurrence in late Eocene and lower Oligocene sediments. Palaeogeographic and palaeosedimentary analyses suggest that the amber is autochthonous (Perkovsky *et al.* 2003). A comparison of the rich arthropod fauna of the Rovno with the fauna in Baltic amber is given by Perkovsky *et al.* (2007) who conclude that the observed differences point to independent origins of their faunas.

Dlussky & Rasnitsyn (in press) studied over 5500 ant inclusions in 12 European collections of the Baltic, Bitterfeld, Rovno and Scandinavian ambers, and fossils of the family are now affecting our understanding of the modern diversity and ecology of ants in significant ways (Dlussky & Rasnitsyn in press). It became apparent during this study that 17 ant species, including *Gesomyrmex hoernesii*, were dominant in all these ambers (these 17 species correspond to 9.8% of the known fossil ant species in these amber types). The same 17 species were prevalent in all studied collections: 93–94% of all inclusions in Baltic amber, 89% in Bitterfeldian amber, and 85% in Rovno and Scandinavian ambers. This consistency of species composition probably indicates that all these ambers have about the same age. However, investigations on the taxonomic composition and the quantitative relationships of all ant species in representative collections showed that there are appreciable differences among all four ambers. The differences found are probably of ecological and not of geochronological nature. The Baltic and Bitterfeld ant assemblages are most similar; the Scandinavian assemblage is the most deviant, and the Rovno amber assemblage is intermediate.

Synopsis of extant and extinct species of *Gesomyrmex*

breviceps Dlussky, Wappler & Wedmann **sp. nov.**; extinct, Middle Eocene, Germany.

chaperi Andre, 1892; extant, Borneo.

= *janeti* Andre, 1892 [synonymy by Wheeler, 1929]

curiosus Dlussky, Wappler & Wedmann **sp. nov.**; extinct, Middle Eocene, Germany.

flavescens Dlussky, Wappler & Wedmann **sp. nov.**; extinct, Middle Eocene, Germany.

hoernesii Mayr, 1868; extinct, Late Eocene, Baltic amber.

= *annectens* Wheeler, 1915 [synonymy by Wheeler, 1929]

= *mayri* (Wheeler, 1915) [synonymy by Wheeler, 1929]

= *theryi* (Emery, 1905) [synonymy by Wheeler, 1929]

howardi Wheeler, 1921; extant, China

germanicus Dlussky, Wappler & Wedmann **sp. nov.**; extinct, Middle Eocene, Germany
kalshoveni kalshoveni Wheeler, 1929; extant, Java
kalshoveni gracilis Hamann, 1957, extant, Java
luzonensis (Wheeler, 1916); extant, Philippines
= *chapmani* Wheeler, 1930 [synonymy by Brown, 1950]
pulcher Dlussky, Wappler & Wedmann **sp. nov.**; extinct, Middle Eocene, Germany
tobiasi Dubovikoff; 2004; extant, Vietnam.

Species excluded from *Gesomyrmex*

Eoformica expectans Théobald, 1937 **comb. nov.**
Formicidae (*incertae sedis*) *miegi* Théobald, 1937 **comb. nov.**

Systematic Section

Family Formicidae Latreille, 1809

Subfamily Formicinae Latreille, 1809

Tribe Gesomyrmecini Ashmead, 1905

Diagnosis (from Bolton 2003). With characters of Formicinae. Palp formula 6,4. Mandible with 6 – 10 teeth. Eye large to enormous; long axes of eyes convergent anteriorly. Scape, when laid back in its normal resting position, passes below the eye. Antennal insertions migrated laterally and widely separated, in line with long axis of eye and in front of anterior margin of eye. Clypeus extends back between antennal sockets, the latter close to or abutting the posterior clypeal margin. Propodeal spiracle circular. Metacoxae closely approximated. Petiolar foramen short. Ventral margin of petiole V-shaped in section. Abdominal sternite III (first gastral) with a transverse sulcus across the sclerite posterior to the helcium sternite. Antenna with 8, 10, 11 or 12 segments.

Genera included: *Gesomyrmex* Mayr, 1868; *Santschiella* Forel, 1916; *Sicilomyrmex* Wheeler, 1915 (extinct); *Prodimorphomyrmex* Wheeler, 1915 (extinct).

Genus *Gesomyrmex* Mayr, 1868

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

Diagnosis. Worker caste polymorphic. Eyes enormously large in workers and males. Antennae geniculate, 8-segmented in worker, 10-segmented in gyne and 8–11-segmented in male. Mandible in worker and gyne with 5–10 acute teeth; mandibles in male reduced, not opposable. Posterolateral corners of the head and propodeum without spines. Fore wings with closed cells 1+2r, 3r and m_{cu}.

Species numbers and distribution. Six extant species are known which are distributed in the Oriental tropics (Fig. 1). Three fossil species were described: *Gesomyrmex hoernesii* Mayr, 1868 (Baltic amber, late Eocene), *G. expectans* Théobald, 1937 (Kleinkembs, France, Oligocene) and *G. miegi* Théobald, 1937 (Haut-Rhin, France, Oligocene). The last two fossil species must be excluded from *Gesomyrmex* (*vide infra*). Five new species from middle Eocene deposits of Germany are described below.

Comments. Mayr (1868) described the genus *Gesomyrmex* with the unique species *G. hoernesii* from Baltic amber from 19 workers and one male. A quarter of a century later André (1892) described two new extant species from Borneo. One of them was similar to fossil *G. hoernesii*, and he described it as *Gesomyrmex chaperi*. The second species differed by its large size, a more elongate head and smaller eyes, and he

described it as *Dimorphomyrmex janeti*. Emery (1905) found in Baltic amber a specimen similar to *D. janeti* and described it as *Dimorphomyrmex theryi*. Finally Wheeler (1915) re-described *G. hoernesii* and *D. theryi* and described two new species from Baltic amber: *Gesomyrmex annectens* and *Dimorphomyrmex mayri*.

Some years later Wheeler (1929) received 18 workers, collected by L.G.K. Kalshoven in Java. All these ants were collected from the same nest, so, naturally, they belonged to the same species described as *Gesomyrmex kalshoveni* Wheeler. Workers from the same colony were very polymorphic. Large, medium and small workers differed by the form of the head, eye size, and mandible form. Moreover large (major) workers had characters of *Dimorphomyrmex*, and small (minor) and medium workers those of *Gesomyrmex*. As a result Wheeler designated *Dimorphomyrmex* as junior synonym of *Gesomyrmex*, and concluded that both species of *Dimorphomyrmex* and both species of *Gesomyrmex*, described from Baltic amber, really belong to one polymorphic species *Gesomyrmex hoernesii* Mayr.

Most extant species of *Gesomyrmex* are known only from the worker caste. A revision of the genus and key for determination of workers was published by Cole (1949). Only three sexuals are known: a winged gyne and a male of *G. luzonensis* (Wheeler 1916, 1930) and a wingless gyne of *G. tobiasi* (Dubovikoff 2004). The last species is known only from this gyne.

***Gesomyrmex hoernesii* Mayr, 1868**

(Fig. 2 and Fig. 6A–E)

Gesomyrmex hörnesii Mayr, 1868, p. 52, tab. II, fig. 38–41 (worker and male); Ern. André, 1895, p. 82; Handlirsch, 1907, p. 859.

Gesomyrmex hörnesii Mayr: Dalla Torre, 1893, p. 176 (misspelling).

Gesomyrmex hoernesii Mayr: Wheeler, 1915, p. 108–111, fig. 53; Wheeler, 1929, p. 11; Burnham, 1978, p.114; Ponomarenko, Schultz, 1988, p. 26; Bolton, 1995, p. 207; Dlussky, 1997, p. 59, fig. 3h.

Dimorphomyrmex theryi Emery, 1905, p. 188, fig. 1 (worker); Handlirsch, 1907, p. 868; Wheeler, 1915, p. 104–106, fig. 50; Burnham, 1978, p.113. Synonymy by Wheeler, 1929, p. 11.

Dimorphomyrmex mayri Wheeler, 1915, p. 106–107, fig. 51 (worker); Burnham, 1978, p.113. Synonymy by Wheeler, 1929, p. 11.

Gesomyrmex annectens Wheeler, 1915, p. 107–108, fig. 52 (worker); Burnham, 1978, p.113. Synonymy by Wheeler, 1929, p. 11.

Types. Mayr (1868) described *G. hoernesii* from 18 workers and a male. Three workers are preserved in NMW (1984/34/141, 1984/34/142 and 1984/34/143). A lectotype was not designated. The holotype of *Dimorphomyrmex theryi* is present at the collection of BMNH (In.29052). The types of *Gesomyrmex annectens* and *Dimorphomyrmex mayri* are lost.

Studied material. **Baltic amber** (workers). BMNH.In.17787 with label “Samland”; BMNH.In.29052 with label “Coll. A. Thery, holotype of *Dimorphomyrmex theryi* Emery”; GMUG.BST.03830 (K2614) determined by Wheeler (1929) as *G. hoernesii*; GMUG.BST.03840 (K2626); GMUG.BST.03977 (α 228, K4302); GMUG.BST.03993 (K4048); GMUG.BST.04076 (K6406); GMUG.BST.04088 (α 181, K4311); GMUG.BST.04097 (\times 10); GMUG.BST.04151 (K4442) determined by Wheeler as *D. theryi*; GMUG.BST.04152 (K4252) determined by Wheeler as *D. theryi*, pictured on fig. 50 in Wheeler (1915); GMUG.BST.04157 (K779) determined by Wheeler as *D. theryi*; GMUG.BST.04200 (α 124) determined by Wheeler as *G. hoernesii*; GMUG.BST.04206 (α 119) determined by Wheeler as *G. hoernesii*; GMUG.BST.04207 (K889) determined by Wheeler as *G. hoernesii*; GMUG.BST.04208 (α 111) determined by Wheeler as *G. hoernesii*; GMUG.BST.04213 (K4466) determined by Wheeler as *G. hoernesii*; GMUG.BST.04214 (α 95) determined by Wheeler as *G. hoernesii*; GMUG.BST.04438 (K6421) determined by Wheeler as *D. theryi*; GMUG.BST.04456 (α 204) determined by Wheeler as *G. hoernesii*; GMUG.BST.04457 (α 171) determined by Wheeler as *G. hoernesii*; MZPW.412; MZPW.2940; MZPW.5864; MZPW.5890; MZPW.8126; MZPW.9561; MZPW.10353; MZPW.15933; MZPW.15980; MZPW.19144; MZPW.19377; MZPW.19959; PIN.964/484; PIN.964/485; PIN964/486; CGC.1632; CGC.2652; CGC.3338. **Bitterfeld amber.** PMHU.7/201 (worker);

HM.7/229 (♀); PMHU.10/225 (worker); PMHU.11/221 (worker); PMHU.13/206 (worker); PMHU.13/210 (worker); PMHU.13/221 (worker); PMHU.15/205 (worker); PMHU.16/227; MKC.F-010 (♂); MKC.F-129 (worker); MKC.F-130 (worker). **Rovno amber** (workers). SIZK.K-419; SIZK.K-5695. **Scandinavian amber** (workers). ZMUC.187 with label “G. Henningsen, 01.07.1966”; ZMUC.188 with label “G.V. Henningsen, 01.02.1969”; ZMUC.189 with label “G.V. Henningsen, 03.05.1960”; ZMUC.190 with label “A. K. Andersen, 28.03.1968”.

Description. Minor worker. BL 2.5–5 mm. Body slender. Head longer than broad, subtrapezoid, narrower in the front than in the back, with convex sides, rounded posterior corners and feebly concave posterior border. Eyes very large, convex, reniform; long axes of eyes distinctive convergent anteriorly. Maximum eye diameter 1.8–2.0 times less than head length and 1.05–1.8 times less than head width. Cheeks very short. Ocelli small but distinct. Frontal area and frontal groove obsolete. Clypeus as long as broad or a little longer than broad. Anterior clypeal margin projecting as a long, rather narrowly rounded lobe over the bases of the mandibles. Antenna short, 8-jointed. Scape does not reach the posterior margin of the eye. Funiculus incrassate, but without distinct club. First funicular joint more than twice as long than thick. The following joints longer than thick. Mandibles very long, decussating when closed, with 9 long, acute teeth, some of which are slightly shorter than the others. External margin of mandible concave in middle part. Maxillary palps do not reach the occipital foramen. Mesosoma long, narrower than the head, constricted in the mesopropodeal region. Pronotum gradually convex, longer than broad. Mesonotum rather flat above, the latter compressed laterally, longer than broad, narrower behind than in front and impressed, but without a suture that divides it from the metanotum. In lateral view propodeal dorsum and declivity are subequal and form a rounded obtuse angle; propodeal dorsum feebly convex, propodeal declivity slightly concave. Legs rather slender. Middle and hind tibiae each with one short simple spur. Petiole as long as broad, with low and thick scale, a little more than twice as broad as long, rounded above, with convex anterior and posterior surfaces. Gaster elongate elliptical, with a circlet of coarse anal cilia. Body rather shiny and lightly shagreened. Mandibles, clypeus and frons usually delicately longitudinally striated. Erect hairs absent on all parts of the body except the top of the gaster. Decumbent pubescence absent.

Major worker (soldier). BL 5–8 mm. Head a little longer than broad, subrectangular, a little narrower in the front than in the back, with straight sides, rounded posterior corners and straight or feebly concave posterior border. Eyes large and convex, elongate elliptical or slightly reniform, situated near the middle of the sides, slightly more approximated in the front than in the back. Maximum eye diameter 2–3 times less than head length and 1.8–3.5 times less than head width. Ocelli usually lacking. Frontal carinae short but prominent, extending to the middle of the anterior orbits. Frontal area small and indistinct. Clypeus broader than long, its posterior border extending back medially between the frontal carinae. Anterior clypeal border projecting in the form of a short broad rounded lobe. Antenna short 8-jointed. Scape not reaching to the posterior orbits. Funiculus incrassated but without distinct clava; joints 1 and 2 of the funiculi subequal, about twice as long as thick, joints 3 and 4 about 1.5 times as long as thick, 5 and 6 scarcely longer than thick, the terminal joint a little longer than thick. Mandibles stout, not decussating when closed, with convex external margin and 8 to 9-toothed masticatory margin. The teeth are stout; the apical tooth is longest; shorter teeth are alternating with the longer ones towards the base. Maxillary palps short, do not reach the occipital foramen. Mesosoma long, narrower than the head, constricted in the mesopropodeal region. Pronotum gradually convex, about as long as broad. Mesonotum longer than broad and broader in front than behind; laterally its surface is straight and gradually sloping backward, its sides compressed. Metanotum distinct, short and transverse, divided from mesonotum and propodeum by sutures or impressions. In lateral view propodeal dorsum and declivity are subequal and form a rounded obtuse angle; propodeal dorsum feebly convex, propodeal declivity slightly concave. Legs long and rather stout, middle and hind tibiae with short simple spurs. Petiole short, with a low and thick scale. Gaster elongate oval. Body rather shiny and lightly shagreened. Mandibles, clypeus and frons sharply and densely longitudinally striated. Erect hairs absent on all parts of the body except the top of the gaster. Decumbent pubescence absent.

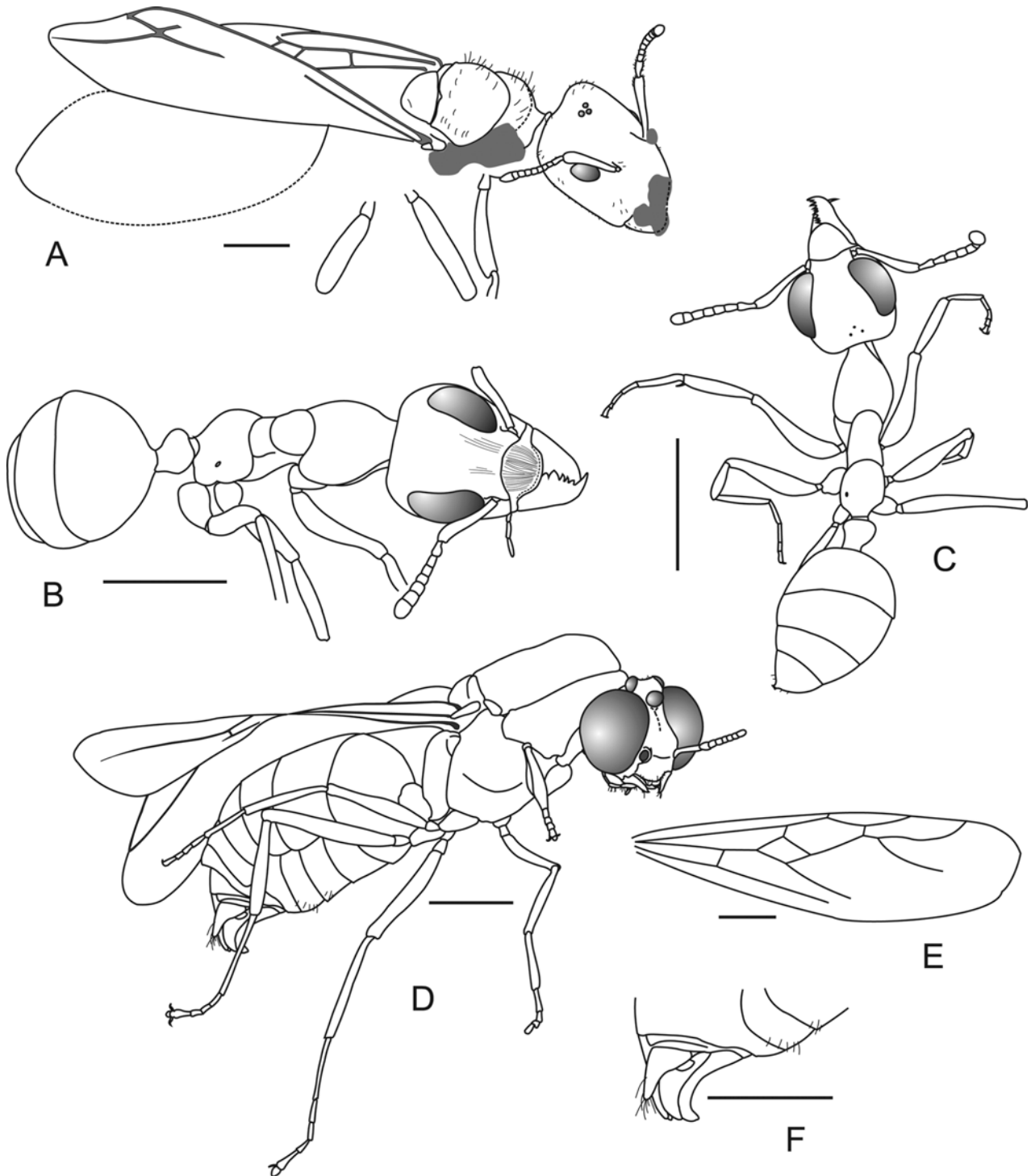


FIGURE 2. *Gesomyrmex hoernesii* Mayr. (A) gyne PMHU.7/229. (B) major worker SIZK.K-419. (C) minor worker GMUG.BST. 04207; (D–F) male MKC.F-010: (D) general view of inclusion, (E) fore wing, (F) genitals. Scale bars = 1 mm.

Gyne (first description). BL 10.5 mm. Head subrectangular, about 1.3 times longer than wide, with rounded posterolateral corners and feebly concave posterior margin. Eyes comparatively smaller than in workers: maximum eye diameter less than 4 times head length. Ocelli large, distance between central and lateral ocelli equals roughly their diameters. Anterior clypeal margin and dentition of mandibles not visible. Antenna 10-jointed. Scape does not reach the posterior margin. Funiculus incrassate, but without distinct club. First funicular joint longer than 2 and 3 together and 2.5 times longer than thick. Following joints except

terminal about as long as thick. Scutum and scutellum wider than long. Gaster, petiole and propodeum covered by white film and not visible. Head and mesosoma with numerous short erect hairs. Legs without erect and semi-erect hairs.

Male. BL 7–8 mm. Head with enormous large convex eyes, which occupy most of the head. Ocelli large and convex. Frontal carinae and lobes absent. Frontal furrow distinct. Anterior clypeal margin projecting as a rounded lobe. Antenna geniculate, small. Mayr (1868) wrote that it is 11-jointed but the studied specimen has only one antenna with 8 joints; perhaps the terminal joints were lost. Mandibles short, not opposable, with an acute apical tooth and without teeth on the masticatory margin. Maxillary palps long, reach the occipital foramen. Pronotum transverse. Scutum with flat dorsal surface strongly rounded anteriorly. Scutellum convex. Propodeal dorsum and declivity form rounded obtuse angle in lateral view; propodeal dorsum much shorter than declivity. Legs rather long and thin. Petiole with rounded scale, higher than long. Gaster cylindrical. Genitalia not retractile.

Body shiny with very delicate shagreened sculpture. Short erect hairs present on mandibles, clypeus, near ocelli, on the last sternites of the gaster, and genital parts. Decumbent pubescence absent.

Forewing with closed cells 1+2r, 3r and mcu. Cell mcu rhomboidal. Veins RS and M partly united and form short section RS+M.

Measurements (in mm). Minor workers. CGC.1632: BL 5.0, AL 1.7, HL 1.2, MdL 0.64, ED 0.61, SL 0.58; CGC.3338: BL 2.3, AL 0.73, HL 0.60, MdL 0.32, ED 0.31, SL 0.30; GMUG.BST.03840: BL 4.7, AL 1.5, HL 1.0, ED 0.52, PtL 0.35, PtH 0.41; GMUG.BST.04206: BL 4.4, AL 1.5, HL 1.0; GMUG.BST.04207: BL 3.9, AL 1.3, HL 0.95, HW 0.68, MdL 0.50, ED 0.50, SL 0.52; GMUG.BST. 04208: BL 4.1, AL 1.35, HL 1.05, HW 0.75, MdL 0.50, ED 0.58, SL 0.48; GMUG.BST.04213: BL 5.0, AL 1.5; GMUG.BST.04214: BL 4.35, AL 1.4, HL 1.1, ED 0.58; GMUG.BST.04456: BL 4.8, AL 1.55, HL 1.1, HW 0.8, ED 0.58, SL 0.55; PIN.964/484: HL 0.99, HW 0.56, MdL 0.53, ED 0.53, SL 0.51; PIN.964/485: BL 5.5, AL 1.75, HL 1.2, HW 1.1, ED 0.61, SL 0.64, PtL 0.35, PtW 0.45, PtH 0.48; PIN.964/486: BL 5.5, AL 1.75. **Major workers.** GMUG.BST.04151: BL 5.7; GMUG.BST.04152: BL 5.8, AL 1.7, HL 1.4, HW 1.3, MdL 0.57, ED 0.47, SL 0.53; GMUG.BST.04157: BL 5.3, AL 1.9; PMHU.13/221: BL 5.3; BMNH.In.29052: BL 5.5, AL 1.75, HL 1.25, HW 1.25, ED 0.53, SL 0.50; SIZK.K-419: AL ~1.8, HL 1.2, HW 1.1, ED 0.62, SL 0.58. **Gyne.** PMHU.7/229: BL 10.5, AL ~3, HL 2.2, HW ~1.6, ED 0.46, SL 0.92, FWL 6.5. **Male.** MKC.F-010: BL about 7, AL 3.0, HL 1.3, MdL 0.36, ED 1.01, SL 0.34, FWL 6.8.

Distribution and horizon. Baltic, Bitterfeld, Rovno and Scandinavian ambers. Late Eocene.

Comments. There is a problem with the association of different castes of fossil ant species as findings of males, females and workers of the same species in the same piece of amber are extremely rare. However we are confident that workers, male and female of *Gesomyrmex* described above belong to the same species. Up to the present 231 workers of *Gesomyrmex* from Baltic and similar ambers are studied: 18 by Mayr (1868), 7 by André (1895), one by Emery (1905), 172 by Wheeler (1915) and 33 (excluding species determined by Wheeler) by one of us (GMD). All these specimens belong to the same species *G. hoernesii*. So there is a high possibility that the two studied males (one by Mayr, and one by us) and above described gyne belong to the same species. The gyne has small eyes relative to those of the workers. This is unusual for ants, but *Gesomyrmex* is evidently an exception to the rule. The only extant species whose workers and gynes are known is *G. luzonensis* (Wheeler, 1916, 1930). Its gynes have comparatively smaller eyes than workers.

Théobald (1937, p. 212) described *Gesomyrmex hoernesii* from Oligocene deposits of France (Kleinkembs, Haut-Rhin). Judged by the description and figures the described insects are really ants but they do not belong to *Gesomyrmex*. The male (Théobald 1937, pl. XIV, fig. 24) has a low nodiform petiole and filiform (not geniculate) antenna with a very short scape, and evidently belongs to Dolichoderinae. One of two specimens described as gynes (Théobald 1937, pl. XIV, fig. 25) has a rounded head and triangulate petiole without a scale. The form of the head of the other «gyne» (Théobald 1937, pl. XIV, fig. 26) is similar to *Formica* or *Camponotus*, but not to *Gesomyrmex*. This specimen also has a small and narrow petiole without a scale. Specimens described as workers (Théobald 1937, pl. XIV, figs. 27, 28) judged by the construction of mesosoma really are poorly preserved gynes without wings. They also have no characters of *Gesomyrmex*.

***Gesomyrmex germanicus* sp. nov.**

(Fig. 3A and Fig. 6I)

Derivation of the name. The species name is derived from the country of origin (Germany).

Holotype. NHMM PE-1997/29 (♀). **Paratype:** NHMM PE-1998/13 (♀). **Other specimens** (♀♀): NHMM PE-1998/1, PE-1998/9.

Type locality and horizon. Eckfeld, Germany. Middle Eocene, ca. 44 Ma (Mertz *et al.* 2000).

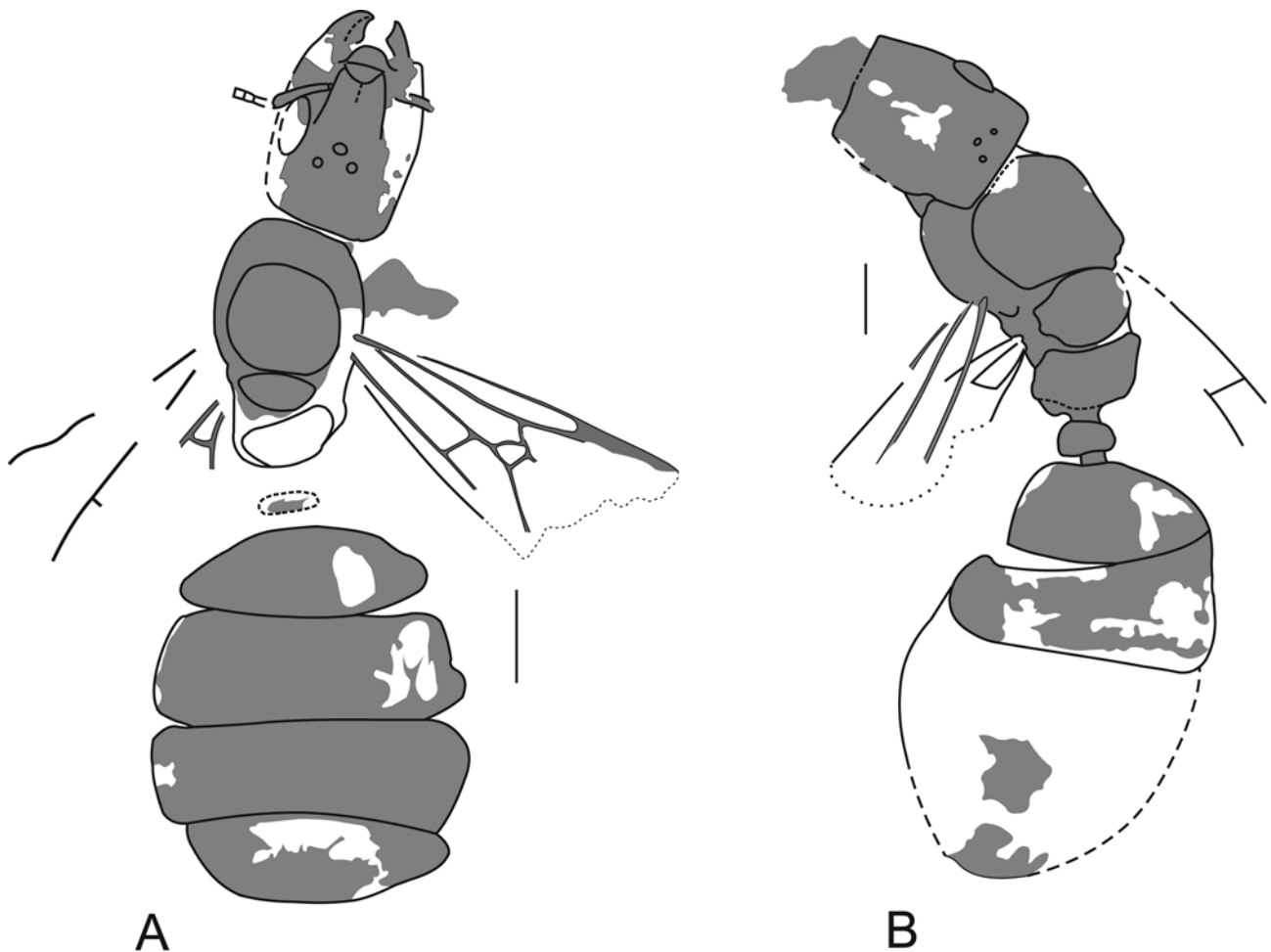


FIGURE 3. *Gesomyrmex* species from Eckfeld maar. (A) *G. germanicus* sp. nov., gyna, holotype PE-1997/29. (B) *G. flavescens* sp. n., gyna, holotype PE-2000/14. Scale bars = 1 mm.

Description. Gyna. BL 9–10 mm. Head subrectangular, about 1.3 times longer than wide, with feebly convex sides and posterior margin and rounded posterolateral corners. Anterior clypeal margin projected as small rounded lobe. Frontal carinae divergent. Eyes ovate, comparatively large: head about 3 times longer than maximum eye diameter. Ocelli large, distance between them a little more than their diameter. Scape does not reach posterior margin of eye, head 3 to 3.5 times longer than scape. Mandibles triangular with an acute apical tooth and some blunt teeth on the masticatory margin. Mesosoma about as wide as head. Scutum about as long as wide. Scutellum transverse. Forewing with very small trapezoid cell *mcu*. Whole body black. Wings colorless with dark veins and pterostigma.

Measurements (in mm). Holotype PE-1997/29: BL 9.7, AL 2.6, HL 2.0, HW 1.5, SL 0.61, ED 0.65; paratype PE-1998/13: BL 9.4, AL 2.7, HL 1.8, SL 0.60; specimen PE-1998/1: HL 1.75, specimen PE-1998/9: BL 9.0, AL 2.35, HL 1.5.

***Gesomyrmex flavescens* sp. nov.**

(Fig. 3B and Fig. 6J)

Derivation of the name. *Flavescens* is Latin for yellowish.

Holotype. NHMM PE-2000/14 (♀).

Type locality and horizon. Eckfeld, Germany. Middle Eocene, ca. 44 Ma (Mertz *et al.* 2000).

Description. Gyne. BL about 13 mm. Head subrectangular, 1.2 times longer than wide, with nearly parallel sides, sharp posterolateral corners and straight posterior margin. Anterior margin of the clypeus straight. Head 3.5 times longer than maximum eye diameter. Ocelli moderate large, distance between them some times greater than their diameter. Mesosoma a little wider than head. Scutum about as long as wide. Petiole with thick scale, longer than wide. Wing venation not preserved. Posterior part of the head, mesosoma, petiole and base of first gastral segment yellowish brown, anterior part of head and gaster varying from black to dark brown. Wings colorless with brown veins and pterostigma.

Measurements (in mm). Holotype PE-2000/14: AL 4.0, HL 2.4, HW 2.0, ED 0.65.

***Gesomyrmex pulcher* sp. nov.**

(Fig. 4A and Fig. 6G)

Derivation of the name. *Pulcher* is Latin for beautiful.

Holotype: SMF MeI 10999 (♀).

Type locality and horizon. Grube Messel, Hesse, Germany. Messel formation, Middle Eocene, ca. 47 Ma (Mertz & Renne 2005).

Description. Gyne. BL 4.8 mm. Head 1.3 times longer than wide, with parallel sides and distinctively concave posterior margin. Clypeus longitudinally striated. Anterior clypeal margin projected as rounded lobe. Eyes large, ovate, head 2.6 times longer than maximum eye diameter. Antenna 10-segmented. Scape reaches the middle of eye; head 3.5 times longer than scape. Funicular joints about as long as thick, or shorter than thick. Mandible triangular with 4 massive blunt teeth. Mesosoma narrower than head. Scutum a little wider than long. Scutellum 1.5 times wider than long. Head and most part of mesosoma yellowish brown, mandibles, central part of scutum, whole scutellum and median parts of gastral tergites dark brown. Legs yellow.

Measurements (in mm). Holotype MeI 10999: AL 1.35, HL 0.95, HW 0.76, SL 0.28, ED 0.37.

***Gesomyrmex breviceps* sp. nov.**

(Fig. 4B and Fig. 6F)

Derivation of the name. *Breviceps* is the Latin expression for “with a short head”.

Holotype. SMF MeI 2305 (♀). **Paratypes** (♀♀). SMF MeI 11054, MeI 13151.

Type locality and horizon. Grube Messel, Hesse, Germany. Messel formation, middle Eocene, ca. 47 Ma (Mertz & Renne 2005).

Description. Gyne. BL 7–9 mm. Head subrectangular, about 1.1 times longer than wide, with feebly concave posterior margin and rounded posterolateral corners. Anterior clypeal margin projected as rounded lobe. Eyes ovate, comparatively small. Head about 3.5 times longer than maximum eye diameter and scape length. Funicular joints shorter than thick. Mandible massive, triangulate. Forewing with closed cells *I+2r*, *3r*, and *mcu*. Cell *mcu* rhomboidal. Vein sections *RS* and *M* with joint start from cell *I+2r* (section *RS+M* practically absent). Coloration completely preserved only in paratype MeI 11054. Posterior part of head and most part of mesosoma yellowish brown, anterior part of head, spot near ocelli, and median parts of gastral tergites dark brown. Coloration of holotype gaster as in MeI 11054. Whole body of paratype MeI 13151 black,

but probably coloration was changed during diagenesis. Wings of all specimens uniformly smoky brown, with darker veins and pterostigma.

Measurements (in mm). Holotype MeI 2305: BL 9.2, AL 2.6, HL 1.6, HW 1.5, ED 0.46, FWL 5.1; paratype MeI 11054: BL 7.2, AL 2.1, ED 0.40, FWL 5.1; paratype MeI 13151: BL 7.1, AL 1.85, FWL 4.3.

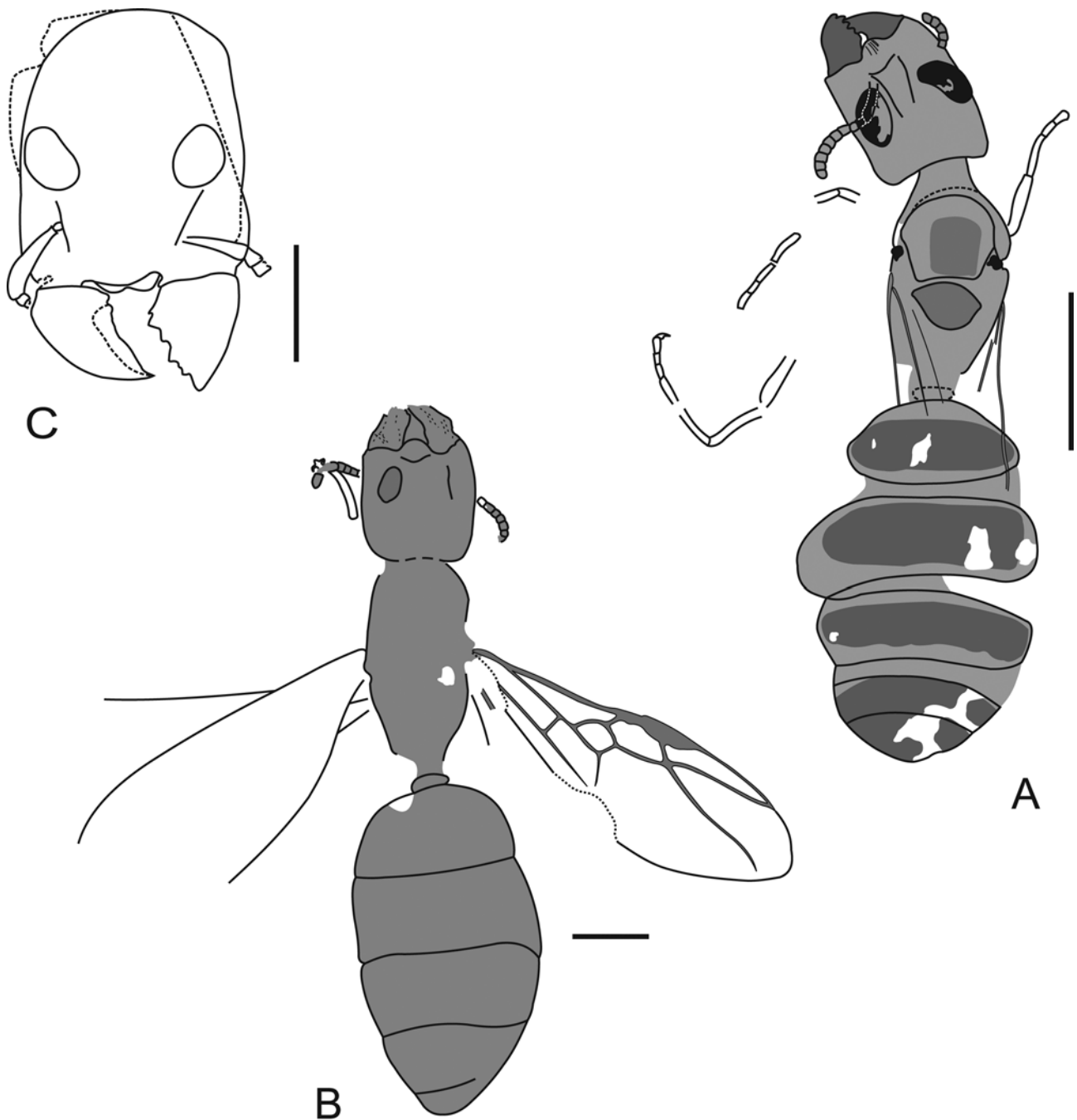


FIGURE 4. *Gesomyrmex* species from Messel. (A) *G. pulcher* **sp. nov.**, gyne, holotype MeI 10999. (B) *G. breviceps* **sp. nov.**, gyne, holotype MeI 2305. (C) *G. curiosus* **sp. nov.**, head of gyne, holotype MeI 11953. Scale bars = 1 mm.

Gesomyrmex curiosus **sp. nov.**
(Fig. 4C and Fig. 6H)

Derivation of the name. *Curiosus* is Latin for funny.

Holotype. SMF MeI 11953 (head of ♀).

Type locality and horizon. Grube Messel, Hesse, Germany. Messel formation, middle Eocene, ca. 47 Ma (Mertz & Renne 2005).

Description. Gyne. Head subtrapezoid, broader in the front than in the back, with gradually rounded posterior margin, without posterolateral corners. Anterior clypeal margin weakly projected, forms a small rounded lobe. Eyes comparatively small: head 4.4 times longer than maximum eye diameter. Frontal carinae short, divergent, reach the anterior margin of eye. Scape does not reach posterior margin of eye; head 3.5 times longer than scape. Mandible triangular, with 5 massive blunt teeth. Most part of the head brownish yellow, anterior part of head and spot near ocelli more dark, mandibles dark brown.

Measurements (in mm). Holotype MeI 11953: HL 2.3, HW 1.6, SL 0.65, ED 0.52.

Comments. Only the head of the unique holotype specimen is well preserved. However it is very different from all fossil and living species.

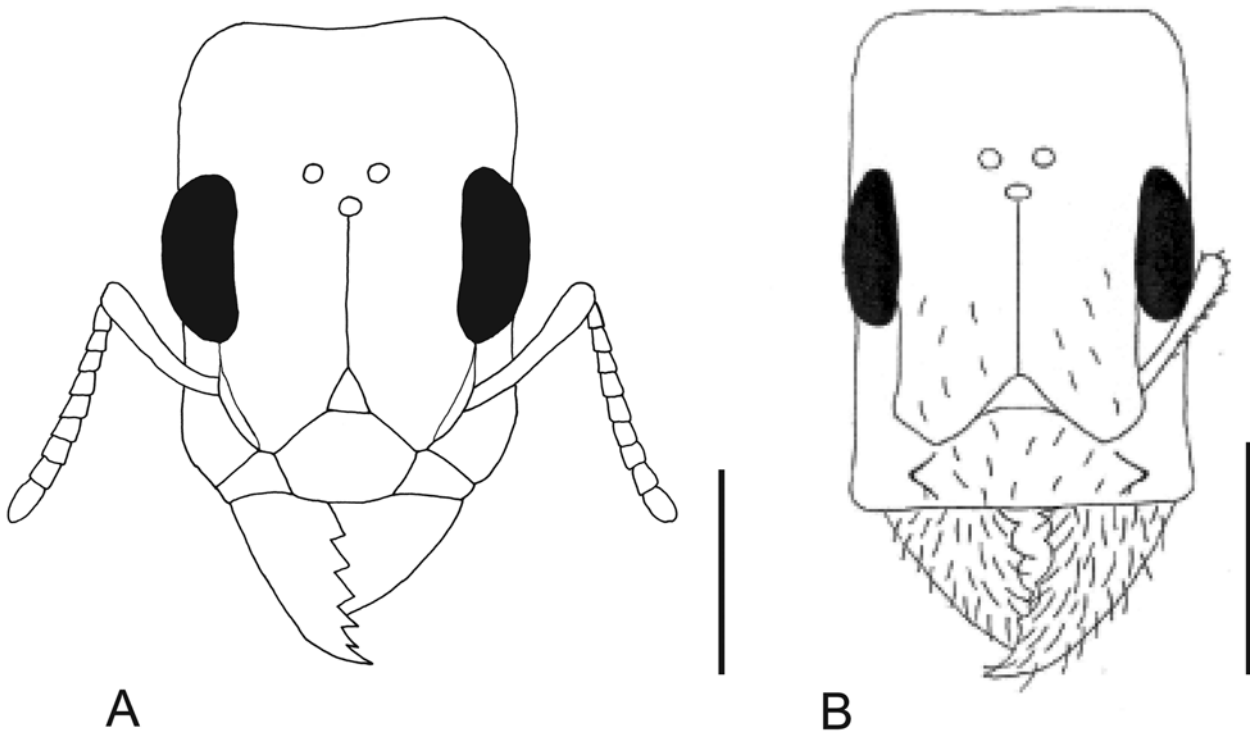


FIGURE 5. Heads of gynes of extant species of *Gesomyrmex*. (A) *G. luzonensis* (Wheeler) (after Wheeler 1916). (B) *G. tobiasi* Dubovikoff (from Dubovikoff 2004). Scale bars = 1 mm.

Key for determination of gynes of *Gesomyrmex*

(gynes of extant species *G. chaperi*, *G. howardi* and *G. kalshoveni* unknown)

1. Anterior margin of clypeus straight or feebly concave (Figs. 3B, 5A, 5B)..... 2
 - Anterior margin of clypeus projects as rounded lobe (Figs. 3A, 4A–4C). Fossil species..... 4
2. Head more than 1.4 times longer than wide (Figs. 5A, 5B). Living species..... 3
 - Head about 1.2 times longer than wide (Fig. 3B). BL about 13 mm. Eckfeld, middle Eocene *G. flavescens* **sp. n.**
3. Propodeum gradually rounded in side view. Eyes larger: head less than 3 times longer than maximum eye diameter. Posterior margin feebly concave (Fig. 5A). BL about 8.5 mm. Philippines..... *G. luzonensis* (Wheeler)
 - Propodeum angulate in side view. Eyes smaller: head more than 3 times longer than maximum eye diameter. Posterior margin straight. (Fig. 5B). BL about 9.5 mm. Vietnam. *G. tobiasi* Dubovikoff
4. Head subrectangular, with feebly concave posterior margin, about 1.1 times longer than wide (Fig. 4B). BL 7–9 mm. Messel, middle Eocene *G. breviceps* **sp. nov.**
 - Head more than 1.2 times longer than wide 5
5. Head subtrapezoid, broader in its anterior part than in its posterior part, with gradually rounded posterior margin,

- without posterolateral corners. Eyes comparatively small: head 4.4 times longer than maximum eye diameter (Fig. 4C). Messel, middle Eocene. *G. curiosus* **sp. nov.**
- Head subrectangular with distinctive rounded posterolateral corners (Figs. 2A, 3A, 4A)..... 6
6. Eyes comparatively small: head 4.7 times longer than maximum eye diameter. Scape comparatively short: head 4.4 times longer than scape. Baltic, Bitterfeld, Rovno and Scandinavian ambers, late Eocene..... *G. henschei* Mayr
- Head 2.5 to 3 times longer than maximum eye diameter, and 3 to 3.3 times longer than scape (Figs. 3A, 5A). 7
7. Posterior margin distinctly concave (Fig. 4A). Head and most part of mesosoma yellowish brown, mandibles, central part of scutum, whole scutellum and median parts of gastral tergites dark brown. BL 4.8 mm. Messel, middle Eocene..... *G. pulcher* **sp. nov.**
- Posterior margin feebly convex (Fig. 8A. Whole body black. BL 9–10 mm. Eckfeld, middle Eocene. *G. germanicus* **sp. nov.**

Species excluded from *Gesomyrmex*

Eoformica expectans (Théobald, 1937) **comb. nov.**

Gesomyrmex expectans Théobald, 1937, p. 210–211, pl. IV, fig. 13; pi. XIV, fig. 21 (♂); Burnham, 1978, p.114; Bolton, 1995, p. 207.

Comments. Described from one imprint from Kleinkembs, Haut-Rhin, France (early Oligocene). The specimen has a small rounded head with comparative small eyes and a comparative long scape, so it cannot be *Gesomyrmex*. Forewings are not preserved. The specimen is assigned to the formal genus (morphogenus) *Eoformica* Cockerell, 1921, which includes poorly preserved wingless imprints of ants in which the waist is one-segmented and narrowly attached to the gaster and the gaster lacks a constriction between the first and second segments. *Eoformica* Cockerell, 1921 includes three species: *E. pinguis* (Scudder, 1877), *E. magna* Dlussky & Rasnitsyn, 2003 and *E. globularis* Dlussky & Rasnitsyn, 2003. *Eoformica expectans* (Théobald) differs from another all other species included in this genus (Dlussky & Rasnitsyn, 2003) by its body proportions.

Formicidae (*incertae sedis*) *miegi* Théobald, 1937 **comb. nov.**

Gesomyrmex Miegi Théobald, 1937, p. 211, pl. XIV, figs. 22, 23 (♂, ♀).

Gesomyrmex miegi Théobald: Burnham, 1978, p.114; Bolton, 1995, p. 207.

Comments. Described from two imprints from Kleinkembs, Haut-Rhin, France (early Oligocene), both without head and wing venation. The poor preservation of these imprints does not permit the assignment of these ants to any living or fossil genus, so we propose to regard these specimens as Formicidae *incertae sedis*.

Discussion

Ecology of *Gesomyrmex*

There is very little information about the mode of life of living *Gesomyrmex* species. The first suggestions were based on indirect evidence. Wheeler (1916) wrote after his study of *G. lusonensis* (described as *Dimorphomyrmex*): “The shape of the body and the peculiar sculpture and pilosity of the anterior portion of the head in this phase, so like the condition of certain species of *Colobopsis* and *Aphomyrmex*, indicate very clearly that colonies of *Dimorphomyrmex* are small and inhabit hollow twigs”. Later Wheeler (1929) added: “The well-developed claws in the worker and female and not infrequent occurrence of *G. hoernesii* in the Baltic amber, suggest that the genus is arboreal. Moreover the structure of the head in maxima and female and the peculiar stubby hairs on the clypeus are reminiscent of some species of *Colobopsis* and allied subgenera of *Camponotus*, which live in hollow twigs or small cavities in bark or wood”.

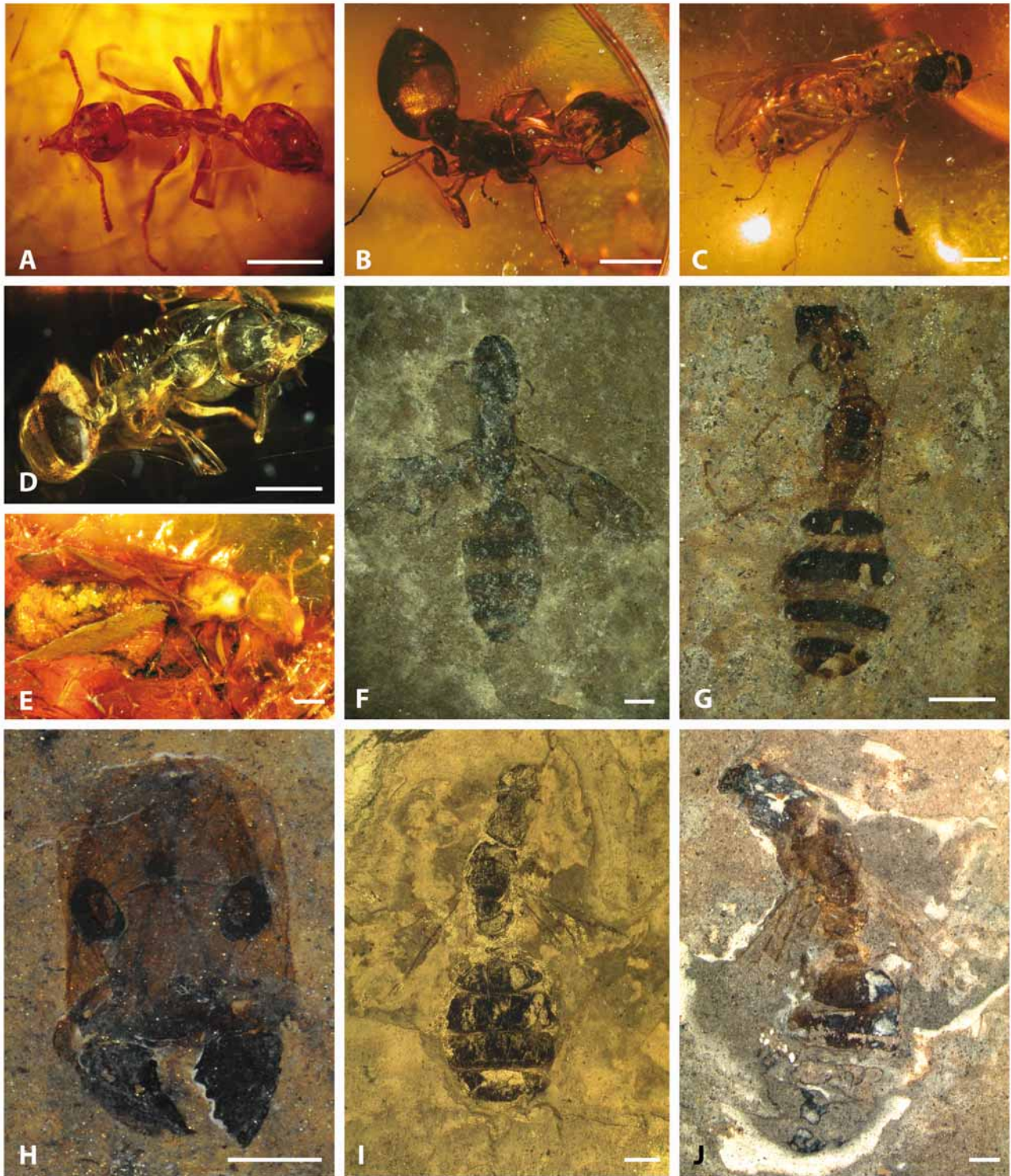


FIGURE 6. Photographs of different casts and species of *Gesomyrmex*. (A) *Gesomyrmex hoernesii* Mayr – minor worker GMUG.BST. 04207. (B) *Gesomyrmex hoernesii* Mayr – worker PMHU.13/221. (C) *Gesomyrmex hoernesii* Mayr – male MKC.F-010. (D) *Gesomyrmex hoernesii* Mayr – major worker SIZK.K-419. (E) *Gesomyrmex hoernesii* Mayr – gyne PMHU.7/229. (F) *G. breviceps* **sp. nov.**, gyne, holotype MeI 2305. (G) *G. pulcher* **sp. nov.**, gyne, holotype MeI 10999. (H) *G. curiosus* **sp. nov.**, head of gyne, holotype MeI 11953. (I) *G. germanicus* **sp. nov.**, gyne, holotype PE-1997/29. (J) *G. flavescens* **sp. n.**, gyne, holotype PE-2000/14. Scale bars = 1 mm.

Only three direct observations on living *Gesomyrmex* are published. Wheeler (1930) cited a letter from Dr. James W. Chapman, who observed and collected a colony of *G. luzonensis* near Dumaguete, Philippines.

During three days Dr. Chapman observed foraging minor workers, which were attracted by ripe bananas. He noticed a peculiar jerky, zigzag gait of these ants. During the day several workers were seen to visit and feed on the bananas. The last one retired to the nest at 5 pm, apparently for the night. The nest was in a pole, which Dr. Chapman cut about two weeks previously and placed diagonally between two of the posts, to serve as a brace. On the third day Dr. Chapman opened the nest and found that “the four entrances were seen to unite to form a single funnel-like passage, which grew narrower towards the end of the pole and opened into the middle of the main nest-cavity. This was about five inches long and one and a quarter inches from the surface. The two ends of the cavity were rounded out and the wood around the excavated pithy centre had been gnawed away to form several irregular galleries. The colony had evidently been nesting in these cavities for some time. There were about 150 adult workers, their queen, male and a number of eggs and larvae”.

The second observation was published by Cole (1949) who described *G. spatulatus* from a series of 25 workers collected at Jorhat, Upper Assam, India. He wrote: “The ants were running up and down on the trunk of a tall tree located in a sunny area beside a rice paddy. They were very agile and ran swiftly with a jerky motion. There was indication that the nest was arboreal, although there was no actual evidence to substantiate this view”.

More recently De Greef (2007, p. 11) reported on a colony of *Gesomyrmex* (possibly *G. tobiasi*) in the Virachey National Park, Cambodia. “Some workers were initially found foraging around the camp area, and were baited with live termites and mosquitoes. After a few hours the nest was found inside a branch of 5 cm diameter, the entrance being a tiny hole of 1 mm diameter. The branch was cut open, delivering dozens of workers of very different sizes, along with larvae and nymphs. Another colony was located nearby and left undisturbed, for further study on their behaviour”. Considering this, it is clear that *Gesomyrmex* is arboreal, inhabiting the lower vegetation or the canopy.

Summarising the citation of Chapman’s letter Wheeler (1930) wrote: “We may conclude that the colonies of *Gesomyrmex* are monometrotic, or possess a single mother queen, that they are not very populous and nest in sound wood. Like other lignicolous ants they probably take possession of the abandoned burrows of other insects and enlarge them by tunnelling in the wood as the colony grows. Dr. Chapman's observations show that the smaller and more numerous workers do most of the foraging, have a peculiar, jerky, zigzag gait and are very timid. He has not observed the guarding of the nest-entrances by the largest workers, though he seems to have seen workers stationed just within the entrance gallery”.

We can add to Wheeler’s conclusions that all living and fossil studied gynes and major workers of *Gesomyrmex* have massive triangular mandibles with large rather blunt teeth. Such mandible construction is characteristic for ants building nests in hard substrate, particularly in wood (Dlussky & Fedoseeva 1988). At the same time minor workers have elongate mandibles with acute teeth, which are more adapted for capturing living prey. An arboreal mode of life of Eocene *G. hoernesii* is supported by the proportions of different castes in the amber inclusions. Mayr (1868) studied 19 workers and one male, André (1895) studied 7 workers and Wheeler (1915) studied 172 workers. We studied 41 workers (except specimens determined by Wheeler), one male and one gyne. So, only three of 242 specimens (1.2%) were sexuals. Such a low proportion of sexuals is characteristic for ants whose workers actively forage on tree trunks and branches (Dlussky & Rasnitsyn 2007).

Notes on the evolution of arboreal ant communities

Gesomyrmex species have been a component of arboreal ant communities since the Eocene. In this context it is interesting to compare the community structure of Tertiary and Recent arboreal ants.

Most ants in extant tropical forests inhabit and forage on trees. Zakharov (1994) studied the distribution of ants in oligodominant tropical forests in Tonga and Western Samoa. He demonstrated that up to 85% of the ant colonies are restricted to arboreal strata. In forests with lianas and epiphytes arboreal ant colonies were most abundant. Concerning the taxonomic composition of Recent arboreal ant complexes, those found in the

tropics and southern subtropics in southern Asia consist mainly of numerous species from the genera *Camponotus* Mayr, *Polyrhachis* F. Smith, *Oecophylla* F. Smith (Formicinae), *Dolichoderus* Lund (Dolichoderinae), *Pheidole* Westwood, *Crematogaster* Lund (Myrmicinae), and *Tetraponera* F. Smith (Pseudomyrmecinae) (e.g. Floren *et al.* 2002).

Since we can observe only the morphology of fossil species, we can draw ecological conclusions only from comparisons with extant species which have special morphological adaptations to their mode of life. However, it is possible to infer that the structure of arboreal ant complexes in the Tertiary was different from today. The most extensively studied fossil fauna originates from Eocene Baltic and similar ambers (Wheeler 1915; Dlussky 1997, 2002, in press; Dlussky & Perkovsky 2002; Dlussky & Rasnitsyn in press). In the Eocene ambers the genera *Polyrhachis*, *Pheidole* and *Crematogaster* were absent and only one *Camponotus* species was present. The most abundant species in these ambers is *Ctenobethylus goepperti* (Mayr) which belongs to an extinct genus (Dlussky & Rasnitsyn 2007). Species of *Dolichoderus* were not so abundant but with 22 different species *Dolichoderus* apparently had a high biodiversity in the late Eocene forests (Dlussky in press) and this is more than in any recent local tropical fauna of southern Asia. Specialized arboreal species of the genus *Tetraponera* are very rarely found in Baltic and similar amber and they are not very speciose (Dlussky 1997, Dlussky in press). Other rather rare specialized arboreal ants known from Eocene ambers were *Gesomyrmex hoernesi*, two species of *Oecophylla*, *Liometopum oligocenicum* Wheeler and two species of the extinct genus *Drymomymex* Wheeler. Possibly the real participation of *Oecophylla* in the fossil ecosystem is not mirrored in their proportion in ambers. Today, these ants construct their nests from living leaves, which means that they live on deciduous trees, whereas the amber formed on coniferous trees.

Recently we began the study of middle Eocene ants from Messel and Eckfeld (Germany). We investigated 412 ant specimens from Messel and 87 ants from Eckfeld, but did not include *Formicium* Westwood, which were described elsewhere (Lutz 1986; Wappler 2003). The most abundant arboreal ants were weaver ants of the genus *Oecophylla* (Dlussky *et al.* 2008). Rare specialized arboreal ants belong to some Dolichoderinae species similar to *Emplastus*, *Ctenobethylus* or *Liometopum*, *Tetraponera*, *Dolichoderus*, and to *Gesomyrmex* which are described in this paper. The last are very interesting because they were not very numerous but unusually diverse with three species in Messel and two species in Eckfeld as recorded in this paper.

A yet unpublished study by one of the authors (Dlussky) shows that among more than a thousand ant impressions from the early Oligocene Bembridge Marls (Isle of Wight, UK) arboreal ants are numerically strongly dominating. There are many impression fossils of two *Oecophylla* species (51% of all ants), and few impressions of *Dolichoderus vectensis* Donisthorpe, *Camponotus* and some species of the dolichoderine genus *Emplastus* Donisthorpe which is morphologically similar to *Ctenobethylus* Brues and *Liometopum* Mayr. Additionally, we studied ants from both the upper Oligocene deposits of Rott (Germany) (60 fossils studied) and Enspel (Germany) (47 fossils studied) and did not find impressions of *Gesomyrmex*, *Tetraponera*, *Polyrhachis*, *Pheidole* or *Crematogaster*. The earliest fossil record of *Polyrhachis*, which nowadays is one of the largest ant genera, was recently found in late Miocene deposits of the island of Crete (Europe) (Wappler *et al.* in press).

We can conclude from these data that the composition of arboreal ant communities changed in the past. The proportion of *Oecophylla* seems to have increased from the middle Eocene to the early Oligocene, and then decreased (Dlussky *et al.* 2008). *Dolichoderus* and *Tetraponera* are present from middle Eocene to Recent times with their maximum diversity in the late Eocene. *Gesomyrmex* was very diverse in the middle Eocene, existed in the late Eocene and then disappeared from the fossil record. At present this genus exists as a relic in the tropical forests of southern Asia.

Acknowledgments

We thank Dr. S. Schaal (Forschungsinstitut Senckenberg, Frankfurt/M) for the loan of the fossils from Messel and for the opportunity to stay at the outpost in Grube Messel. The team of the outpost made the stay most

agreeable. We thank Dr. H. Lutz (Naturhistorisches Museum Mainz) for the loan of the Eckfeld fossils, Dr. Andrew Ross (Natural History Museum, London), Dr. Mike Reich (Geowissenschaftliches Zentrum der Universität Göttingen, Museum), Dr. Alexander Rasnitsyn (Paleontological Institute, Moscow) and Dr. Evgeny Perkovsky (Schmalhausen Institute of Zoology, Kiev) for their help in the study of amber ants and Dr. Dmitry Dubovikoff (Zoological Institute, St.-Petersburg) for valuable discussion about the manuscript. Thanks also to the museum team in the Geowissenschaftliches Zentrum der Universität Göttingen for making possible the pleasant stay in Göttingen. Valuable comments on the manuscript were provided by Dr. Barry Bolton (Natural History Museum, London), Dr. John T. Longino (The Evergreen College, Olympia), and an anonymous reviewer.

This work was supported by grants of the Russian Fund of Fundamental Investigations (RFFI) No 08-04-00-701 (to G.D.), the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) No 436 RUS 17/17/07 (to G.D. and S.W.) and DFG project No RU 665/3-2 (to S.W.). This is contribution No. 116 of the “Fossilfundstätte Eckfeld Maar (Mittel-Eozän)”.

References

- André, E. (1892) Voyage de M. Chaper à Bornéo. Catalogue des fourmis et description des espèces nouvelles. *Mémoires de la Société Zoologique de France*, 5, 46–55.
- André, E. (1895) Notice sur les fourmis fossiles de l'ambre de la Baltique et description de deux espèces nouvelles. *Bulletin de la Société Zoologique de France*, 20, 80–84.
- Barthel, M. & Hetzer, H. (1982) Bernstein-Inklusen aus dem Miozän des Bitterfelder Raumes. *Zeitschrift für angewandte Geologie*, 28, 314–336.
- Beattie, A.J. & Hughes, L. (2002) Ant-plant interactions. In: Herrera, C.M. & Pellmyr, O. (Eds.), *Plant-Animal Interactions: An Evolutionary Approach*. Blackwell Science, Oxford, pp. 211–235.
- Bolton, B. (1994) *Identification guide to the ant genera of the world*. Harvard University Press, Cambridge, 222 pp.
- Bolton, B. (1995) *A new general catalogue of the ants of the world*. Harvard University Press, Cambridge, 504 pp.
- Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1–370.
- Bolton, B., Alpert, G., Ward, P.S. & Nasrecki, P. (2006) *Bolton's Catalogue of ants of the world*. Harvard University Press, Cambridge, Massachusetts, CD-ROM.
- Brown, W. L., Jr. (1950) Morphological, taxonomic, and other notes on ants. *Wasmann J. Biol.* 8, 241–250.
- Burnham, L. (1978) Survey of social insects in the fossil records. *Psyche*, 89, 85–133.
- Cole Jr., A.C. (1949) A study of the genus *Gesomyrmex* Mayr, and a description of a species new to the genus (Hymenoptera: Formicidae). *Annals of the Entomological Society of America*, 42, 71–76.
- Dalla Torre von., K.W. (1893) *Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus*. Vol. 7. *Formicidae (Heterogyna)*. W. Engelmann, Leipzig, 289 pp.
- De Greef, S. (2007) Ant survey. In: Preliminary Report for the Rapid Assessment Programm (RAP) survey in Virachey National Park, Cambodia, 1–5 October 2007, Conservation International editor, pp. 10–12.
- Dlussky, G.M. (1997) Genera of ants (Hymenoptera: Formicidae) from Baltic amber. *Paleontologicheskii Zhurnal*, 1997 (6), 50–62 [in Russian, English translation: *Paleontological Journal*, 31 (6): 616–627].
- Dlussky, G.M. (2002) Ants of the genus *Dolichoderus* (Hymenoptera: Formicidae) from the Baltic and Rovno ambers. *Paleontologicheskii Zhurnal*, 2002 (2), 54–68 [in Russian, English translation: *Paleontological Journal*, 36, 50–63].
- Dlussky, G.M. (in press) New data on ants of the genus *Dolichoderus* Lund (Hymenoptera, Formicidae) from late Eocene ambers of Europe. *Vestnik Zoologii*. (in Russian).
- Dlussky, G.M. & Fedoseeva, E.B. (1988) The origin and early evolutionary steps of ants (Hymenoptera: Formicidae) [in Russian]. In: Ponomarenko, A.G. (Ed.), *Cretaceous biocenotic crisis and evolution of the insects*. Nauka Press, Moscow, pp. 70–144.
- Dlussky, G.M. & Perkovsky, E.E. (2002) Ants (Hymenoptera, Formicidae) from the Rovno amber. *Vestnik Zoologii*, 36, 3–20.
- Dlussky, G.M. & Rasnitsyn, A.P., 2003 [2002]. Ants (Hymenoptera: Formicidae) of formation Green River and some other middle Eocene deposits of North America. *Russian Entomological Journal*, 11, 411–436.
- Dlussky, G.M. & Rasnitsyn, A.P. (2007) Paleontological record and stages of ant evolution. *Uspekhi Sovremennoy Biologii*, 127, 118–134. (in Russian).

- Dlussky, G.M. & Rasnitsyn, A.P. (in press) Ants (Insecta: Vespida: Formicidae) in the Upper Eocene amber of Europe. *Transactions of the Paleontological Institute of the Russian Academy of Sciences*.
- Dlussky, G.M., Wappler, T. & Wedmann, S. (2008) New middle Eocene formicid species from Germany and the evolution of weaver ants. *Acta Palaeontologica Polonica*, 53, 615–626.
- Dubovikoff, D.A. (2004) A new species of the genus *Gesomyrmex* Mayr, 1868 (Hymenoptera: Formicidae) from Vietnam. *Trudy Russkogo Entomologicheskogo Obshchestva*, 75, 219–221.
- Emery, C. (1895) Die Gattung *Dorylus* Fab. und die systematische Eintheilung der Formiciden. *Zoologische Jahrbücher (Systematik, Oekologie, Geographie der Tiere)*, 8, 685–778.
- Emery, C. (1905) Deux fourmis de l'ambre de la Baltique (Hym.). *Bulletin de la Société Entomologique de France*, 1905, 187–189.
- Emery, C. (1925) Hymenoptera. Fam. Formicidae. Subfam. Formicinae. *Genera Insectorum*, 183, 1–302.
- Felder, M. & Harms F.-J. (2004) Lithologie und genetische Interpretation der vulkano-sedimentären Ablagerungen aus der Grube Messel anhand der Forschungsbohrung Messel 2001 und weiterer Bohrungen. *Courier Forschungsinstitut Senckenberg*, 252, 151–203.
- Floren, A., Biun, A. & Linsenmair, K.E. (2002) Arboreal ants as key predators in tropical lowland rainforest trees. *Oecologia*, 131, 137–144.
- Fuhrmann, R. (2005) Die Bernsteinlagerstätte Bitterfeld, nur ein Höhepunkt des Vorkommens von Bernstein (Succinit) im Tertiär Mitteldeutschlands. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften*, 156, 517–529.
- Hamann, H. H. F. (1957) On a new record of *Gesomyrmex* Mayr (Formicidae). *Idea* 10(4), 1–6.
- Handlirsch, A. (1907) *Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. Lieferung 6*. Wilhelm Engelmann, Leipzig, pp. 801–960.
- Hoffeins, C. & Hoffeins, H.W. (2003) Untersuchungen über die Häufigkeit von Inkluden in Baltischem und Bitterfelder Bernstein (Tertiär, Eozän) aus unselektierten Aufsammlungen unter besonderer Berücksichtigung der Ordnung Diptera. *Studia Dipterologica*, 10, 381–392.
- Hölldobler, B. & Wilson, E.O. (1990) *The ants*. Springer Verlag, Berlin, 732 pp.
- Knuth, G., Koch, T., Rappsilber, I., & Volland, L. (2002) Zum Bernstein im Bitterfelder Raum - Geologie und genetische Aspekte. *Hallesches Jahrbuch für Geowissenschaften, (ser. B)*, 24, 35–46.
- Koenigswald von, W. & Storch, G. (1998) Messel. Ein Pompeji der Paläontologie. Jan Thorbecke Verlag, Sigmaringen, 151 pp.
- Lutz, H. (1986) Eine neue Unterfamilie der Formicidae (Insecta: Hymenoptera) aus dem mittel-eozänen Ölschiefer der "Grube Messel" bei Darmstadt (Deutschland, S-Hessen). *Senckenbergiana Lethaea*, 67, 177–218.
- Lutz, H. (1990) Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg*, 124, 1–165.
- Lutz, H. (1993) Zur Taphonomie der aquatischen und terrestrischen Fauna des „Eckfelder Maares“ (Mittel-Eozän; Deutschland): Ergebnisse aus den Grabungen 1990–1992. *Mainzer Naturwissenschaftliches Archiv*, 31, 85–113.
- Lutz, H. & Kaulfuß, U. (2006) A dynamic model for the meromictic lake Eckfeld Maar (Middle Eocene, Germany). *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften*, 157, 433–450.
- Lutz, H., Neuffer, F.O., Frankenhäuser, H. & Gwosdek, S. (1998) Forschungsprojekt Eckfelder Maar: Jahresbericht 1997. *Mitteilungen der Rheinisch Naturforschenden Gesellschaft*, 19, 35–37.
- Lutz, H. & Neuffer, F.O. (2000) The middle Eocene fossiliferous site Eckfeld Maar. *GFF*, 122, 95–96.
- Mayr, G. (1867) Vorläufige Studien über die Radoboj-Formiciden, in der Sammlung der k. k. geologischen Reichsanstalt. *Jahrbuch der K.-K. Geologischen Reichsanstalt Wien*, 17: 47–62.
- Mayr, G. (1868) Die Ameisen des baltischen Bernsteins. *Beiträge zur Naturkunde Preussens Königlischen Pysikalisch-Ökonomischen Gesellschaft zu Königsberg*, 1, 1–102.
- Mertz, D.F., Harms, F.-J., Gabriel, G. & Felder, M. (2004) Arbeitstreffen in der Forschungsstation Grube Messel mit neuen Ergebnissen aus der Messel-Forschung. *Natur und Museum*, 134, 289–290.
- Mertz, D.F. & Renne, P.R. (2005) A numerical age for the Messel fossil deposit (UNESCO World Heritage Site) derived from ⁴⁰Ar/³⁹Ar dating on a basaltic rock fragment. *Courier Forschungsinstitut Senckenberg*, 255, 67–75.
- Neuffer, F.O., Gruber, G., Lutz, H. & Frankenhäuser, H. (1996) *Das Eckfelder Maar – Zeuge tropischen Lebens in der Eifel*. Mainzer Naturhistorisches Museum, Mainz, 102 pp.
- Perkovsky, E.E., Zosimovich, V.Yu. & Vlaskin, A.P. (2003) A Rovno amber fauna: a preliminary report. *Acta Zoologica Cracoviensia*, 46 (suppl.- Fossil insects), 423–430.
- Perkovsky, E.E., Rasnitsyn, A.P., Vlaskin, A.P. & Taraschuk, M.V. (2007) A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates*, 48, 229–245.
- Pirung, M., Büchel, G. & Jacoby, W. (2001) The Tertiary volcanic basins of Eckfeld, Enspel and Messel (Germany). *Zeitschrift der Deutschen Geologischen Gesellschaft*, 152, 27–59.
- Ponomarenko, A.G. & Schultz, O. (1988) Typen der Geologisch-Paläontologischen Abteilung: Fossile Insekten // Kataloge der wissenschaftl. Sammlung des Naturhistorischen Museum in Wien. *Paläozoologie*, 6, 1–30.
- Röschmann, F. (1997) Ökofaunistischer Vergleich von Nematoceren-Faunen des Baltischen und Sächsischen Bernsteins.

Paläontologische Zeitschrift, 71, 79–87.

- Richter, G. & Baszio, S. (2001) Traces of a limnic food web in the Eocene lake Messel – a preliminary report based on fish coprolite analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166, 345–368.
- Richter, G. & Wedmann, S. (2005) Ecology of the Eocene Lake Messel revealed by analysis of small fish coprolites and sediments from a drilling core. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 223, 147–161.
- Ritzkowski, S. (1997) K-Ar-Altersbestimmungen der bernsteinführenden Sedimente des Samlandes (Paläogen, Bezirk kaliningrad). *Sonderheft Metalla*, 1997, 19–23.
- Schaal, S. & Ziegler, W. (Eds.) (1992) *Messel. An insight into the history of life and of the Earth*. Clarendon Press, Oxford, 322 pp.
- Schulz, R., Harms, F.-J. & Felder, M. (2002) Die Forschungsbohrung Messel 2001: Ein Beitrag zur Entschlüsselung der Genese einer Ölschieferlagerstätte. *Zeitschrift für angewandte Geologie*, 2002, 9–17.
- Théobald, N. (1937) *Les insectes fossiles des terrains oligocènes de France*. G. Thomas, Nancy, 473 pp.
- Tröster, G. (1991) Eine neue Gattung der Elateridae (Insecta: Coleoptera) *Macropunctum* gen. n. aus der Messel-Formation des unteren Mittel-Eozän der Fundstätte Messel. *Courier Forschungsinstitut Senckenberg*, 139, 99–117.
- Tröster, G. (1993) Fossile Schnellkäfer der Gattung *Lanelater* Arnett 1952 (Coleoptera, Pyrophorinae, Agrypnini) aus dem Eozän der Grube Messel bei Darmstadt. *Senckenbergiana Lethaea*, 73, 49–60.
- Wappler, T. (2003) Die Insekten aus dem Mittel-Eozän des Eckfelder Maares, Vulkaneifel. *Mainzer Naturwissenschaftliches Archiv*, Beiheft, 27, 1–234.
- Wappler, T. & Andersen, N.M. (2004) Fossil water striders from the Middle Eocene fossil sites Eckfeld and Messel, Germany (Hemiptera, Gerromorpha). *Paläontologische Zeitschrift*, 78, 41–52.
- Wappler, T. & Ben-Dov, Y. (2008) Preservation of armoured scale insects (Hemiptera: Coccoidea: Diaspididae) on angiosperm leaves from the Eocene of Germany. *Acta Palaeontologica Polonica*, 53, 627–634.
- Wappler, T., Dlussky, G.M. & Reuter, M. (in press) The first fossil record of Polyrhachis (Hymenoptera: Formicidae: Fomicinae) from the upper Miocene of Crete (Greece). *Paläontologische Zeitschrift*
- Wappler, T. & Engel, M.S. (2003) The middle Eocene bee faunas of Eckfeld and Messel, Germany (Hymenoptera: Apoidea). *Journal of Paleontology*, 77, 908–921.
- Wappler, T. & Engel, M.S. (2006) New record of Mastotermes from the Eocene of Germany (Isoptera: Mastotermitidae). *Journal of Paleontology*, 80, 380–385.
- Wappler, T., Smith, V.S. & Dagleish, R.C. (2004) Scratching an ancient itch: an Eocene bird louse fossil. *Proceedings of the Royal Society, B (Suppl.)*, 271, 255–258.
- Wedmann, S. (2005) Annotated taxon-list of the invertebrate animals from the Eocene fossil site Grube Messel near Darmstadt, Germany. *Courier Forschungsinstitut Senckenberg*, 255, 103–110.
- Wedmann, S., Bradler, S. & Rust, J. (2007) The first fossil leaf insect: 47 million years of specialized cryptic morphology and behavior. *Proceedings of the National Academy of Science*, 104, 565–569.
- Wedmann, S. & Yeates, D. (2008) Eocene records of bee flies (Insecta, Diptera, Bombyliidae, *Comptosia*): Their paleobiogeographic implications and remarks on the evolutionary history of bombyliids. *Palaeontology*, 51, 231–240.
- Weitschat, W. (1997) Bitterfelder Bernstein – Ein eozäner Bernstein auf miozäner Lagerstätte. *Metalla*, 66, 71–84.
- Weitschat, W. & Wichard, W. (1998) *Atlas der Pflanzen und Tiere im Baltischen Bernstein*. Verlag Dr. Friedrich Pfeil, München, 256 pp.
- Wheeler, W.M. (1915) The ants of the Baltic Amber. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg*, 55, 1–142.
- Wheeler, W.M. (1916) Four new and interesting ants from the mountains of Borneo and Luzon. *Proceedings of the New England Zoological Club*, 6, 9–18.
- Wheeler, W. M. (1921) Chinese ants collected by Prof. C. W. Howard. *Psyche*, 28, 110–115.
- Wheeler, W.M. (1929) The identity of the ant genera *Gesomyrmex* Mayr and *Dimorphomyrmex* Ernest André. *Psyche*, 36, 1–12.
- Wheeler, W.M. (1930) A second note on *Gesomyrmex*. *Psyche*, 37, 35–40.
- Zakharov, A.A. (1994) Ant population structure on the islands of Tonga and Western Samoa In: Puzatchenko, Y.G., Golovatch S.I., Dlussky, G.M., Diakonov, K.N., Zakharov, A.A. & Korganova, G.A. (Eds.), *Animal population of the islands of Southwestern Oceania (Ecogeographic studies)*. Nauka Press, Moscow, pp. 94–142. (in Russian).