Journal of Systematic Palaeontology, Vol. 10, Issue 4, December 2012, 725–753

The poneromorph ants (Hymenoptera, Formicidae: Amblyoponinae, Ectatomminae, Ponerinae) of Grube Messel, Germany: high biodiversity in the Eocene

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(Received 17 September 2010; accepted 27 March 2011; printed 5 December 2012)

Ants are a very successful group among insects, but the course of evolution of their biodiversity is still unclear. This study sheds light on ant diversification during the Eocene. Analysis of the ant taphocoenosis of the fossil site Grube Messel, Germany (47 Ma) yielded three poneromorph subfamilies and 22 new species in six genera, four of which are new: *Pseudectatomma* gen. nov., *Cephalopone* gen. nov., *Cyrtopone* gen. nov. and *Messelepone* gen. nov. Only one extant genus, *Pachycondyla*, is present in the taphocoenosis from Messel. The high diversity of poneromorph ants from Messel is very striking in comparison with middle to late Eocene European ambers. A significantly lower proportion of species in ambers can be assigned to poneromorph ants, and fewer poneromorph species are known from European ambers than from Messel. A possible gradual decline of the diversity of poneromorphs from the Eocene to the Miocene seems to be detectable worldwide. These insights are discussed in the context of the morphology and ecology of Poneromorpha and Formicomorpha. The proportion of ant castes in amber seems to indicate that already during the Eocene poneromorphs inhabited preferably litter and soil, whereas formicomorphs preferred the arboreal realm. The 'ponerine paradox' of having only a primitive social organization, yet being an old phylogenetic line with global distribution, is discussed with emphasis on palaeontological data but still remains unsolved. The evolutionary history of Myrmicinae is discussed. With the newly available palaeontological data, the timing and the dynamics of dominance by different subgroups of ants can be traced more precisely than before.

Keywords: biodiversity; evolution; ecology; fossil record; Tertiary; Palaeogene

Introduction

Ants (Hymenoptera: Formicidae) are the most successful group of social insects, with a present day biodiversity that exceeds 14,000 species (www.antweb.org, accessed 21 January 2011) and an enormous biomass placing them in an ecologically very important position (e.g. Hölldobler & Wilson 1990). Together with termites, ants constitute an impressive part of the animal biomass in tropical rainforests and savannas (Hölldobler & Wilson 1990). Ant biomass is estimated to be several times greater than the biomass of the mammals present in the central Amazonian rainforest (Fittkau & Klinge 1973).

Many studies have addressed the early evolution, the former biodiversity and the higher phylogenetic relationships of ants, including morphological analyses, palaeontological analyses and ever more molecular analyses (e.g. Wheeler 1915; Baroni Urbani *et al.* 1992; Dlussky 1997; Grimaldi *et al.* 1997; Grimaldi & Agosti 2000; Dlussky & Rasnitsyn 2003; Wilson & Hölldobler 2005; Brady *et al*. 2006; Moreau *et al.* 2006; Perrichot *et al.* 2008a, b; Rabeling *et al.* 2008; Moreau 2009). Nevertheless, important questions remain under discussion, e.g. concerning the age of the first Formicidae, the origin of their eusociality, phylogenetic relationships among the higher clades and the evolutionary course resulting in today's biodiversity.

Until Bolton (2003) reorganized their higher classification, the ants described in this article were united in the subfamily Ponerinae. Fossil species of the former Ponerinae could be determined by the following complex of key characters: a one-segmented waist, constriction between the first and second gastral (III and IV abdominal) segments, distal position of the cross vein cu-a of the forewing, etc. Bolton (2003) divided the former Ponerinae into six separate subfamilies, which are united in the poneromorph subfamily group. Most myrmecologists accepted his proposal. However, it creates problems for palaeoentomologists as most of the key characters proposed for the distinction of these new subfamilies cannot be seen in fossil imprints.

In this paper, we attempt to offer criteria for the distinction of poneromorph subfamilies usable for fossil imprints. We analyse the previously unstudied poneromorph ants

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ISSN 1477-2019 print / 1478-0941 online

http://dx.doi.org/10.1080/14772019.2011.628341
http://www.tandfonline.com

from the Middle Eocene of Grube Messel, Germany, and compare observed diversity and composition from Messel with those found in other European taphocoenoses and other sites, especially in China and North America. The dynamics of dominance of different ant subgroups during the Cenozoic is discussed.

Material and methods

The investigated fossils are housed in the insect collection at the Forschungsstation Grube Messel of the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main (FIS).

Fossil specimens were photographed using a digital camera, and enlarged prints were hand traced by pen. The resultant drawings were scanned and improved using standard graphics software. In the line drawings, full lines indicate visible sclerite boundaries, dashed lines supposed sclerite boundaries, and dotted lines visible margins of incomplete sclerites. Preserved original sclerites of the impressions are coloured in grey.

Nomenclature of wing venation (Fig. 1) follows Dlussky (2009). Other morphological terminology is after Bolton (1994), while higher classification follows Bolton (2003).

Ant impression fossils are significantly 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.

Measurements taken (Fig. 2) 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; FrW, frons width; FWL, forewing length; G1H, height of first gastral (III abdominal) segment; G1L, length of first gastral segment from helcium to posterior margin in side view; G1W, width of first gastral segment; G2H, height of second gastral (IV abdominal) segment; G2L, length of second gastral segment without presclerite; G2W, width of second gastral segment; HL, head length without mandibles; HW, maximum head width without eyes; MdL, mandible length; PtL, petiole length; PtW, maximum petiole width; ScL, scutum length; SctL, scutellum length; SL, scape length.

All colour photographs of holotypes will be available online in the fossil catalogue at www.antweb.org.

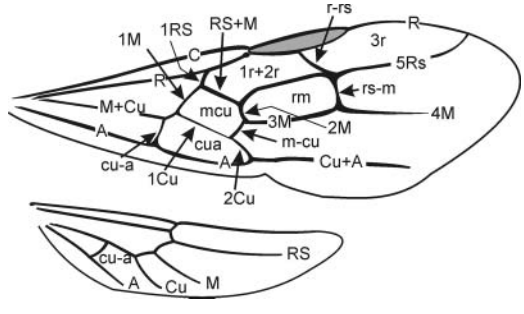

Figure 1. Wings of a gyne *Gnamptogenys europaea* (Mayr 1868), Late Eocene, Rovno amber. Abbreviations: C, R, RS, M, Cu, A: longitudinal veins; 1RS, RS + M, 2M, etc.: longitudinal vein sections; r-rs, r-m, m-cu, etc.: crossveins; 1r + 2r, rm, 3r, mcu, cua: cells. From Dlussky (2009).

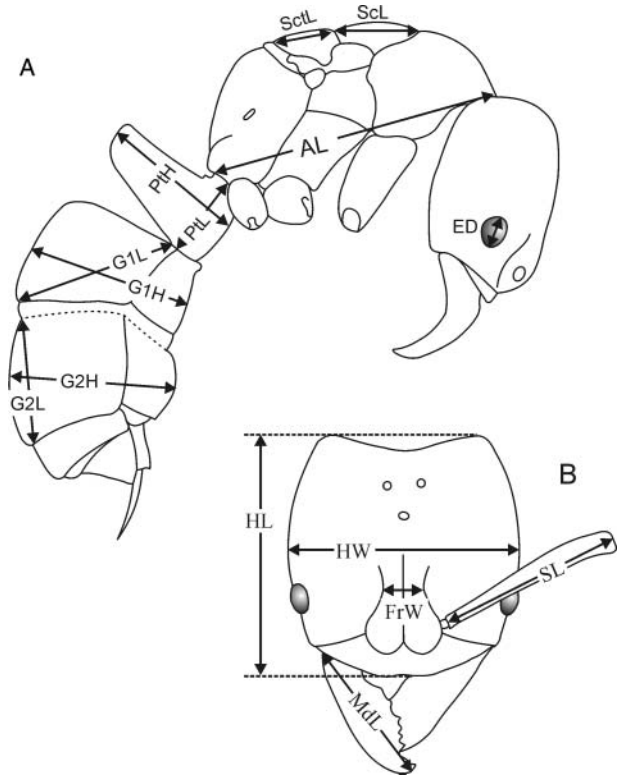

Figure 2. Gyne of *Pachycondyla astuta* F. Smith, Recent, Vietnam, showing measurements (explanation of abbreviations in the text).

Geological setting

Grube Messel is located on the eastern shoulder of the Rhine rift valley in Germany, situated between the cities of Frankfurt am Main and Darmstadt. Presently, the site is a large pit with a diameter of about 0.7 km × 1 km and a depth of about 60 m. The Messel pit is the site of a former isolated lake, infilled by sediments, interpreted as a Maar lake created by explosive volcanic activity (e.g. Schulz *et al*. 2002; Felder & Harms 2004). The lake basin had a diameter of about 1.5 km and was initially 300 to 400 m deep; laminated and fossiliferous 'oilshale' sediments were deposited in the upper 140 m (Harms 2002; Felder & Harms 2004). The water body of the former lake was meromictic, chemically and thermally stratified (e.g. Goth 1990). A recent

absolute dating of the Messel Formation revealed an age of about 47 Ma (Mertz & Renne 2005). Ongoing excavations have yielded a multitude of fossils that offer unique insights into the Eocene ecosystem (e.g. Schaal & Ziegler 1992; von Koenigswald & Storch 1998). After plant remains, insects are the most abundant fossils. They document a highly diverse, mostly terrestrial fauna (e.g. Lutz 1990; Tröster 1991, 1993; Hörnschemeyer & Wedmann 1994; Wedmann & Hörnschemeyer 1994; Wappler & Engel 2003; Wappler 2003, 2006; Wedmann 2005, 2007; Wedmann & Makarkin 2007; Wedmann *et al.* 2007, 2009; Wedmann & Yeates 2008; Fikácek *et al.* 2010). After beetles, ants are the most common terrestrial insects among the more than 13,000 fossil insects currently in the Messel insect collection of the Senckenberg Forschungsinstitut. Initial studies on different ant taxa have been published already (Lutz 1986; Dlussky *et al.* 2008, 2009), and together with the current study show the high diversity of the Messel ant taphocoenosis.

Systematic palaeontology

Subfamily **Amblyoponinae** Forel, 1893

Type genus. *Amblyopone* Erichson, 1842.

Diagnosis (for impression fossils). Waist of one segment (petiole). Petiole essentially sessile, with steep broad anterior face but without distinctly descending posterior face, markedly broadly attached to first gastral (III abdominal) segment. Helcium projects from very high on anterior face of first gastral; first gastral segment above the helcium has no free anterior face. Eyes when present (sometimes absent in workers) situated behind midlength of sides of head. Antenna of workers and gynes geniculate, with 7–12 segments, antenna of male filiform, 13-segmented, with very short scape. Pretarsal claws without a preapical tooth. Sting well developed. Forewing either with closed cells 1+2r, 3r, rm and mcu, or section 3RS reduced and united cell 1+2r+rm is present. Cell 3r rather short, shorter than 1/3 of forewing length. Crossvein cu-a meeting M+Cu near cell mcu proximal to section 1M at distance not more than cu-a length.

Composition. Amblyoponinae includes 11 extant genera with 282 extant species (www.antweb.org, accessed 21 January 2011) which are distributed mainly in the tropics. There is one extinct genus, *Casaleia* Pagliano & Scaramozzino, 1990. Four extinct species have been described: *Amblyopone groehni* Dlussky, 2009, *A. electrina* Dlussky, 2009 (Baltic amber, Eocene), *Casaleia inversa* (Dlussky, 1981) (Chon-Tuz, Kotchkorka District, Kirghizsta, Miocene) and *Myopopone sinensis* Zhang, 1989 (Shanwang, Shandong, China, Miocene). A new representative of this subfamily is described below.

Genus **Casaleia** Pagliano & Scaramozzino, 1990
(= *Protamblyopone* Dlussky, 1981 [nec Wheeler, 1927])

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

Diagnosis. Gyne. Mandible triangulate. Eyes large. Antenna 12-segmented. Petiole trapezoid 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.

Species composition. *Casaleia inversa* (Dlussky, 1981) (Chon-Tuz, Kotchkorka District, Kirghizstan, Miocene), and *C. eocenica* sp. nov.

Casaleia eocenica sp. nov.
(Fig. 3)

Etymology. The species name refers to its Eocene age.

Holotype. FIS MeI 5565, dorsal imprint of winged gyne.

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

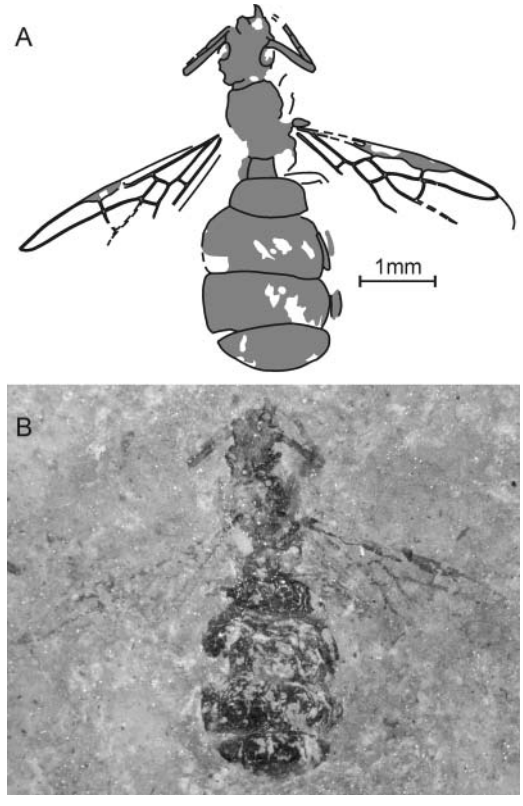

Figure 3. *Casaleia eocenica* sp. nov., gyne, holotype, FIS MeI 5565. **A,** line drawing; **B,** photograph.

Description. Gyne. BL 4.9 mm. Head longer than wide. Eyes rather large, oval, situated nearly at midlength of head sides. Antennal insertions widely separated. Scape protrudes beyond the posterior corners of the head. Petiole wider than long. First gastral segment width is 65% of second and third segments, however this may be result of different deformation connected with different chitinization of segments. Forewing with closed cells 1 + 2r, 3r, rm and mcu. Length of cell 3r is 31% of forewing length. Crossveins rs-m and r-rs meet RS almost at one point, appearing as a single cross vein. Cell rm triangular; its distal corner levelled proximally with distal corner of pterostigma. Cell mcu rectangular, nearly one and a half times longer than wide. Section 2M+Cu nearly as long as cross vein cu-a.

Comparison. The new species differs from *Casaleia inversa* in its size (body length of *C. inversa* = 6.5 mm), the longer scape (in *C. inversa* the scape does not reach the posterior corner of the head) and the more compact mesosoma.

Measurements (in mm). Holotype MeI 5565: AL = 1.1, HL = 0.83, HW = 0.69, SL = 0.76, FWL = 3.2.

Subfamily **Ectatomminae** Emery, 1895

Type genus. *Ectatomma* F. Smith, 1858.

Diagnosis (for impression fossils). Waist of one segment (petiole). Petiole with node, narrowly attached to first gastral (III abdominal) segment, with a distinctly descending posterior face. Helcium projects from about the midheight of the anterior face of first gastral segment; no high vertical anterior face of first gastral segment above the helcium. G1L usually is more than 75% of G2L (60% in *Canopone*), G1H is more than 88% of G2H, and G1W is more than 90% of G2W. Usually with distinctive constriction between first and second gastral segments. Antenna of workers and gynes geniculate, 12-segmented, antenna of male filiform, 13-segmented, with very short scape. Mesotibia and metatibia each with one spur or without spurs in workers and gynes and with one to two spurs in males. Pretarsal claws usually with a median tooth. Forewing with closed cells 1 + 2r, 3r, rm, mcu, and usually also cua. Crossvein cu-a meeting M+Cu near cell mcu proximal to section 1M at distance not more than cu-a length.

Composition. Ectatominae includes 4 extant genera with 298 species (www.antweb.org, accessed 21 January 2011), plus two monotypic extinct genera: *Electroponera* Wheeler, 1915 and *Canapone* Dlussky, 1999. Ten fossil species have been described: *Canapone dentata* Dlussky, 1999 (Canadian amber, Late Cretaceous); *Ectatomma gracile* Emery, 1891 (Sicilian amber, Early Oligocene); *Electroponera dubia* Wheeler, 1915, *Gnamptogenys europaea* (Mayr, 1868) and *G. rohdendorfi* Dlussky, 2009 from Baltic amber (Eocene); *G. brunoi* Lattke, 2002, *G. casca* Lattke, 2002, *G. levinates* Baroni Urbani, 1980 and *G. pristina* Baroni Urbani, 1980 from Dominican amber (Miocene); and *Rhytidoponera kirghizorum* Dlussky, 1981 (Chon-Tuz, Kirghizia, Miocene). Described on the basis of a male, *Ectatomma gracile* undoubtedly belongs to this subfamily but should be reassigned either to *Gnamptogenys* Roger, 1863 or *Rhytidoponera* Mayr, 1862. Hong (2002, p. 538, figs 2.8.331–2.8.340) described *Curticorna leptogastrosa* from the Upper Eocene Fushun amber of China and attributed this species to the subfamily Dorylinae. This is an appreciable error: the wing venation of this ant differs from that of Dorylinae and is similar to poneromorphs. The position of the helcium, form of the gastral segments, and presence of one simple spur on both meso- and metatibia indicate that *Curticorna* may belong to the subfamily Ectatomminae. However, a final decision on this is possible only after restudy of the original material.

The oldest described genus of Ectatomminae is *Canapone*, described by Dlussky (1999) from Grassy Lake Canadian amber (79–78 Ma, McKellar *et al*. 2008). Judging from Anderson's photographs (2009, figs 1–3), an undescribed 'primitive ant' from Burmese amber (Albian, *c*. 100 Ma) is undoubtedly the most ancient known representative of poneromorph ants and most likely belongs to subfamily Ectatomminae. A new genus with two new species is described below.

Genus ***Pseudectatomma*** gen. nov.

Etymology. This genus is named from the Greek word '*pseudo*' (ψευδο) – false, and the ant genus name *Ectatomma*.

Type species. *Pseudectatomma eocenica* sp. nov.

Diagnosis. Gynes. Anteroventral angle of pronotum rounded, without tooth. Metatibia with one pectinate spur. Pretarsal claws lack a median tooth. Petiole nodiform. Second gastral segment trapezoid in side view, its dorsal surface not strongly convex.

Remarks. The new genus differs from Recent genera of Ectatomminae in the form of the gaster. The dorsal surface of the second gastral segment of *Gnamptogenys* Roger, 1863 and *Rhytidoponera* Mayr, 1862 is strongly convex in profile and the tip of the gaster is directed downward. Also in *Rhytidoponera* the anteroventral angle of the pronotum is armed with an acute tooth. The new genus differs from the extinct *Electroponera* Wheeler in the form of its petiole. The petiole of *Electroponera* is angulated in side view and has a concave anterior and a more flattened posterior declivity, both bordered by a sharp ridge.

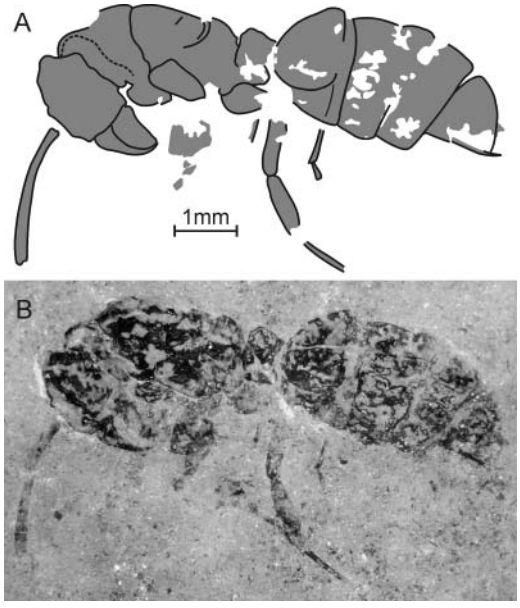

Figure 4. *Pseudectatomma eocenica* sp. nov., gyne, holotype, FIS MeI 400. **A,** line drawing; **B,** photograph.

Pseudectatomma eocenica sp. nov.
(Fig. 4)

Etymology. The species name refers to the Eocene.

Holotype. FIS MeI 400, lateral imprint of gyne.

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

Description. Gyne (indicated by the visible boundaries of the scutellum and postnotum of the mesosoma). BL 9.2 mm. Head longer than wide, with distinctive occipital corners and concave occipital margin. Anterior margin of clypeus weakly convex. Scape nearly 1.5 times longer than head, protrudes beyond the occipital margin of the head. Mandibles wide, triangular, about 66% of head length. Dentition of masticatory margin not visible. Mesosoma about twice longer than high. Propodeum uniformly rounded in side view. Petiole nodiform, subtriangular in side view with rounded upper corner. First gastral segment nearly as high as second. Sting well developed. Eyes, funiculus, tibial spurs and pretarsal claws not preserved in unique imprint.

Measurements (in mm). Holotype, MeI 400: AL = 2.9, HL = 1.5, HW = 1.0, SL = 2.2, G1L = 1.2, G1H = 1.8, G2L = 1.3, G2H = 1.9.

Pseudectatomma striatula sp. nov.
(Fig. 5)

Etymology. From the Latin *striatulus*, marked by parallel lines or ridges.

Holotype. FIS MeI 5762, lateral imprint of winged gyne.

Paratype. FIS MeI 8153, dorsal imprint of head, mesosoma and part of left forewing.

Other material. FIS MeI 10798, lateral imprint of gyne.

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

Description. Gyne. BL 15–16 mm. Head nearly as long as wide, with convex sides, rounded posterior corners and feebly convex posterior margin. Eyes rounded, situated slightly posteriorly of the midlength of head sides. Ocelli form equilateral triangle. Anterior margin of clypeus convex and uniformly rounded. Antennal sockets relatively widely separated. Scape protrudes beyond the posterior margin of the head, about as long as head length. Funicular joints elongate. Mandibles triangular, with large teeth (at least 5). Mandible a little more than half of head length. Mesosoma robust. Scutum small, slightly convex in side view, 1.1 times longer than wide, and 3 times shorter than mesosoma. Scutellum 1.5 times shorter than scutum. Propodeum flat in side view. Petiole not visible. Head with distinct sculpture formed by longitudinal rugae. Forewing venation only partially preserved on paratype imprint. Cross vein cu-a situated near proximal angle of cell mcu, and section 2M+Cu nearly as long as cu-a. Section 1M 3.5 times longer than 1RS.

Measurements (in mm). Holotype, MeI 5762: AL = 5.7, HL = 2.9, ED = 0.1. Paratype MeI 8153: AL > 5.7, HL = 3.0, HW = 3.0, SL = 3.0, ED = 0.67.

Remarks. Petiole and articulation of helcium of this ant are not visible. However, the anterior face of the first gastral segment is gradually rounded (there is no high vertical anterior face above the helcium as in most Ponerinae). Therefore, we infer that the helcium projects from about the midheight of the anterior face of the first gastral segment. Additionally, this ant has one spur both on meso- and metatibia. Because of these features we include *P. striatula* in the subfamily Ectatomminae.

Subfamily **Ponerinae** Lepeletier de Saint-Fargeau, 1835

Type genus. *Ponera* Latreille, 1804.

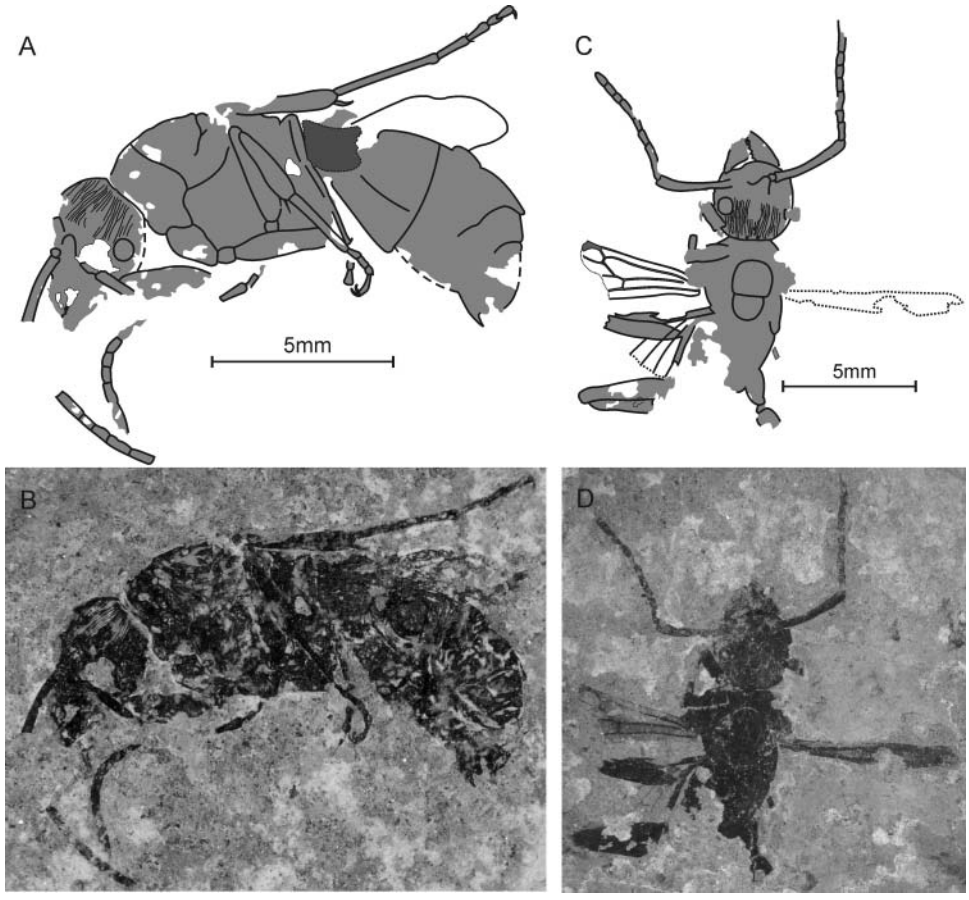

Figure 5. *Pseudectatomma striatula* sp. nov., gynes. **A, B,** holotype, FIS MeI 5762; **A,** line drawing; **B,** photograph. **C, D,** paratype, FIS MeI 8153; **C,** line drawing; **D,** photograph.

Diagnosis (for impression fossils). Waist of one segment (petiole) of different shape narrowly attached to first gastral (III abdominal) segment, with a distinctly descending posterior face. Gaster usually with constriction between first and second gastral (III and IV abdominal) segments. Helcium projects from very low down on the anterior face of first gastral segment, the latter usually with a high vertical anterior face above the helcium. G1L is more than 80% of G2L, G1H more than 85% of G2H, and G1W more than 85% of G2W. Sting always present; often large and strongly developed. Antenna of workers and gynes geniculate, 12-segmented, antenna of male filiform, 13-segmented, with very short scape. Mesotibia and metatibia each with one or two spurs or without spurs. Forewing with closed cells 1 + 2r, 3r, rm and mcu. Crossvein cu-a meeting M+Cu near cell mcu proximal to section 1M at distance not more than cu-a length.

Remarks. Projection of helcium and form of first gastral segment are reliable characters for distinction of most Ponerinae from other poneromorph subfamilies (Amblyoponinae, Ectatomminae, Heteroponerinae, Paraponerinae and Proceratiinae). Representatives of some genera have their first gastral tergite rounded in side view like Ectatomminae, however these species have mesotibiae and metatibiae with two spurs (only one spur in Ectatomminae).

The subfamily Ponerinae includes 28 extant genera with 1798 species (www.antweb.org, accessed 25 January 2011) and 8 extinct genera with 31 species: *Protopone* Dlussky, 1988 (Palaeocene, Sakhalin amber, Russia, monobasic); *Eogorgites* Hong, 2002 *Eoponerites* Hong, 2002, *Furcisutura* Hong, 2002 and *Longicapitia* Hong, 2002 (Early Eocene, Fushun amber, China; all monobasic); *Archiponera* Carpenter, 1930 (Late Eocene, Florissant, USA, monobasic); *Ponerites* Dlussky & Rasnitsyn, 2003 (Middle Eocene–Miocene, 6 species); and *Poneropsis* Heer, 1867 (Oligocene–Miocene, 19 species). However, the data on the fossil species need correction. Some species included by Heer (1867) in the genus *Poneropsis* actually belong to the subfamily Dolichoderinae (Mayr, 1867b). Judging from the drawings, some genera described by Hong (2002) from Eocene Fushun amber as Formicinae and Myrmicinae may belong to Ponerinae. The data of Hong (2002) indicate that a rich fauna of poneromorph ants existed in eastern

Asia during the Early Eocene. However, none of the genera are similar to Recent genera and the true taxonomic position of most poneromorph genera from the Fushun amber is unclear. Some of these genera probably belong to an undescribed extinct subfamily (or subfamilies). However, restudy of the original material is required.

Following Bolton (2003), the subfamily Ponerinae includes three tribes: Thaumatomyrmecini with the sole genus *Thaumatomyrmex* Mayr, 1887; Platythyreini with the sole genus *Platythyrea* Roger, 1863; and Ponerini which includes all other genera. Species of the South American genus *Thaumatomyrmex* have an unusual mandible with a small number (3–5) of extremely attenuated slender teeth. Fossil representatives of this genus are as yet unknown. Species of *Platythyrea* have the following combination of characters which may be seen in fossil imprints: clypeus broadly inserted between horizontal frontal lobes; antennal sockets relatively widely separated, not closely approximated; mesotibia and metatibia each with two pectinate spurs; pretarsal claws each usually with a preapical tooth. None of the specimens from Grube Messel have such a combination of characters. A key character of the tribe Ponerini is the combination of a low position of the helcium and closely approximated antennal sockets. All species from Grube Messel that we include in the subfamily Ponerinae have a low position of the helcium; however, only some of them have approximated antennal sockets. We include the species with approximated antennal sockets in the genus *Pachycondyla*, and the species with widely separated antennal sockets in the extinct genus *Protopone* or in three new genera described below.

The diagnoses of the genera proposed below include only characters visible on fossil imprints. Generic placement of some of the fossils is very difficult because only a very limited number of characters is preserved in fossil imprints, a common problem with fossil species preserved as imprints. As our main aim is to document species diversity in the Messel Pit fossil site, we describe all species even if their generic assignment is uncertain.

Genus ***Pachycondyla*** F. Smith, 1858

(= *Ectomomyrmex* Mayr, 1867a (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Bothroponera* Mayr, 1862 (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Megaponera* Mayr, 1862 (syn. by Bolton 1994))
(= *Paltothyreus* Mayr, 1862 (syn. by Bolton 1994))
(= *Euponera Forel*, 1891 (syn. by Bolton 1994))
(= *Brachyponera* Emery, 1900a (provisional syn. by Snelling 1981, syn. by Bolton 1994))
(= *Pseudoponera* Emery, 1900a (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Ophthalmopone* Forel, 1890 (syn. by Bolton 1994))
(= *Mesoponera* Emery, 1900b (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Neoponera* Emery, 1901 (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Eumecopone* Forel, 1901a (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Hagensia* Forel, 1901b (syn. by Bolton 1994))
(= *Trachymesopus* Emery, 1911 (provisional syn. by Brown, 1973, syn. by Snelling 1981))
(= *Xyphopelta* Forel, 1913 (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Syntermitopone* Wheeler, 1936 (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Termitopone* Wheeler, 1936 (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Wadeura* Weber, 1939 (provisional syn. by Brown 1973, syn. by Snelling 1981))
(= *Pseudoneoponera* Donisthorpe, 1943 (provisional syn. by Brown 1973, syn. by Snelling 1981))

Type species. *Formica crassinoda* Latreille, 1802, by subsequent designation of Emery (1901).

Diagnosis (for impression fossils). Head less than 1.7 times shorter than mesosoma. Antennal sockets closely approximated. Frons width less than 25% of head width. Mandible of gyne and worker subtriangular with dentate masticatory margin, less than 65% of head length. Male with very reduced and not opposable mandibles. Middle and hind tibiae each with a large pectinate spur and a small simple spur. Pretarsal claws simple. Petiole with thick scale or high node. Helcium projects from very low down on the anterior face of first gastral segment, the latter with a high vertical anterior face above the helcium. G1L is more than 106–175% of G2L, G1H is 95–120% of G2H, and G1W is more than 93–105% of G2W. Pygidium of male with distinct terminal spine.

Remarks. The genus includes 366 extant (www.antweb.org, accessed 25 January 2011) and 12 described extinct species. However, some species included in *Pachycondyla* by Bolton (1995) do not belong to this genus. Judging from descriptions and drawings, the species described by Théobald (1937) as *Brachyponera dubia*, *Euponera globiventris* and *E. calcarea* (Kleinkembs, France, Oligocene), which were transferred to *Pachycondyla* by Bolton (1995), probably really belong to the subfamily Dolichoderinae, but this has to be confirmed from the original material. The construction of the metasoma of these ants is typical for representatives of the formicomorph subfamily group. The forewings of *B. dubia* and *E. calcarea* have closed cells 1 + 2r, 3r, rm and mcu as in most poneromorphs and Dolichoderinae, but cross vein cu-a seems to be displaced to the wing base (character of Dolichoderinae). The species described by Donisthorpe (1920) from Bembridge, UK (Oligocene) as *Euponera (Mesoponera) crawleyi*, which was transferred by Bolton

(1995) to *Pachycondyla*, belongs to Ponerinae, but no key characters of *Pachycondyla* are visible on the imprints (unpublished data of Dlussky). The taxonomic position of species described by Zhang (1989) from Miocene deposits of Shanwang (China) as *Euponera nubeculata* and *E.? minutansata* (*Euponera* is a junior synonym of *Pachycondyla*) are unclear, partly because the quality of the drawings is not good. The narrow frons and the closely approximated antennal sockets may be an indirect indication that *E. nubiculata* belongs to Ponerinae. But the comparatively large size (9 mm) precludes inclusion of this species in the morphogenus *Ponerites* Dlussky & Rasnitsyn, 2003. The species described as *E. minutansata* undoubtedly does not belong in Ponerinae. The feature accepted by Zhang as a constriction between the first and second gastral segments is probably the result of gaster deformation during fossilization. Such deformations are often found in imprints of ants with a fat gaster. In side view, a petiole with a high vertical scale with an acute top is visible. Such a construction of the petiole is characteristic for most Formicinae and some Dolichoderinae.

Consequently, only six described fossil species can be placed with confidence in *Pachycondyla*: *P. labandeirai* Dlussky & Rasnitsyn, 2003 (Green River Formation, USA, Middle Eocene); *P. succinea* (Mayr, 1868), *P. gracilicornis* (Mayr, 1868) and *P. baltica* Dlussky, 2003 (Baltic amber, Eocene); *P. conservata* Dlussky, 2009 (Rovno amber, Eocene); and *P. tristis* Dlussky, 2009 (Bitterfeld amber, Eocene). Gynes of only three of these species are known, and these gynes all differ from the six species described below from Grube Messel. Of the described species, *P. labandeirai* is unique in its wide head (HW > HL), *P. tristis* is distinguished by its wide and thin scale of petiole, while *P. succinea* has an angulate propodeum and a rounded top of the scale in side view like *P. eocenica* and *P. messeliana* from Grube Messel but differing from these species in its smaller size (BL 4–6 mm).

Pachycondyla eocenica sp. nov.
(Fig. 6)

Etymology. The species name refers to the Eocene.

Holotype. FIS MeI 10889, lateral imprint of winged gyne.

Paratype. FIS MeI 8710, head of gyne or worker in full face view.

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

Description. Gyne. BL 8.8 mm. Head as long as wide, with convex sides, rounded posterior corners and weakly concave posterior margin. Anterior margin of clypeus uniformly convex. Eyes oval, situated in front of the midlength of head; head about 5 times longer than maximum eye diameter. Gena longer than maximal eye diameter. Frons width nearly 23% of head width. Scape almost reaching the posterior margin of the head. Head 1.3 times as long as scape length. Funiculus gradually incrassate to the apex but without distinctly differentiated club. Funicular segments (except first and apical) less than 1.5 times longer than thick. Mandibles subtriangular with 9–10 comparatively large teeth. Mandible length is about half (51% in holotype and 53% in paratype) of head length. Mesosoma robust. Scutum flat in side view, 3.7 times shorter than mesosoma. Scutellum small, 6.5 times shorter than mesosoma. Propodeal dorsum and declivity form rounded obtuse angle. Petiole with high and thick scale, its top is gradually rounded in side view. First gastral segment 1.3 times longer than second.

Measurements (in mm). Holotype, MeI 10889: AL = 2.6, HL = 1.5, HW = 1.5. Paratype MeI 8710: HL = 1.5, HW = 1.5, SL = 1.1, ED = 0.35, MdL = 0.81.

Remarks. Conspecificity of the holotype and paratype specimen can be questioned. Mesosoma and metasoma of the holotype specimen are preserved, but the head is seen only as a contour, only the outer ridges of the mandibles are preserved, and eyes and antennae are not preserved. At the same time only the head of the paratype specimen is preserved. However, we consider that the specimens are conspecific as the form of their heads is similar and different from all other ponerines of the same size.

Pachycondyla lutzi sp. nov.
(Fig. 7)

Etymology. In honour of the palaeoentomologist Herbert Lutz, who was one of the first to study ants from Grube Messel.

Holotype. FIS MeI 11958, lateral imprint of winged gyne.

Paratypes. FIS MeI 11481, dorsal imprint of worker without gaster; FIS MeI 1361, FIS MeI 3553, FIS MeI 2078, FIS MeI 10526, dorsal imprints of winged gynes; FIS MeI 11679, lateral imprint of gyne.

Other specimens (gynes). FIS MeI 10564, FIS MeI 12975, FIS MeI 13507.

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

Description. Gyne. BL 11–15 mm. Head with convex sides, rounded posterior corners and weakly convex posterior margin. Head 1.04–1.13 times wider than long.

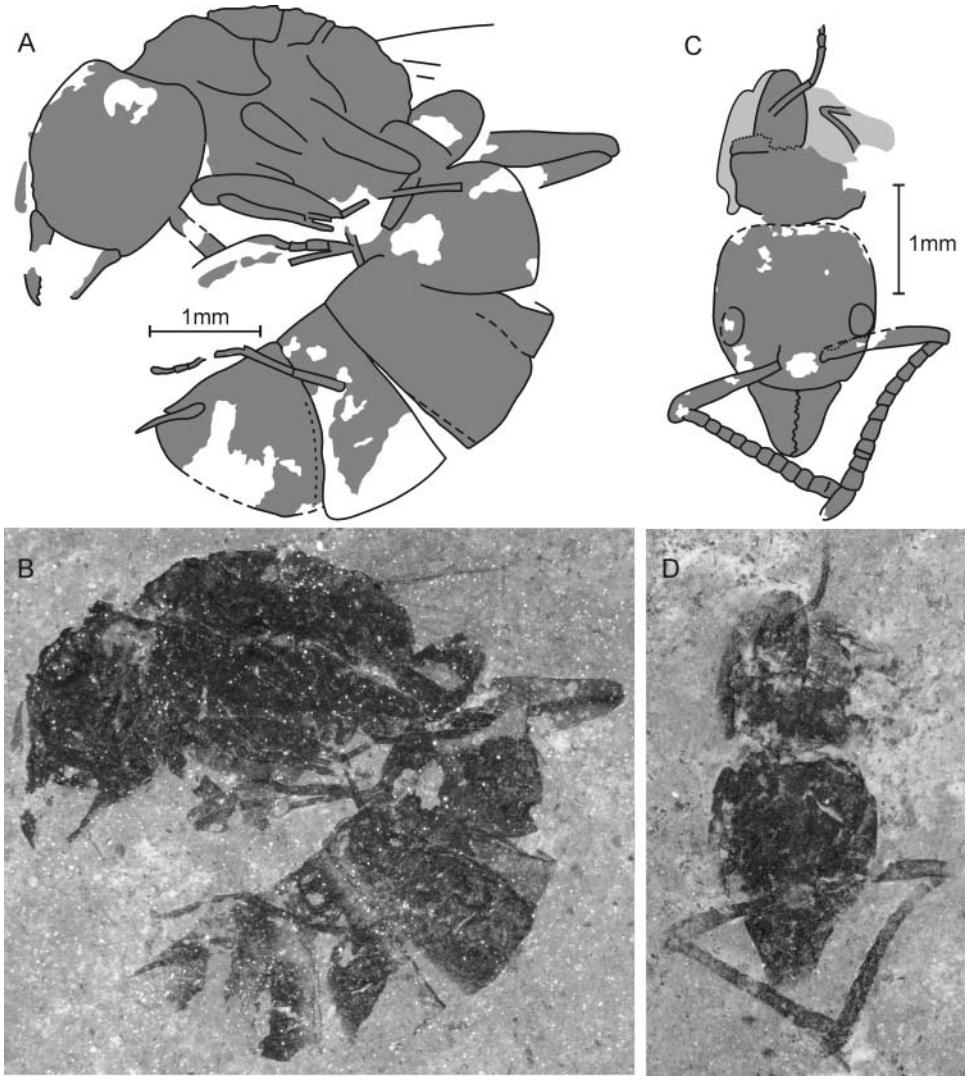

Figure 6. *Pachycondyla eocenica* sp. nov. **A, B,** gyne, holotype, FIS MeI 10889; **A,** line drawing; **B,** photograph. **C, D,** gyne or worker, paratype, FIS MeI 8710; **C,** line drawing; **D,** photograph.

Eyes shortly oval, almost round, displaced forward; head about 5 times longer than maximum eye diameter. Anterior margin of clypeus gradually rounded or (in MeI 3553) with small and shallow concavity in the middle. Frons width is 18–23% of head width. Scape protrudes not beyond the posterior margin of the head. Head nearly 1.4 times as long as scape length. Funiculus gradually incrassate to the apex but without distinctly differentiated club. Funicular segments (except first and apical) less than 1.5 times longer than thick. Mandibles subtriangular with 5–6 comparatively large teeth. Mandible length is about half (50–55%) of head length. Scutum small, transverse, 3.5 times shorter than mesosoma. Propodeum rounded in side view. Petiole with thick and high scale, wider than long. First gastral segment nearly as wide as second. Tibial spurs and pretarsal claws not visible at any specimens. Forewing with closed cells 1 + 2r, 3r, rm, mcu and cua. Section 5RS straight or slightly bent towards anterior margin of wing. Cross vein rs-m more distal than r-rs, so cell rm pentagonal. 1RS shorter than 1M. Cell mcu pentagonal. Cross vein cu-a meeting 1M + Cu near proximal angle of mcu, so 2M + Cu shorter than cu-a. Hind wing with all longitudinal and transverse veins.

Worker. Gaster absent, so precise measurement is impossible, but evidently about 8 mm. Head about as long as wide. Scape does not reach the occipital corner of the head. Head nearly 1.4 times as long as scape length. Frons width is 16% of head width. Eyes small: head about 7 times longer than maximum eye diameter. Clypeus with slightly emarginated anterior margin. Mesosoma 2.5 times longer than wide.

Measurements (in mm). Gyne: Holotype, MeI 11958: AL = 3.7, HL = 2.9, HW = 3.1, SL = 2.6, FWL = 6.8.

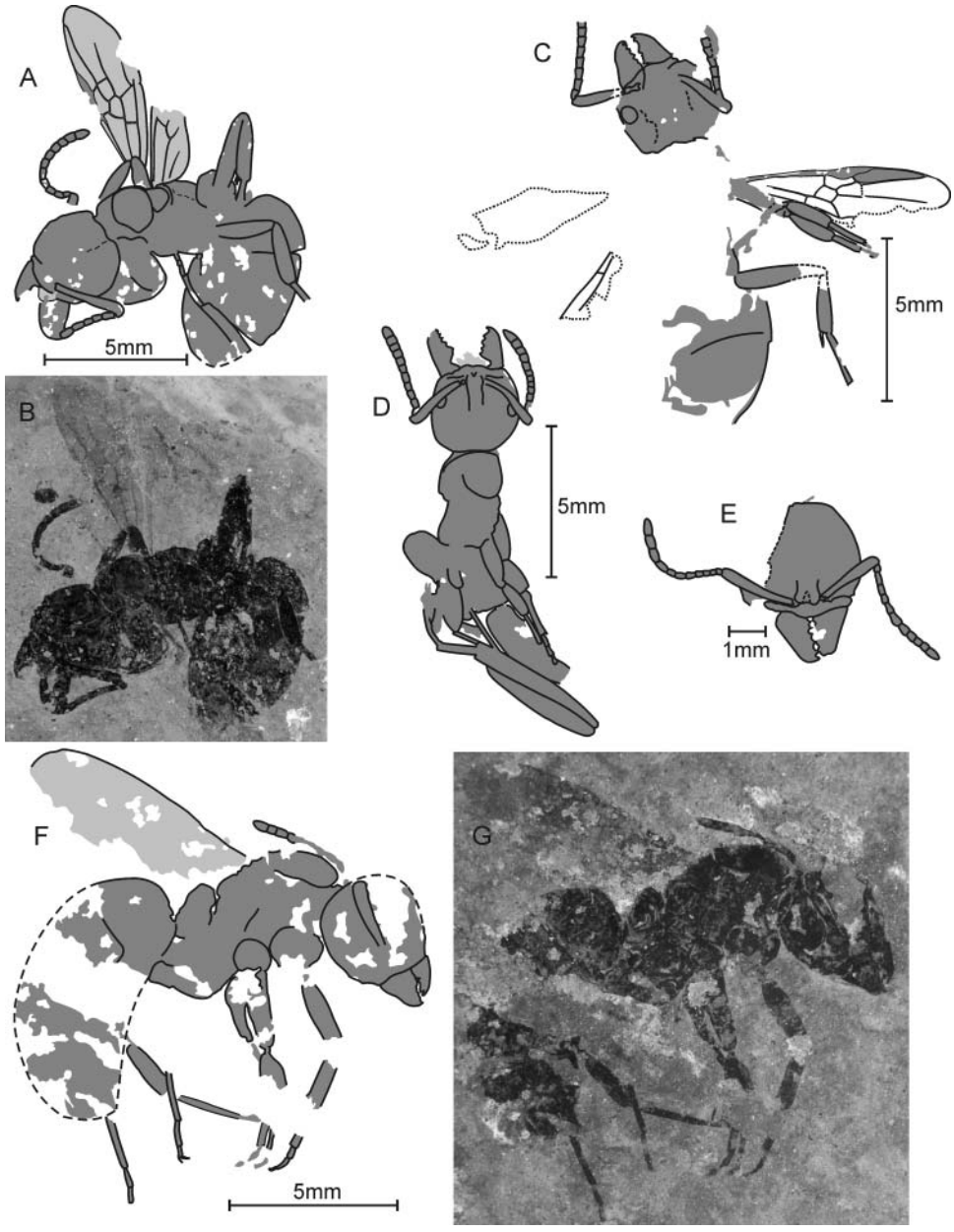

Figure 7. *Pachycondyla lutzi* sp. nov. **A, B,** gyne, holotype, FIS MeI 11958; **A,** line drawing; **B,** photograph. **C,** gyne, paratype, FIS MeI 1361, line drawing. **D,** worker, paratype, FIS MeI 11481, line drawing. **E,** head of gyne or worker, paratype, FIS MeI 3553, line drawing. **F, G,** gyne, paratype, FIS MeI 11679; **F,** line drawing; **G,** photograph.

Paratypes: MeI 2078: HL ~ 2.5, HW = 2.4, SL = 1.8, MdL = 1.0; MeI 10526: AL = 3.9, HW = 2.8; MeI 3553: HL = 3.1, SL = 2.1, MdL = 1.6; MeI 1361: HL = 2.6, HW = 2.9, SL = 1.8, ED = 0.52, MdL = 1.4, FWL = 6.8. MeI 11679: AL = 4.15, HL = 2.8. Worker: paratype, MeI 11481: AL ~ 3.2, HL = 1.70, HW = 1.76, SL = 1.25, ED = 0.25.

Pachycondyla? messeliana sp. nov.
(Fig. 8)

Etymology. Named after the type locality (Messel).

Holotype. FIS MeI 4744, lateral imprint of winged gyne.

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

Description. Gyne. BL 14.5 mm. Head massive, 1.3 times shorter than mesosoma. Scape does not protrude beyond the posterior margin of the head. Mesosoma robust, 1.8 times longer than high. Scutum convex in side view. Propodeal dorsum and declivity both nearly straight, they form

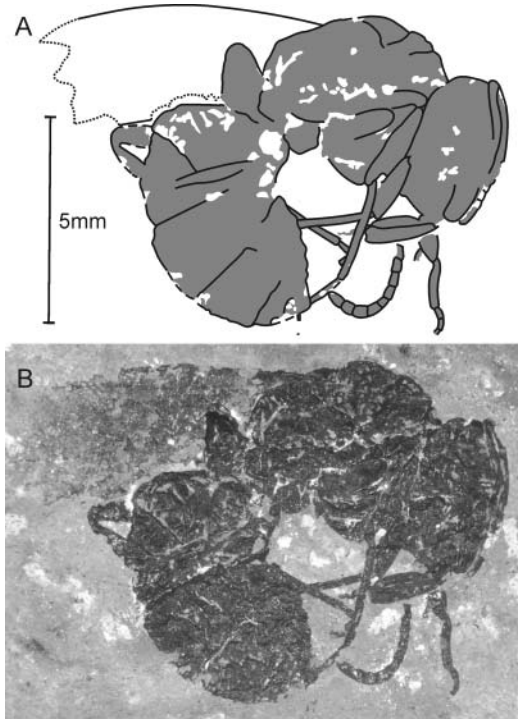

Figure 8. *Pachycondyla*? *messeliana* sp. nov., gyne, holotype FIS MeI 4744. **A,** line drawing; **B,** photograph.

distinctive obtuse angle in side view. Petiolar scale tapered upward. Anterior and posterior sides of scale slightly convex in side view, apex rounded.

Measurements (in mm). Holotype, FIS MeI 4744: AL = 4.5, HL = 3.5.

Remarks. Most of the key characters are not visible on the imprint. But the form of the second gastral tergite (presence of presclerite) indicates that this species belongs to Poneromorpha. As the helcium of the specimen projects from very low down on the anterior face of the first gastral segment, it cannot belong to either Amblyoponinae or Ectatomminae. It has a petiole with a high scale and therefore cannot belong to *Protopone*, *Cephalopone* or *Messelepone*. The comparatively large head precludes assignment to *Cyrtopone*. Consequently, the new species either belongs to *Pachycondyla* or is a new genus. As the poor preservation of the specimen does not permit establishment of a new genus, the species is placed provisionally in the genus *Pachycondyla*.

Pachycondyla minuta sp. nov.
(Fig. 9)

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

Holotype. FIS MeI 10638, lateral imprint of gyne (the construction of the mesosoma undoubtedly indicates that it

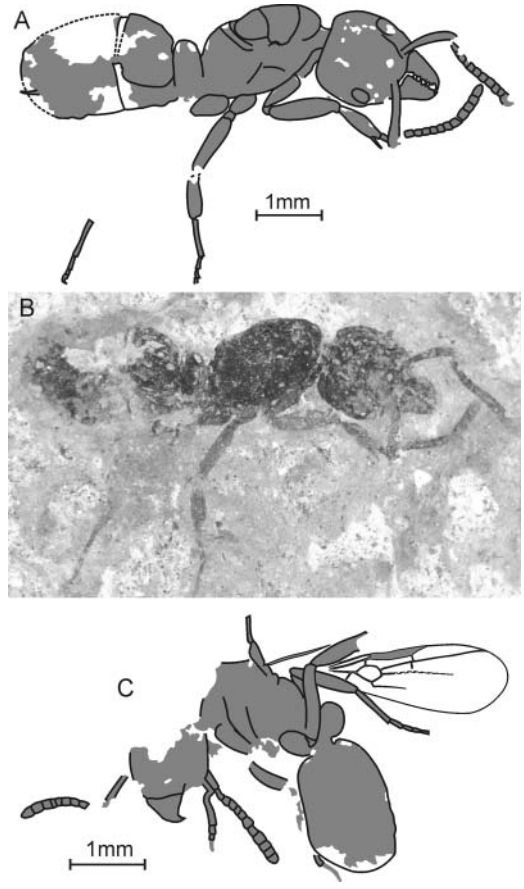

Figure 9. *Pachycondyla minuta* sp. nov., gynes. **A, B,** holotype, FIS MeI 10638; **A,** line drawing; **B,** photograph. **C,** paratype, FIS MeI 12250, line drawing.

is a gyne: the mesonotum is distinctly divided in scutum and scutellum).

Paratypes. Gynes. FIS MeI 10167, FIS MeI 12250.

Other specimens. Gynes. FIS MeI 10093, FIS Mel 13789, FIS Mel 14219.

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

Description. Gyne. BL 6–7.3 mm. Head 1.1 times wider than long, with convex sides, rounded posterior corners and straight posterior margin. Anterior margin of clypeus gradually rounded. Eyes rather small, situated in front of lateral midlength of head; head 4.5–5 times longer than maximum eye diameter. Gena a little longer than maximal eye diameter. Scape does not reach the posterior margin of the head. Head 1.1 times as long as scape length. Funiculus gradually incrassate to the apex but without a distinctly differentiated club. Funicular segments (except first and apical) less than

1.5 times longer than thick. Mandibles subtriangular with 7 large acute teeth. Mandible length is about 57% of head length. Scutum transverse, 3.5 times shorter than mesosoma. Scutellum 4 times shorter than mesosoma, longer than wide. Propodeum rounded in side view. Petiole with high and thick scale. Anterior and posterior sides of scale in side view subparallel, weakly convex, apex rounded. Forewing of gyne with closed cells 1 + 2r, 3r, rm, mcu and cua. Section 5RS straight or slightly bent in a direction of anterior margin of wing. 1RS shorter than 1M. Cell mcu pentagonal. Section 2M + Cu nearly 1.5 times as long as cross vein cu-a.

Measurements (in mm). Holotype, MeI 10638: AL = 2.1, HL = 1.3, HW = 1.4, SL = 1.0, ED = 0.28, MdL = 0.7. Paratype MeI 10167: HL = 0.86; AL ~ 1.0. Paratype, MeI 12250: AL = 1.6, HW = 1.0, FWL = 2.7.

Pachycondyla petiolosa sp. nov.
(Fig. 10)

Etymology. From the Latin *petiolosus*, with a conspicuous petiole.

Holotype. FIS MeI 1893, lateral imprint of winged gyne.

Paratype. FIS MeI 1427, lateral imprint of winged gyne.

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

Description. Gyne. BL 20–22.5 mm. Large massive ant. Head subquadrate with rounded posterior corners and straight or weakly convex posterior margin. Eyes oval, situated slightly behind the lateral midlength of head; head 3.4–5 times longer than maximal eye diameter. Anterior margin of clypeus not visible. Scape protrudes slightly beyond the occipital margin of the head. Middle funicular segments 1.5–2 times longer than thick. Mandibles shorter than half of head length. Mesosoma robust. Petiole with high and thick scale. Scale 1.5–1.7 times higher than long; anterior and posterior sides of scale subparallel in side view, apex rounded. Last gastral tergite of paratype with visible hairs which stick out.

Measurements (in mm). Holotype, MeI 1893: AL = 7.1, HL = 4.7, SL = 3.2, ED = 1.2. Paratype, MeI 1427: AL = 7.2, SL = 3.1, ED = 1.2, FWL = 12.9.

Pachycondyla petrosa sp. nov.
(Fig. 11)

Etymology. From the Greek *petros* ($\pi\varepsilon\tau\rho o\varsigma$) (stone).

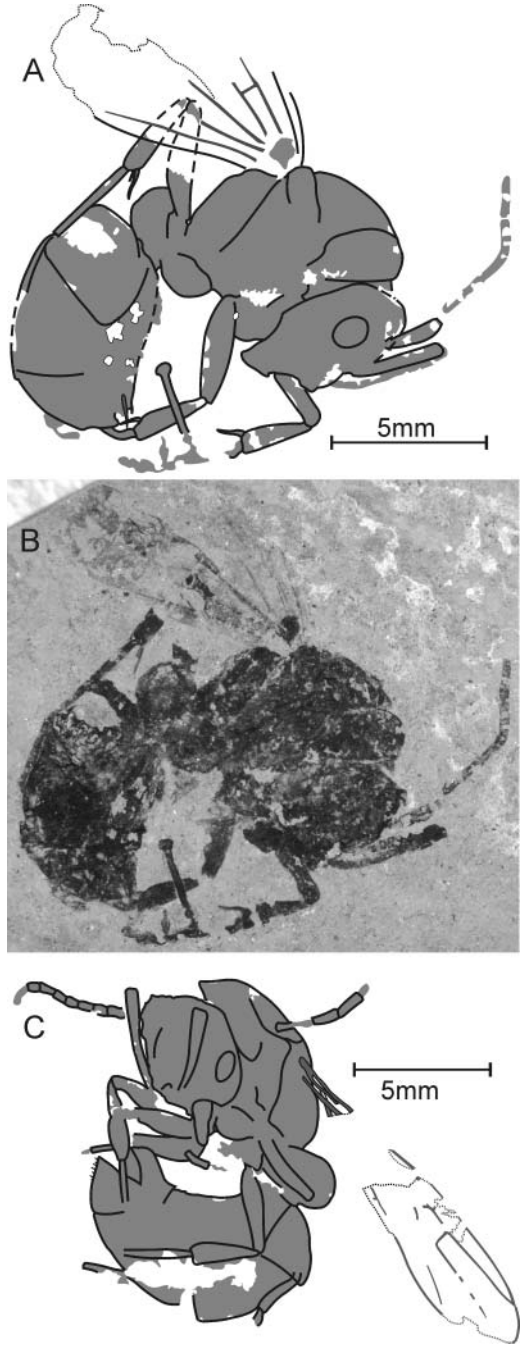

Figure 10. *Pachycondyla petiolosa* sp. nov., gynes. **A, B,** holotype, FIS MeI 1893; **A,** line drawing; **B,** photograph. **C,** paratype, FIS MeI 1427, line drawing.

Holotype. FIS MeI 12273, lateral imprint of gyne or worker.

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

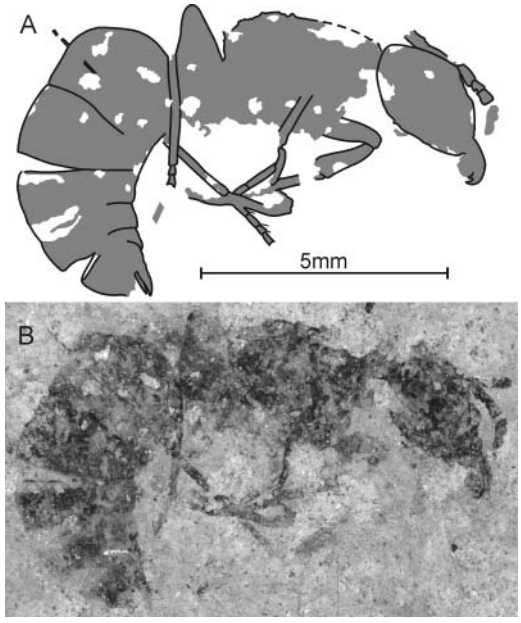

Figure 11. *Pachycondyla petrosa* sp. nov., gyne, holotype, FIS MeI 12273. **A,** line drawing; **B,** photograph.

Description. Gyne or worker. BL 12.4 mm. Mandibles triangulate with large teeth, shorter than half of head length. Propodeum angulated in side view. Petiole with high scale, triangulate in side view, with narrowly rounded top. First gastral segment longer than second and as high as second.

Measurements (in mm). Holotype, MeI 12273: AL = 3.25, HL = 2.55, PtL = 1.1, PtH = 1.8, G1L = 2.5, G2L = 1.5, G1H = G2H = 2.4.

Remarks. Habitually, this new species is very similar to Recent *Pachycondyla* from the former subgenus *Mesoponera*.

Genus ***Protopone*** Dlussky, 1988

Type species. *Protopone primigena* Dlussky, 1988.

Diagnosis (for impression fossils). Gyne. Head at most 1.7 times shorter than mesosoma. Antennal sockets relatively widely separated, not closely approximated. Frons width more than 30% of head width. Mandible subtriangular with dentate masticatory margin, less than 70% of head length. Middle and hind tibiae each with a large pectinate spur and a small simple spur. Pretarsal claws simple. Petiole nodiform. Helcium projects from very low down on the anterior face of first gastral segment, the latter with a high vertical anterior face above the helcium.

Remarks. The type species was described from Sakhalin amber (Palaeocene) from a wingless gyne specimen and six new species are described below. The type species differs from the new species described below on the basis of gynes by the following combination of characters: the scape does not reach the posterior margin of the head; the eyes are shifted forwards (the gena is shorter than the maximal eye diameter); the petiolar node is triangular in side view; and body length is about 3.5 mm.

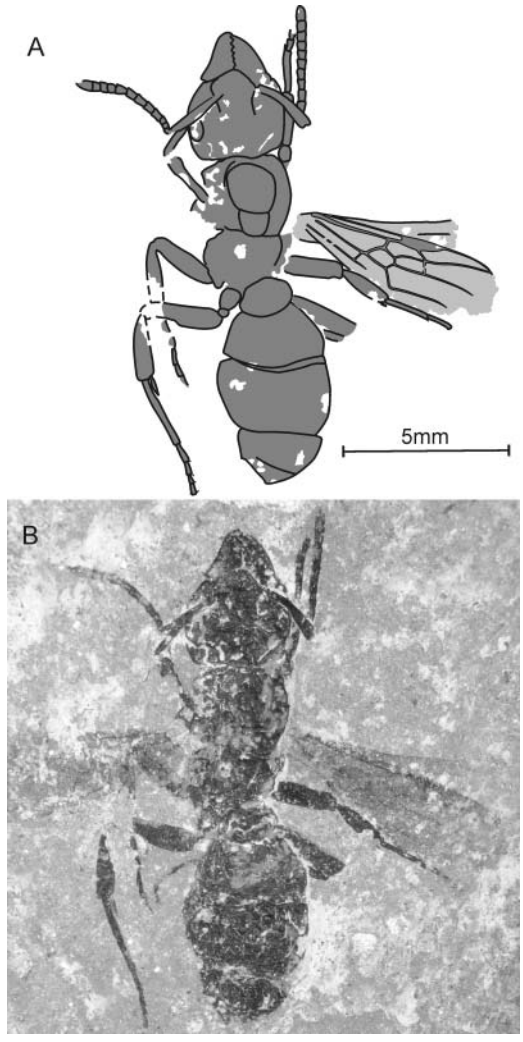

Figure 12. *Protopone germanica* sp. nov., gyne, holotype, FIS MeI 10841. **A,** line drawing; **B,** photograph.

Protopone germanica sp. nov.
(Fig. 12)

Etymology. The species name is derived from the country of origin.

Holotype. FIS MeI 10841, dorsal imprint of winged gyne.

Other material. FIS MeI 12360 (head).

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

Description. Gyne. BL 13.7 mm. Head 1.15 times wider than long with weakly convex sides, rounded posterior corners and weakly convex posterior margin. Mesosoma 1.6 times longer than head. Anterior margin of clypeus rounded. Eyes oval, situated slightly behind the lateral midlength of head. Head about 4 times longer than maximum eye diameter. Frons width about 45% of head width. Scape reaches the posterior margin of the head. Head about 1.4 times longer than scape length. Funiculus slightly incrassate to the apex, without a differentiated club. Funicular segments longer than thick. Mandibles massive, subtriangular, about 60% of head length, with 6 teeth on the masticatory margin. Mesosoma robust, 1.6 times longer than wide. Scutum small, longer than wide, 2.7 times shorter than mesosoma. Petiole nodiform, 1.5 times wider than long. First gastral segment 1.9 times wider than petiole and about as wide as second gastral segment. Left metatibia with pectinate spur; second (simple) spur not visible. Forewing with closed cells 1 + 2r, 3r and mcu. Cell 1 + 2r 2.75 times longer than wide. Cross vein r-rs strongly inclined forward. Cell 3r 5 times longer than wide; section 5RS slightly S-formed. Cell mcu pentagonal, 1.6 times longer than wide. Cross vein rs-m closed, cell rm absent on the imprint, however some brown spots are preserved which may be remains of the cross vein. If so, cell rm was quadrangular, 2.4 times longer than wide, and cross veins r-rs and rs-m start from RS from the same point. Cross vein cu-a situated near proximal corner of cell mcu; section 2M+Cu about as long as two widths of vein.

Measurements (in mm). Holotype, MeI 10841: AL = 4.3, HL = 2.6, HW = 2.95, SL = 1.9, ED = 0.65, MdL = 1.6, PtL = 1.1, PtW = 1.6, FWL ~ 6.8.

Protopone? dubia sp. nov.
(Fig. 13)

Etymology. From the Latin *dubius*, uncertain or doubtful.

Holotype. FIS MeI 10142, head and fragments of mesosoma and forewing of winged gyne.

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

Description. Head apparently longer than wide, with rounded posterior corners and convex posterior margin. Anterior margin of clypeus rounded. Eyes oval, situated slightly in front of lateral midlength of head. Head about 5 times longer than maximum eye diameter. Gena nearly as long as maximal eye diameter. Antennal sockets relatively widely separated. Scape protrudes slightly beyond the posterior margin of the head. Head 1.3 times longer than scape. Funiculus slightly incrassate to the apex, without a differentiated club. Funicular segments except first and apical nearly 1.5 times longer than thick. Mandibles subtriangulate, with numerous (10 or more) teeth, comprising nearly 65% of head length.

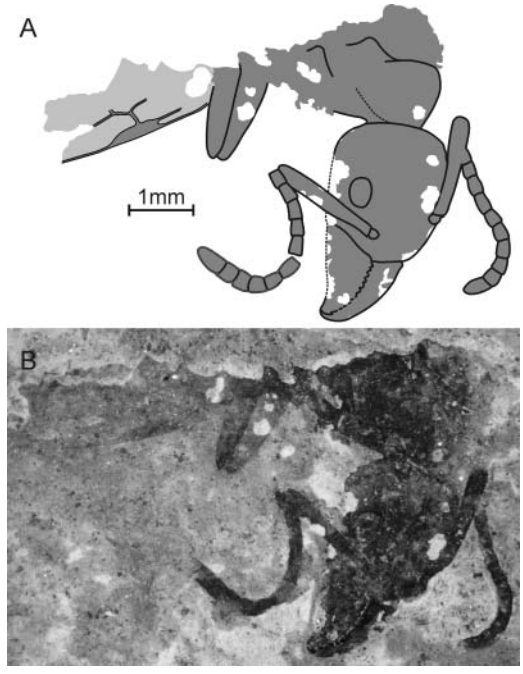

Figure 13. *Protopone*? *dubia* sp. nov., gyne, holotype, FIS MeI 10142. **A,** line drawing; **B,** photograph.

Measurements (in mm). Holotype, MeI 10142: HL = 2.2, SL = 1.7, ED = 0.46.

Remarks. In spite of the fact that only the head and pronotum of this specimen are preserved, we believe that enough characters are visible to allow the naming of a separate species. This species cannot belong to the genus *Pachycondyla* as the antennal sockets are widely separated, nor to the genus *Cephalopone*, as its mandibles are less than 80% of head length, or to the genera *Cyrtopone* and *Messelpone*, as its mandibles are more than 50% of head length. *Pseudectatomma eocenica* has mandibles of similar length, but they are more massive and the scape is much longer. Therefore, this species is provisionally placed in the genus *Protopone*. It differs from all known species of *Protopone* by the combination of comparative long multidentate mandibles and comparatively small eyes.

Protopone magna sp. nov.
(Fig. 14)

Etymology. From the Latin *magnus*, large.

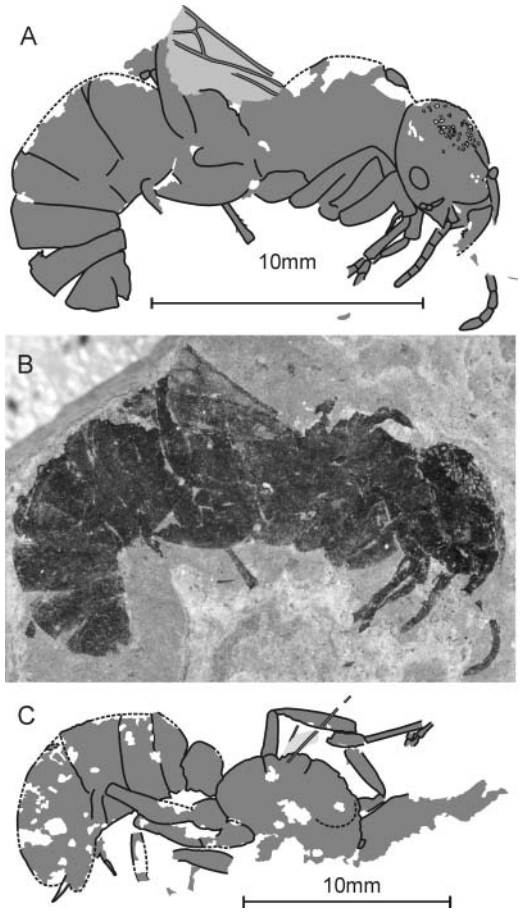

Figure 14. *Protopone magna* sp. nov., gynes. **A, B,** holotype, FIS MeI 8790; **A,** line drawing; **B,** photograph. **C,** paratype, FIS MeI 8789, line drawing.

Holotype. FIS MeI 8790, lateral imprint of winged gyne.

Paratype. FIS MeI 8789, lateral imprint of winged gyne without head.

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

Description. Gyne. BL *c*.26 mm. Large massive ant. Head 1.5 times shorter than mesosoma. Anterior margin of clypeus rounded. Antennae without club; middle funicular segments nearly twice longer than thick. Mandibles preserved only partially, but it seems that they are comparatively short, perhaps shorter than half of head length. Mesosoma comparatively short and high. Scutum longer than in other *Protopone* species. Propodeum rounded in side view. Petiole nearly as long as high, nodiform with very short peduncle. In side view anterior and dorsal surfaces gradually rounded, without distinct boundary; posterior surface of petiole straight and forms distinct rounded angle with dorsal surface. First gastral segment nearly as long and high as second. Head with distinctive foveolate sculpture.

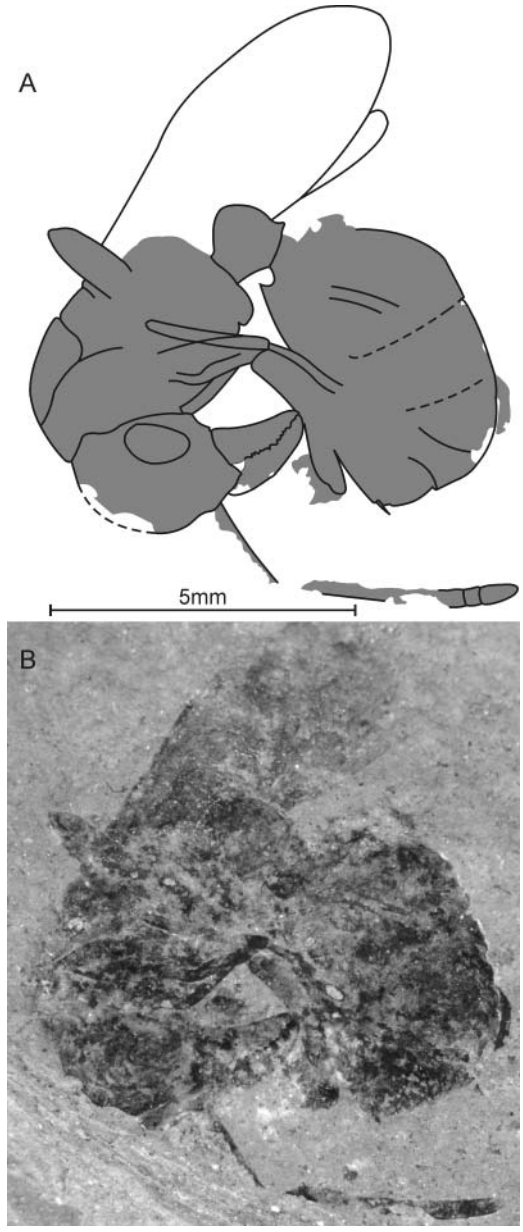

Figure 15. *Protopone oculata* sp. nov., gyne, holotype, FIS MeI 2334. **A,** line drawing; **B,** photograph.

Measurements (in mm). Holotype, MeI 8790: AL = 6.6, HL = 4.4, ED = 0.87. Paratype MeI 8789: AL = 7.2.

Protopone oculata sp. nov.
(Fig. 15)

Etymology. From the Latin *oculatus* (eyed), referring to its large eyes.

Holotype. FIS MeI 2334, lateral imprint of winged gyne.

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

Description. Gyne. BL 14 mm. Head 1.6 times shorter than mesosoma. Anterior margin of clypeus rounded. Eyes large, oval, situated slightly in front of lateral midlength of head. Head 2.3 times longer than maximal eye diameter. Gena shorter than maximal eye diameter. Mandibles subtriangulate, with numerous (10 or more) teeth, nearly 58% of head length. Mesosoma robust. Scutum slightly convex, 2.3 times shorter than mesosoma. Dorsal and declivous surfaces of propodeum in side view form rounded right angle. Petiole a little higher than long, with node rounded in side view and short peduncle. First gastral segment longer than second.

Measurements (in mm). Holotype MeI 2334: AL = 4.1, HL = 2.6, ED = 1.07, MdL = 1.45, PtL = 1.30, PtH = 1.18.

Protopone sepulta sp. nov.
(Fig. 16)

Etymology. From the Latin *sepultus*, buried.

Holotype. FIS MeI 5329, imprint of winged gyne.

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

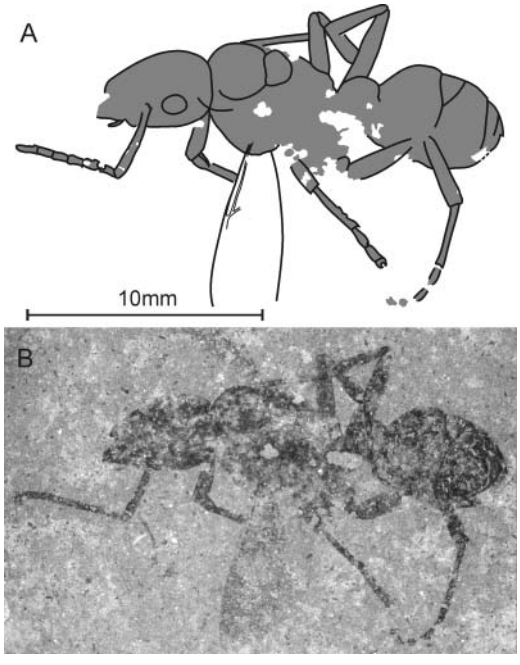

Figure 16. *Protopone sepulta* sp. nov., gyne, holotype, FIS MeI 5329. **A,** line drawing; **B,** photograph.

Description. Gyne. BL 16.5 mm. Head longer than wide, with rounded posterior corners and straight posterior margin. Mesosoma nearly 1.3 times longer than head. Eyes oval, situated on the midlength or slightly behind the lateral midlength of head. Head about 4 times longer than maximal eye diameter. Gena longer than maximal eye diameter. Scape 1.3 times shorter than head, protrudes slightly beyond the posterior margin of the head. Funicular segments elongated, about twice longer than thick. Mesosoma robust. Scutum nearly 2.6 times shorter than mesosoma. Petiole with rounded node and short peduncle. First gastral segment longer than second.

Measurements (in mm). Holotype, MeI 5329: AL = 5.0, HL = 4.2, SL = 3.05, ED = 0.95, PtL = 1.8.

Protopone vetula sp. nov.
(Fig. 17)

Etymology. From the Latin *vetulus*, old, wizened.

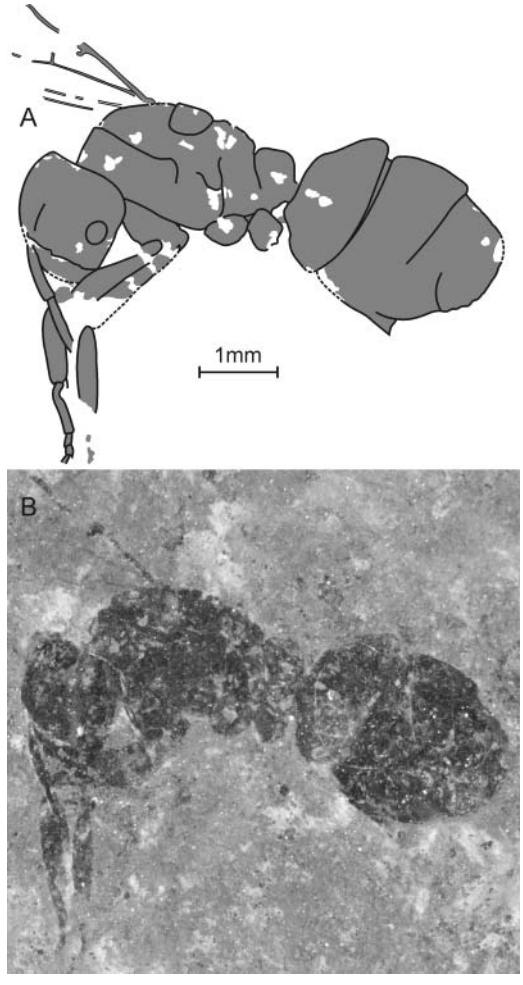

Figure 17. *Protopone vetula* sp. nov., gyne, holotype, FIS MeI 7679. **A,** line drawing; **B,** photograph.

Holotype. FIS MeI 7679, lateral imprint of winged gyne.

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

Description. Gyne. BL 7 mm. Head 1.15 times wider than long, subrectangular, with nearly straight sides, rounded posterior corners, and straight posterior margin. Mesosoma 1.7 times longer than head. Eyes oval, situated slightly in front of lateral midlength of head. Head 3.7 times longer than maximal eye diameter. Gena longer than maximal eye diameter. Mandibles shorter than half of head length. Mesosoma robust, 1.4 times longer than high. Scutum convex in side view, 2.2 times shorter than mesosoma. Scutellum 4.5 times shorter than mesosoma. Dorsal and declivous surfaces of propodeum form rounded obtuse angle. Propodeal dorsum slightly convex, and declivity slightly concave. Petiole with high node with flat dorsal surface. First gastral segment nearly as long and wide as second.

Measurements (in mm). Holotype, MeI 7679: AL = 2.3, HL = 1.15, HW = 1.3, ED = 0.31.

Genus ***Cephalopone*** gen. nov.

Etymology. Named after the Greek word *cephale* ($\kappa\varepsilon\varphi\alpha\lambda\eta$), head, and the ant genus *Ponera*.

Type species. *Cephalopone potens* sp. nov.

Diagnosis (for impression fossils). Gynes. Large ants: body length more than 20 mm. Head nearly 1.7 times shorter than mesosoma. Antennal sockets relatively widely separated, not closely approximated. Antenna 12-segmented, without a club. Mandible very large (more than 80% of head length), subtriangular with dentate masticatory margin. Middle and hind tibiae each seem to have a large pectinate spur and a small simple spur (visible only on middle tibia of *C. potens*). Petiole nodiform. Helcium projects from very low down on the anterior face of first gastral segment, the latter rounded in side view.

Species composition. *Cephalopone potens* sp. nov. and C. grandis sp. nov.

Remarks. Differs from other fossil Ponerinae by the large massive multidentate mandibles.

Cephalopone potens sp. nov.
(Fig. 18)

Etymology. From the Latin *potens* (strong, powerful).

Holotype. FIS MeI 10860, dorsal imprint of winged gyne.

Paratype. FIS MeI 11830, dorsal imprint of winged gyne.

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

Description. Gyne. BL 21–22.5 mm. Head subrectangular, 1.1–1.2 times wider than long, with rounded posterior corners and weakly concave posterior margin. Mesosoma 1.5–1.6 times longer than head. Anterior margin of the clypeus gradually convex. Eyes oval, rather small, situated in front of lateral midlength of head. Head 3.8 times longer than maximal eye diameter in holotype. Scape does not protrude or protrudes only slightly beyond the posterior margin of the head. Funicular segments 1.5–2 times longer than thick. Mandibles subtriangulate, about as long as head. Masticatory margin with nine teeth, and large teeth alternate with smaller. Mesosoma rather massive. Legs rather short and thick. Two spurs (large pectinate and small simple) are visible on mesotibia of paratype specimen. Petiole 1.15 times longer than high, with cubical node and very short peduncle; dorsal and ventral surfaces of petiole subparallel; anterodorsal and posterodorsal corners rounded. Gaster oval and compact. G1L is 78% of G2L, G1W and G2W subequal.

Measurements (in mm). Holotype, MeI 10860: AL = 6.1, HL = 4.3, HW = 4.5, MdL = 3.4, SL = 3.5, ED = 1.06. Paratype MeI 11830: AL = 6.7, HL = 4.0, HW = 4.9, MdL ~ 4.0, FWL = 13.05.

Cephalopone grandis sp. nov.
(Fig. 19)

Etymology. From Latin *grandis*, large.

Holotype. FIS MeI 5361, dorsal imprint of winged gyne.

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

Description. BL *c.*26 mm. Head subquadrate, about as long as wide, with rounded posterior corners and weakly convex posterior margin. Anterior margin of the clypeus with convex middle part and pair of lateral tubercles. Scape protrudes slightly beyond the posterior margin of the head. Funicular segments 1.5–2 times longer than thick. Mandibles 87% of head length, subtriangular with 10 teeth. Apical and preapical teeth large, and then large teeth alternate with smaller; teeth 4, 6, 8 and 10 are large, and teeth 3, 5, 7 and 9 are small. Petiole nodiform, sessile, subrectangular in side view; anterior side is nearly straight, its dorsal side is flat and its posterior side is convex; the anterodorsal corner is sharp and the posterodorsal corner is rounded.

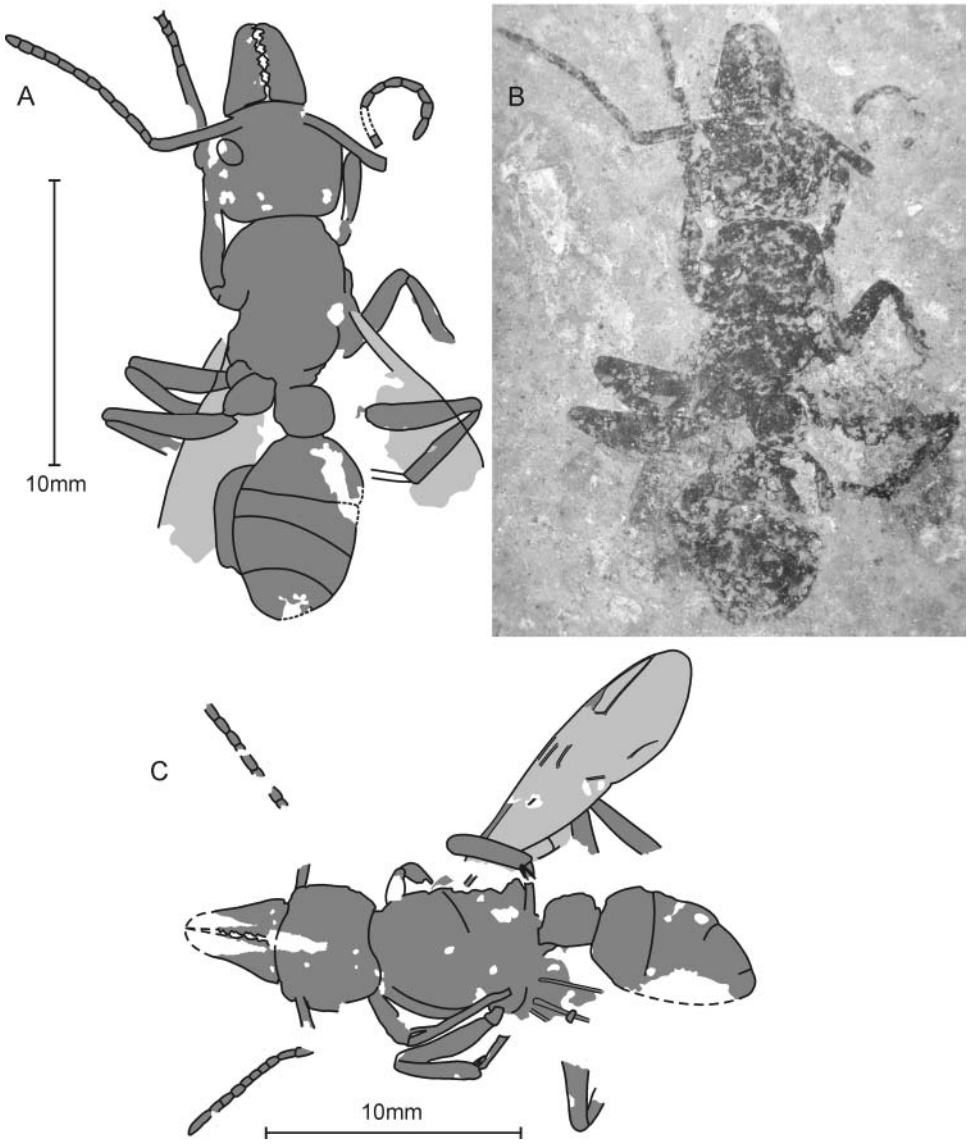

Figure 18. *Cephalopone potens* sp. nov., gynes. **A, B,** holotype, FIS MeI 10860; **A,** line drawing; **B,** photograph; **C,** paratype, FIS MeI 11830, line drawing.

Part only of forewing veins preserved. Cell mcu pentagonal. Section 1M more than 3 times longer than 1RS. Cross vein cu-a situated nearly proximal angle of cell mcu, so 2M + Cu distinctly shorter than cu-a.

Measurements (in mm). Holotype, MeI 5361: AL = 7.5, HL = 3.4, SL = 3.55, MdL = 3.5, FWL = 12.2.

Genus ***Cyrtopone*** gen. nov.

Etymology. This genus is named after the Greek word '*cyrtos*' (κυρτος), curved, and the ant genus name *Ponera*.

Type species. *Cyrtopone microcephala* sp. nov.

Diagnosis (for impression fossils). Gyne. Head small, nearly 2 times shorter than mesosoma. Antennal sockets relatively widely separated, not closely approximated. Mandible subtriangular with dentate masticatory margin, not more than half of head length. Pretarsal claws simple. Petiole nodiform, higher than long. Helcium projects from very low down on the anterior face of first gastral segment, the latter with a high vertical anterior face above the helcium. First gastral segment longer than second.

Remarks. Differs from *Pachycondyla*, *Protopone* and *Cephalopone* by its small head.

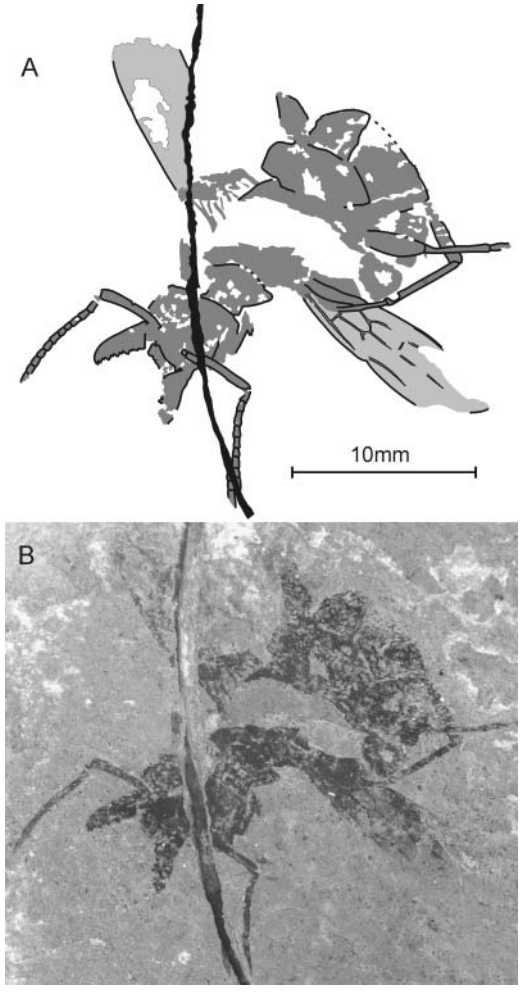

Figure 19. *Cephalopone grandis* sp. nov., gyne, holotype, FIS MeI 5361. **A,** line drawing; **B,** photograph.

Cyrtopone microcephala sp. nov.
(Fig. 20)

Etymology. From the Greek microcephalos ($\mu\iota\kappa\rho o\kappa\varepsilon\varphi\alpha\lambda o\varsigma$), with a small head.

Holotype. FIS MeI 2407, lateral imprint of winged gyne.

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

Description. Gyne. BL 12.5 mm. Head about as long as wide and 1.8 times shorter than mesosoma. Anterior margin of clypeus trapezoidal. Eyes small, rounded, situated on the midlength of head; gena longer than maximal eye diameter. Scape reaches, but does not protrude the occipital margin of the head. Head 1.3 times longer than scape. Funicular segments about twice longer than thick. Mandibles subtriangular, dentate, shorter than half of head

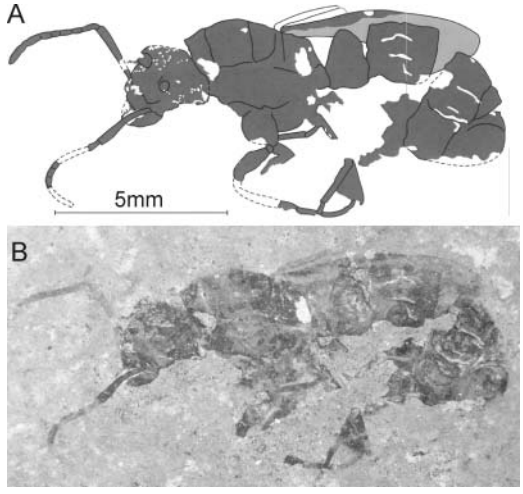

Figure 20. *Cyrtopone microcephala* sp. nov., gyne, holotype, FIS MeI 2407. **A,** line drawing; **B,** photograph.

length. Mesosoma robust, less than twice as long as high. Scutum weakly convex, 3.3 times shorter than mesosoma. Propodeum angulate in side view, propodeal dorsum shorter than declivity. Petiole with high and thick triangulate scale, 1.4 times higher than long. In side view anterior side of petiole nearly straight, posterior side convex and top rounded. Anterior and dorsal surfaces of first gastral tergite form distinctive obtuse angle in side view. First gastral segment 1.5 times longer than second. Head with foveolate sculpture. Gaster of imprint with longitudinal ditches, which evidently resulted from deformation during the fossilization process; this indicates that the gaster of living ants was rather strongly sclerotized.

Measurements (in mm). Holotype, MeI 2407: AL = 4.1, HL = 2.2, SL = 1.75, MdL = 1.1, PtL = 1.2, PtH = 1.7.

Cyrtopone curiosa sp. nov.
(Fig. 21)

Etymology. From the Latin *curiosus*, funny.

Holotype. FIS MeI 6075, lateral imprint of gyne (indicated by the visible boundaries of the scutellum and postnotum of the mesosoma).

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

Description. Gyne. BL *c.*7.5 mm. Head subrectangular, a little longer than wide, with nearly straight sides, rounded posterior corners and weakly convex posterior margin. Mesosoma twice as long as head. Eyes oval, situated slightly behind the lateral midlength of head. Frons width is nearly 25% of head width. Scape protrudes slightly beyond

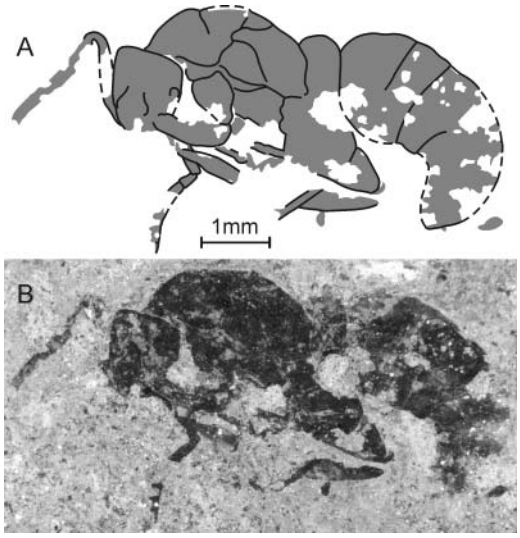

Figure 21. *Cyrtopone curiosa* sp. nov., gyne, holotype, FIS MeI 6075. **A,** line drawing; **B,** photograph.

the posterior margin of the head. Mesosoma massive. Scutum weakly convex in side view. Mesosoma 3.2 times longer than scutum and 6.7 times longer than scutellum. Propodeum rounded in side view. Petiole with high and very thick scale; in side view posterior side straight and top gradually rounded. First gastral segment distinctly longer than second.

Measurements (in mm). Holotype, MeI 6075: AL = 2.4, HL = 1.2, HW = 1.1, SL ~ 1.4.

Cyrtopone elongata sp. nov.
(Fig. 22)

Etymology. From the Latin *elongates*, elongated.

Holotype. FIS MeI 10617, dorsal imprint of winged gyne.

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

Description. Gyne. BL *c.*5.7 mm. Head subrectangular, 1.1 times longer than wide, with subparallel sides, rounded posterior corners and straight or weakly concave posterior margin. Mesosoma twice longer than head. Anterior margin of clypeus gradually convex. Eyes oval, situated slightly in front of lateral midlength of head. Head 3.7 times longer than maximal eye diameter. Gena longer than maximal eye diameter. Scape does not protrude beyond the posterior margin of the head. Funiculus gradually incrassate to the apex but without distinctly differentiated club. Funicular segments about as long as thick. Mandibles subtriangular, 45–50% of head length. Mesosoma twice as long than wide.

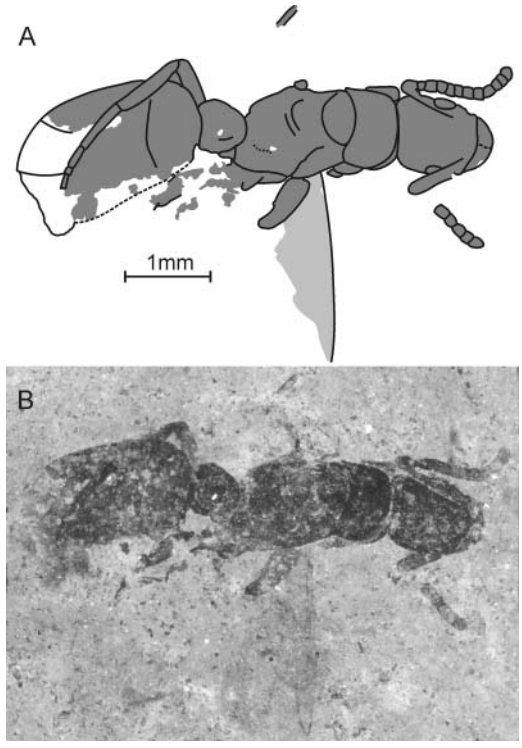

Figure 22. *Cyrtopone elongata* sp. nov., gyne, holotype, FIS MeI 10617. **A,** line drawing; **B,** photograph.

Scutum small, transverse. Petiole nodiform, a little shorter than wide.

Measurements (in mm). Holotype, MeI 10617: AL = 1.93, HL = 0.94, HW = 0.86, SL = 0.73, ED = 0.25, MdL = 0.42, PtL = 0.54.

Cyrtopone striata sp. nov.
(Fig. 23)

Etymology. From the Latin *striatus* (ridged, striped).

Holotype. FIS MeI 1392, lateral imprint of winged gyne.

Description. Gyne. BL 14.5 mm. Head small, 2.5 times shorter than mesosoma. Eyes small, round, situated at about the middle of head sides; gena 1.4 times longer than maximal eye diameter. Scape nearly 1.4 times longer than head, extending about one-third its length beyond the posterior margin of the head. Scutum weakly convex in side view, nearly 3.5 times shorter than mesosoma. Propodeum with very short dorsum and long straight declivity in side view; propodeal dorsum and declivity form rounded obtuse angle. Metatibia with large pectinate spur and small simple spur. Petiole not seen. Head and scutum with sculpture formed by longitudinal rugae.

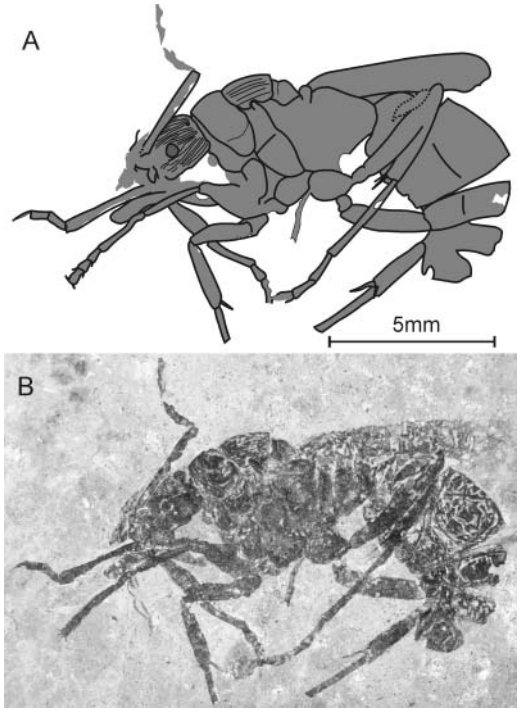

Figure 23. *Cyrtopone striata* sp. nov., gyne, holotype, FIS MeI 1392. **A,** line drawing; **B,** photograph.

Measurements (in mm). Holotype, MeI 1392: AL = 5.5, HL = 2.2, SL = 3.0, ED = 0.41.

Genus ***Messelepone*** gen. nov.

Etymology. The genus name is derived from the type locality (Messel) and the ant genus name *Ponera*.

Diagnosis (for impression fossils). Gyne. Head small, nearly two times shorter than mesosoma. Antennal sockets relatively widely separated, not closely approximated. Mandible subtriangular, not more than half of head length. Pretarsal claws simple. Petiole rectangular in side view. Helcium projects from very low down on the anterior face of first gastral segment, the latter with a high vertical anterior face above the helcium. First gastral segment shorter than second.

Male. Mandibles opposable. Antennae 13-segmented, filiform, with short scape. Petiole rectangular in side view. First gastral segment shorter than second. Helcium projects from low down on the anterior face of first gastral segment. Dorsum of first gastral tergite gradually rounded. Pygidium without terminal spine.

Remarks. The new monospecific genus differs from other Eocene ant genera by the combination of a small head, a distinctive form of petiole and a short first gastral segment. Males also differ from *Pachycondyla* by their more developed mandible and the absence of a pygidial spine. Many Recent species of the genus *Leptogenys* Roger, 186l have a similar construction of the petiole, but these ants differ from *Messelepone* in other characters. In particular, they have pectinate pretarsal claws and their first gastral segment is longer than the second.

Messelepone leptogenoides sp. nov.
(Fig. 24)

Etymology. Derived from the ant genus name *Leptogenys*.

Holotype. FIS MeI 4808, lateral imprint of winged gyne.

Paratype. FIS MeI 7198, lateral imprint of male.

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

Description. Gyne. BL 14 mm. Head 2.1 times shorter than mesosoma. Scape protrudes slightly beyond the posterior margin of the head. Eyes oval, situated slightly in front of lateral midlength of head; head 3.4 times longer than maximal eye diameter. Gena a little shorter than maximal eye diameter. Mandibles short, subtriangulate. Dentation not preserved. Mesosoma robust, twice longer than high. Scutum flat, 3 times shorter than mesosoma. Petiole without peduncle, rectangular in side view, a little higher than long, with subparallel anterior and posterior sides and weakly convex dorsum. G1L is 72% of G2L.

Male. BL 7.3 mm. Eyes rounded; maximal eye diameter 2.7 times shorter than head. Gena length about half of maximal eye diameter. First antennal segment (scape) nearly 1.5 times longer than thick. Second segment is shortest, nearly as long as thick. Third segment is longest, 3.5 times longer than thick and a little longer than first and second segment together. Mandibles subtriangulate, well developed. Dentation not preserved. Mesosoma 1.5 times longer than high. Scutum weakly convex in side view, 2.7 times shorter than mesosoma. Pretarsal claws simple. G1L is 83% of G2L, G1H and G2H subequal.

Measurements (in mm). Holotype (gyne), Mel4808: AL = 4.4, HL = 2.1, SL = 1.6, ED = 0.61, PtL = 1.3. Paratype (male) MeI 7198: AL = 2.3, HL = 1.1, SL = 0.22, ED = 0.40, PtL = 0.59, PtH = 0.69.

Remarks. Usually it is almost impossible to prove the conspecificity of females and males of fossil ants. However, we consider that this case is an exception as the structure of the petiole is very similar in the gyne and in the male and differs strongly from all other species found at Grube Messel.

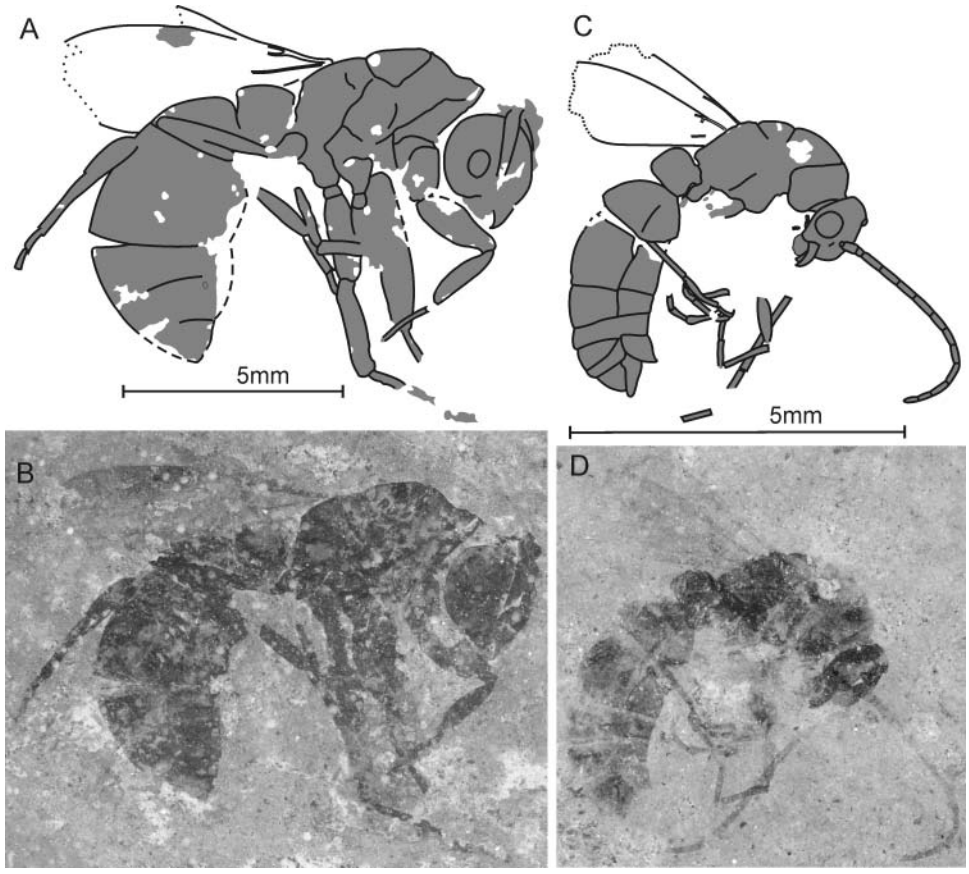

Figure 24. *Messelepone leptogenoides* sp. nov. **A, B,** holotype, gyne, FIS MeI 4808; **A,** line drawing; **B,** photograph. **C, D,** paratype, male, FIS MeI 7198; **C,** line drawing; **D,** photograph.

Ponerinae incertae sedis

Remarks. The following imprints undoubtedly belong to Ponerinae, but cannot be determined precisely because of their insufficient preservation: MeI 202, MeI 662, MeI 7055, MeI 7222, MeI 7369, MeI 7751, MeI 7758, MeI 8298, MeI 8551 (forewing), MeI 10805, MeI 11007, MeI 12307, MeI 12377, MeI 12628, MeI 12641, MeI 13220, MeI 13339, MeI 13585, MeI 13802.

Key for the determination of gynes of poneromorph ants from Grube Messel

1. Petiole essentially sessile, with a steep broad anterior face but without a distinctly descending posterior face, markedly broadly attached to first gastral (III abdominal) segment (Fig. 3) (subfamily Amblyoponinae). Mandible rather short, triangulate. Petiole trapezoid in dorsal view. BL 4.9 mm . . . . . *Casaleia eocenica* sp. nov.
— Petiole narrowly attached to first gastral (III abdominal) segment, with a distinctly descending posterior face (Figs 4, 8, 10) 2
2. Helcium projects from about the midheight of the anterior face of first gastral segment; no high vertical anterior face to first gastral segment above the helcium (Fig. 4) (subfamily Ectatomminae). Anteroventral angle of pronotum rounded, without tooth. Metatibia with one pectinate spur. Pretarsal claws lack a median tooth. Petiole nodiform. Second gastral segment trapezoid in side view, its dorsal surface not strongly convex. (genus *Pseudectatomma*) 3
— Helcium projects from very low down on the anterior face of first gastral segment, the latter usually with a high vertical anterior face above the helcium (Figs 10, 11, 20, 24, etc.) (Subfamily Ponerinae) 4
3. Head with distinct sculpture formed by longitudinal rugae (Fig. 5) . . . *Pseudectatomma striatula* sp. nov.
— Head without visible sculpture. Petiole with triangulate node (Fig. 4) . . . . . *Pseudectatomma eocenica* sp. nov.

4. Mandibles very large, more than 80% of head length, subtriangular with dentate masticatory margin. Head nearly 1.7 times shorter than mesosoma. First gastral segment rounded in side view. Petiole nodiform. BL>20 mm (genus *Cephalopone*) 5
— Mandibles shorter, less than 70% of head length. First gastral segment with a high vertical anterior face above the helcium 6
5. Clypeus with a pair of lateral tubercles. Anterior side of petiolar node is nearly straight, dorsal side is flat and posterior side is convex; anterodorsal corner sharp and posterodorsal corner rounded (Fig. 19). BL ∼ 26 mm . . . . . *Cephalopone grandis* sp. nov.
— Clypeus gradually rounded, without tubercles. Petiole with cubical node and very short peduncle; dorsal and ventral surfaces of petiole subparallel; anterodorsal and posterodorsal corners rounded (Fig. 18). BL 21–22.5 mm . . . . . *Cephalopone potens* sp. nov.
6. Head small; mesosoma 1.8–2.5 times as long as head 7
— Mesosoma not more than 1.7 times longer than head 11
7. Petiole rectangular in side view, a little higher than long, with subparallel anterior and posterior sides and weakly convex dorsum. First gastral segment shorter than second (Fig. 24). BL 14 mm . . . . . *Messelepone leptogenoides* sp. nov.
— Petiole of other form. First gastral segment longer than second (genus *Cyrtopone*) 8
8. Head and scutum with longitudinal rugae. Scape longer than head, extends about 1/3 of its length beyond the posterior margin of the head (Fig. 23). BL 14.5 mm . . . . . *Cyrtopone striata* sp. nov.
— Head and scutum without rugose sculpture. Scape does not reach posterior margin of the head or protrudes only slightly beyond the posterior margin 9
9. Head with foveolate sculpture. Scape reaches but does not protrude the occipital margin of the head. Funicular segments about twice longer than thick. Petiole with high and thick triangulate scale, 1.4 times higher than long. In side view anterior side of petiole nearly straight, posterior side convex, and top rounded (Fig. 20). BL 12.5 mm . . . . . *Cyrtopone microcephala* sp. nov.
— Head without visible sculpture 10
10. Scape does not protrude beyond the posterior margin of the head. Funicular segments about as long as thick. Petiole nodiform (Fig. 22). BL ∼ 5.7 mm . . . . . *Cyrtopone elongata* sp. nov.
— Scape protrudes slightly beyond the posterior margin of the head. Petiole with high and very thick scale; in side view anterior and posterior sides subparallel and top gradually rounded (Fig. 21). BL ∼7.5 mm . . . . . *Cyrtopone curiosa* sp. nov
11. Antennal sockets closely approximated; frons width less than 25% of head width (Figs 6C, 7B, D). Petiole with thick scale (Figs 7E, 8–11). (genus *Pachycondyla*) 12
— Antennal sockets relatively widely separated, not closely approximated; frons width more than 30% of head width (Figs 12, 13). Petiole nodiform (Figs 12, 15, 16). (genus *Protopone*) 17
12. BL 20–22.5 mm. Scape protrudes slightly beyond the occipital margin of the head. Eyes situated slightly behind the lateral midlength of head. Petiole with high and thick scale; anterior and posterior sides of scale subparallel in side view, apex rounded. (Fig. 10A, B) . . . . . *Pachycondyla petiolosa* sp. nov.
— BL less than 16 mm. Scape does not reach the posterior margin of the head. Eyes displaced forward from the head midlength (not seen in *P. petrosa* and *P. messeliana*) 13
13. Head massive, 1.3 times shorter than mesosoma. Petiolar scale tapered upward. Anterior and posterior sides of scale slightly convex in side view, apex rounded (Fig. 8). BL 14.5 mm . . . . . *Pachycondyla? messeliana* sp. nov.
— Head 1.6–1.7 times shorter than mesosoma 14
14. Petiole with high scale, triangulate in side view, with narrowly rounded top (Fig. 11). BL 12.4 mm . . . . . *Pachycondyla petrosa* sp. nov.
— Petiolar scale with nearly parallel anterior and posterior sides 15
15. Head nearly as long as wide (Fig. 6). Mandible 51–53% of head length. BL 8.8 mm . . . . . *Pachycondyla eocenica* sp. nov.
— Head a little wider than long 16
16. BL 11–15 mm . . . .*Pachycondyla lutzi* sp. nov.
— BL 6–7.3 mm . . . . . *Pachycondyla minuta* sp. nov.
17. Head with coarse foveolata sculpture. Funicular segments nearly twice longer than thick (Fig. 14 A). BL 26 mm . . . .*Protopone magna* sp. nov.
— Head without distinctive sculpture. Funicular segments longer than thick 18
18. Eyes situated slightly in front of lateral midlength of head. Head 2.3 times longer than maximal eye diameter. Gena shorter than maximal eye diameter. Petiole with node rounded in side view and short peduncle (Fig. 15). BL 14 mm . . . . . *Protopone oculata* sp. nov.
— Eyes smaller: head 3.5–5 times longer than maximal eye diameter. Gena longer than maximal eye diameter (Figs 12, 13, 16, 17) 19
19. Head longer than wide. Scape protrudes beyond the posterior margin of the head. (Figs 14, 18) 20

— Head wider than long. Scape reaches the posterior margin of the head (Figs 12, 17) 21

20. Eyes situated in front of the lateral midlength of head (Fig. 13). HL 2.2 mm . . . .*Protopone? dubia* sp. nov.

— Eyes situated on the midlength or slightly behind the lateral midlength of head (Fig. 16). HL 4.2 mm. BL 16.5 mm . . . . . .*Protopone sepulta* sp. nov.

21. Eyes situated slightly behind the lateral midlength of head. Gena nearly twice longer than maximal eye diameter (Fig. 12). BL 13.7 mm . . . . . .*Protopone germanica* sp. nov.

— Eyes situated slightly in front of lateral midlength of head. Gena less than 1.5 times longer than maximum eye diameter (Fig. 17). BL 7 mm . . . . . .*Protopone vetula* sp. nov.

Discussion

Composition of fossil ant assemblages during the early Cenozoic

In the Messel insect collection of the Forschungsinstitut Senckenberg, ants account for 1086 of 13,508 (8%) insect compression fossils. Almost half of these (535 = 49%) are specimens of two species of the genus *Titanomyrma* Archibald, Johnson, Mathewes & Greenwood, 2011, which belongs to the extinct subfamily Formiciinae (Lutz 1986). These two species are the largest of all known ants worldwide (up to 70 mm long), and they dominate the formicid taphocoenosis from Messel. The body lengths of other ants from Messel, which belong to extant subfamilies, do not exceed 25 mm, and most of them are less than 10 mm long. Because of their abundance, only well-preserved fossils of the giant ants are collected and therefore their proportion in the taphocoenosis from Messel is under-represented in the Senckenberg collection. Therefore, giant ants are excluded from further calculations regarding the composition of the ant taphocoenosis.

To date we have determined 447 ant imprints from Messel to subfamily level. Most of these (369 = 80.5%) are representatives of the formicomorph subfamily group (Formicinae and Dolichoderinae). Of the imprints 64 (14.3%) belong to the poneromorph subfamilies Amblyoponinae, Ectatomminae and Ponerinae, 15 (3.4%) to Myrmicinae, and seven (1.6%) to the smaller subfamilies Myrmecinae, Pseudomyrmecinae and Cerapachyinae. Since not all subfamilies of the Messel material have been studied yet, we cannot definitively specify the exact number of species in every subfamily. However, a preliminary estimate of species numbers is: Dolichoderinae ∼8, Formicinae ∼12, Formicinae or Dolichoderinae ∼3, Myrmicinae ∼8, Ponerinae ∼22, Myrmeciinae ∼1, Pseudomyrmecinae ∼2, Cerapachyinae ∼2.

Poneromorph ants are the third most common group with regard to specimen numbers (after Dolichoderinae and Formicinae), and the most speciose group in the ant taphocoenosis of Messel. Moreover, the number of poneromorph species in Messel is higher than in any other fossil site known so far. Until recently, the poneromorph ant fauna of Eocene Baltic amber (16 described species) was considered as the most speciose (Dlussky 2009). However, it is necessary to consider the difference in the quantity of studied material: nearly 14,000 inclusions of ants have been studied in total from Baltic amber (Dlussky & Rasnitsyn 2009), compared to less than a thousand imprints from Messel. More similar to Messel in respect to the quantity of studied material are the Eocene amber inclusions of Bitterfeld (1129 studied ant inclusions) and Rovno (729 studied ant inclusions), from which seven poneromorph species each were described (Dlussky 2009). In Baltic, Bitterfeld and Rovno amber the ratio of poneromorph ants to all ant species is similar: 16 of 124 (12.9%) species in Baltic amber, seven of 71 (9.9%) species in Bitterfeld amber, and seven of 64 (10.9%) species in Rovno amber. In contrast, at Messel we found 24 species of poneromorphs among about 60 supposed total ant species, nearly 40%.

The ant assemblages of the middle to late Eocene ambers and Messel differ even more clearly with regard to the proportion of specimens. In Baltic amber, specimens of poneromorphs comprise 0.7% of all ant specimens, in Bitterfeld amber 1.7%, in Rovno amber 1.6%, whereas in Messel poneromorphs comprise 14% of all ant specimens. In the Late Eocene deposits of the Bembridge Marls, UK (936 ant imprints studied) we found 20 ant species including seven species of Ponerinae, which comprised 2.1% of the ant specimens (unpublished data of Dlussky). The contribution of poneromorphs to European Oligocene and Miocene ant assemblages was also insignificant. We did not find them in the Late Oligocene deposits of Rott, Germany (61 imprints studied), and only one out of 47 studied specimens from the Late Oligocene fossil site Enspel was a poneromorph. In the Middle Miocene deposits from Vishnevaya balka, Stavropol, Russia (75 imprints studied) two of five species belong to Ponerinae and these species represent 2.7% of all ant specimens (Dlussky 1981). In the Late Miocene deposits from Radoboj, Croatia, studied by Mayr (1867b), Ponerinae comprised 0.7% of all ants in 131 specimens studied. These comparisons document a decrease of the species diversity of poneromorph ants in Europe from the Middle Eocene towards the Miocene.

Although the data are sparse, similar trends can be observed in North America and eastern Asia. For example, in the Middle Eocene deposits of the Green River, USA, four out of 16 described species belong to Ponerinae, while the specimens of these species comprise 10% of all ants (Dlussky & Rasnitsyn 2003). Only two of 5592 studied specimens (33 species) from the Late Eocene deposits of Florissant, USA, belong to the unique ponerine species *Archiponera wheeleri* Carpenter (Carpenter 1930). More than five of 35 described species from the Early Eocene

Fushun amber (China) (Hong 2002) are poneromorph ants, and only four of 45 described species from the Miocene Shanwang deposits (China) (Zhang 1989) belong to poneromorph subfamilies. A decline of the diversity of poneromorphs from the Eocene towards the Miocene seems to be detectable worldwide.

Evolution of some ant subgroups during the early Cenozoic

To facilitate further interpretation of the findings presented above, some background explanation is required. From the very beginning of ant history two basic branches have stood apart: Formicomorpha (Aneuretinae, Formicinae and Dolichoderinae) and Poneromorpha. The second abdominal segment (petiole) of the Formicomorpha has a frail coupling with the third segment, and only two pairs of muscles remain in it. Such a petiole (especially a petiole in the form of a scale) allows unrestricted motions of the gaster in a vertical plane. The subsequent segments form the compact gaster, which makes it possible for these ants to move quickly and with agility across substratum surfaces. Subsequently, the ability to compress and stretch the gaster (together with modifications of the proventriculus) has allowed these ants to store liquid food in a crop, preadapting them to symbiosis with plant lice and other Homoptera. Additionally, Formicinae and Dolichoderinae have lost the sting and have instead developed the ability to spray poison a considerable distance (up to 30 cm in some *Formica*). This behaviour can provide effective protection against attacks.

The evolution of the metasoma of Poneromorpha was different. This group specialized on movement in the clefts of dense substrata. Along with a mobile articulation of the second and third abdominal segments in which the form of the corbel of III segment is approximately spherical, the subsequent segments also have considerable degrees of freedom of movement thanks to ring joints (tubulation). Such a gaster which consists of rigid chitinous rings allows these ants to move ahead successfully in narrow twisting courses of soil or wood and it makes it possible for them to use their sting effectively in any direction (Dlussky & Fedoseeva 1988).

Thus, the differing morphological features of the two groups suggest that their evolution from the very beginning occurred in two different realms: Formicinae and Dolichoderinae inhabited the soil and foraged on the soil surface and in the arboreal realm, while Poneromorpha inhabited soil and leaf litter. Perhaps some Aneuretinae coexisted with Poneromorpha in soil and leaf litter. The Palaeocene aneuretine ant *Aneuretellus* (Dlussky, 1988) and the Eocene *Protaneuretus* (Wheeler, 1915) have small eyes which are shifted strongly towards the front and have an incrassate funiculus with thick terminal segments. Such characters are typical for modern ants inhabiting soil and leaf litter. Recent poneromorphs that live in leaf litter surpass formicomorphs both in number of specimens and species diversity. Ward (2000) analysed the composition of 110 Winkler samples collected from many forested localities in different biogeographical regions. The dominant subfamily in forest leaf litter was Myrmicinae, which composed 65.2% of species and 73.7% of specimens. Poneromorphs (mostly Ponerinae) made up 22.2% of species and 12.4% of specimens, Formicinae 10.6% of species and 12.9% of specimens, and Dolichoderinae only 1.1% of species and 0.5% of specimens. The pattern changes clearly if one goes vertically up into the forest canopy. For example, in Amazonian and Bornean forest canopies subfamily dominance is nearly reversed: Formicinae and Dolichoderinae rise considerably in numbers compared to Myrmicinae, and Ponerinae drop to very low levels (Brühl 1998; Wilson & Hölldobler 2005).

A similar stratification of poneromorphs and formicomorphs seems to have existed also in European Eocene forests. This is reflected in the proportions of ant castes preserved in amber. All Dolichoderinae and Formicidae, except *Nylanderia pygmaea* (Mayr, 1868), are represented in amber inclusions mostly by workers (Dlussky & Rasnitsyn 2007). This indicates that the workers climbed up the tree trunks where they became easily trapped in outflowing resin. Moreover, a connection of the most abundant dolichoderine species *Ctenobethylus goepperti* (Mayr, 1868) and the formicine species *Lasius schiefferdeckeri* Mayr, 1868 with aphids and coccids has been documented (Perkovsky 2006, 2007, 2008). In contrast, poneromorph ants (except *Bradoponera* Mayr, 1868) in Baltic and other European ambers are represented predominantly by alate sexuals. This is explained primarily by the fact that the vast majority of Ponerinae live in soil and leaf litter, and workers almost never climb up tree trunks. During their nuptial flight, however, the gynes and males first ascend up grass or tree trunks and from there they eventually take flight (Dlussky 2009). In contrast to Recent forests, Myrmicinae are rare and all species in amber are represented mostly by workers; there is no evidence that they inhabited soil or litter.

Despite belonging to a very ancient phylogenetic group and despite their high diversification and global distribution, recent poneromorphs remain remarkably primitive in their social organization. Wilson & Hölldobler (2005, p. 7412) called this "the ponerine paradox" and proposed the "dynastic-succession" hypothesis as an explanation. Their hypothesis was based on general reasoning and hardly on palaeontological data. Wilson & Hölldobler (2005, p. 7414) described the following scenario. At the end of the Mesozoic flowering plants had replaced much of the old gymnosperm flora worldwide and, as a result, forest litter became more complex and better suited as a habitat for ants. During the Palaeocene and Early Eocene, the ponerines inhabiting soil and ground litter underwent an adaptive

radiation, with some of the genera appearing at that time surviving until today. At the same time, or perhaps more toward the end of the ponerine expansion, but probably no later than the Early Eocene, myrmicines radiated and competed with ponerines for both prey and nest sites. After some time, they equalled and then surpassed ponerines in biomass and diversity. Dolichoderines and formicines also diversified, perhaps at the same time as the myrmicines but more likely later, in the Early to Middle Eocene. They were less successful than ponerines and myrmicines in colonizing ground and leaf litter sites, having been pre-empted there by the other two groups. Through coevolution with symbiotic homopterans, dolichoderines and formicines became very successful in penetrating environments less available to predators, including cool-temperate climates and the canopies of tropical forests. This success is reflected in their high abundance, especially of worker specimens in amber, and of alate specimens in rock/impression fossils.

With the newly available palaeontological data, the timing and course of the evolution of ponerines can be traced more precisely. Flowering plants replaced the gymnosperm flora during the Cretaceous and ants, including poneromorphs, were rare at that time (Wilson & Hölldobler 2005; Dlussky & Rasnitsyn 2007). Since fossils of poneromorph ants from the Palaeocene and Early Eocene are very rare, we cannot say much concerning this time period. Only two deposits have yielded fossil ants from the Palaeocene: Sakhalin amber (eight ant specimens, comprising seven species, with only one poneroid species, *Protopone primigena*) and Tadushi, Russian Far East (two wings of Formicinae). Ants are known from the Early Eocene Fur and Olst Formation, Denmark (numerous imprints of one species, *Ypressiomyrma rebekkae*) and from the Fushun amber from China, whose fauna urgently needs to be revised as stated earlier in this paper.

The data of Hong (2002) and our new data from Messel confirm the assumption that poneromorphs flourished during the Early and Middle Eocene in Europe and East Asia. However, *Protopone* from Palaeocene Sakhalin amber and all genera described from the Early Eocene Fushun amber are extinct; only *Pachycondyla* from the Middle Eocene of Messel belongs to an extant genus. Towards the end of the Eocene the situation began to change. Only five of 20 poneromorph species described from Middle to Late Eocene ambers (Dlussky 2009) belong to extinct genera; these are four species of *Bradoponera* Mayr, 1868, and *Electroponera dubia* Wheeler, 1915. All other species belong to the extant genera *Amblyopone* Erichson, 1842 (two species) (Amblyoponinae), *Gnamptogenys* Roger, 1863 (two) (Ectatomminae), *Hypoponera* Santschi, 1938 (one), *Pachycondyla* F. Smith, 1858 (five), *Ponera* Latreille, 1804 (three), *Platythyrea* Roger, 1863 (one) (Ponerinae) and *Proceratium* Roger, 1863 (one) (Proceratiinae). Thus, based on palaeontological data, it can be assumed that an intensive adaptive radiation of Poneromorpha took place during the Eocene, with many extant genera appearing.

However, the hypothesis of Wilson & Hölldobler (2005) that Myrmicinae began their radiation not later than the Early Eocene, and that they then surpassed Ponerinae in biomass and diversity, is not supported by palaeontological data. Myrmicinae compose 13% of the species (eight of 60) and 3.4% of the specimens in the Middle Eocene ant taphocoenosis of Messel, and 13% (two of 16) of the species and 2.1% of the specimens in the Middle Eocene of the Green River (Dlussky & Rasnitsyn 2007). In European Middle to Late Eocene ambers the proportion of Myrmicinae increases to 28–30% of species, but the proportion of specimens remains low: 1.7% in Baltic amber, 9.1% in Bitterfeld amber, 5.5% in Rovno amber, and 14.3% in Scandinavian amber (Dlussky & Rasnitsyn 2009). Moreover, Myrmicinae are mostly represented by workers in the ambers, so they probably did not inhabit the litter and were not competitors of Ponerinae. The higher proportion of Myrmicinae in Bitterfeld and Scandinavian ambers is connected with the high abundance of the extinct genus *Fallomyrma* Dlussky & Radchenko, 2006. A low participation of Myrmicinae is documented in several Late Eocene sites: myrmicines comprise 24% (eight of 33) of species and 4.8% of specimens at Florissant, and 10% (two of 20) of species and 0.5% of specimens in the Bembridge Marl.

The dominant group of ants all through the Palaeogene were formicomorphs: they account for 81% of the specimens at Messel, 81.8% from the Green River, 81–97% in European ambers, 95.2% at Florissant and 95.5% at Bembridge. Only during the Late Oligocene to Miocene did the proportion of Myrmicinae increase and became similar to recent levels. This is illustrated by the 50% of myrmicine specimens at Rott, 40% at Vishnevaya balka and 22% in Radoboj (Dlussky & Rasnitsyn 2007, 2009).

Thus, judging from available palaeontological data, the evolutionary dynamics of ant subfamilies was much more complex than assumed by the dynastic-succession hypothesis. An explanation of the Ponerine Paradox demands new data. It would be especially important to study the palaeontological history of ants in Africa, which is unknown at the present due to the lack of fossils, as there is an assumption that the main radiation of Myrmicinae might have taken place on this continent (Dlussky *et al.* 2004; Dlussky 2005).

Acknowledgements

We thank Dr K. Perfilieva (Moscow State University) for help in the reconstruction of ant wing venation. The comments of two anonymous reviewers helped us to improve the manuscript. We thank the Senckenberg digging team members for their efforts, Uta Kiel (FIS) for taking photographs, and Stephan Schaal for his support. This work

was financially supported by grants of the Russian Fund of Fundamental Investigations (RFFI) No 08-04-00-701 (to GD) and the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) No 436 RUS 17/17/07 (to GD and SW).

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