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New Fossil Ants of the Subfamily Myrmeciinae (Hymenoptera, Formicidae) from Germany

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Abstract—Two new fossil members of the subfamily Myrmeciinae are described: *Archimyrmex wedmannae*, sp. nov (Grube Messel, Germany, Middle Eocene) and *Prionomyrmex wappleri*, sp. nov. (Rott, Germany, Late Oligocene). Members of the genus *Archimyrmex* were known earlier from Eocene deposits of the United States and Argentina, and members of the genus *Prionomyrmex* were known from Late Eocene Baltic amber.

Keywords: ants, Myrmeciinae, *Archimyrmex, Prionomyrmex*, new species, Middle Eocene, Late Oligocene.
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INTRODUCTION

The subfamily Myrmeciinae has always attracted the attention of myrmecologists studying the origins and evolution of ants. These ants have the highest number of plesiomorphic characters, compared to members of the other extant families, and were long viewed as forms especially close to the hypothetical ancestors of the whole family. In the recent fauna, members of this subfamily live exclusively in the Australian region and are represented by only two genera, but in the past their distribution was considerably wider.

Examination of collections of fossil ants in museums of Germany has revealed two new species of Myrmeciinae, described below. As will be shown, these findings extend our notion of the history of this subfamily.

SYSTEMATIC PALEONTOLOGY

Subfamily Myrmeciinae Emery, 1877

Type genus. *Myrmecia* Fabricius, 1804.

Diagnosis (for fossil impressions). Petiole one- or two-segmented. Abdominal segment III (postpetiole in species with two-segmented waist or first gastral segment in species with one-segmented waist) always smaller than abdominal segment IV: 45–75% as long, 50–80% as high, and 40–80% as wide. Mandibles elongate, usually with many teeth, 70–125% as long as head. Antenna 12-segmented in workers and gynes and 13-segmented in males. Maxillary palpus 6-segmented. Metatibia with two spurs, one of them always pectinate. Claws with additional tooth on internal margin. Pygidium simple, convex in profile. Forewing[1] with closed cells 1+2r, 3r, rm, mcu, and usually also cua. Cell 3r relatively short, no longer than 30% wing length. Segment 5RS almost straight. Segment 2+3RS usually curved, often angulate. Cell rm pentagonal. Its distal corner level with distal corner of pterostigma. Cell mcu large, usually pentagonal, sometimes hexagonal. Its distal corner at least level with first basal third of pterostigma. Transverse vein cu-a branching off M+Cu near divergence of 1M and 1Cu.

Composition. The subfamily Myrmeciinae is represented in the recent fauna by only two genera, *Myrmecia* Fabricius, 1804, which includes 90 species, and the monotypic *Nothomyrmecia* Clarck, 1934. Members of both families live only in Australia and on neighboring islands (Bolton et al., 2006). The subfamily also includes six known extinct genera: *Archimyrmex* Cockerell, 1923 (three species, Middle Eocene; United States, Argentina), *Avitomyrmex* Archibald, Cover et Moreau, 2006 (three species, Early Eocene; Canada), *Macabeemyrma* Archibald, Cover et Moreau, 2006 (one species, Early Eocene; Canada), Myrmeciites Archibald, Cover et Moreau, 2006 (three species, Early Eocene; United States, Canada), *Prionomyrmex* Mayr, 1868 (two species, Late Eocene; Baltic amber), and *Ypresiomyrma* Archibald, Cover et Moreau 2006 (three species, Early Eocene; Denmark, Canada) (Baroni Urbani, 2000; Dlussky and Perfilieva, 2003; Archibald, Cover, and Moreau, 2006). *Cariridris* bipetiolata Brandão et Martins-Neto, 1989 (Lower Cretaceous, Brazil), described as Myrmeciinae, in fact belongs to the subfamily Ampulicidae (Dlussky and Rasnitsyn, 2003).

Remarks. In the capital study by Ward and Brady (2003) on the phylogeny of Myrmeciinae, over 85 alternative characters distinguishing members of this subfamily from members of other subfamilies are

[1] Venation nomenclature used here has been discussed in earlier publications (e.g., Dlussky, 2009).

given. However, only three groups of characters can be used to distinguish between fossil species of Myrmeciinae and Poneromorpha: shape and relative size of mandibles, size ratio between abdominal segments III and IV, and wing venation pattern.

According to the author's data (80 specimens belonging to 42 species were measured), in gynes and workers of recent Myrmeciinae abdominal segment III is 45–74% as long, 50–81% as high, and 44–80% as wide as abdominal segment IV. In *Nothomyrmecia macrops* the mandible is 72–80%, and in *Myrmecia* 83–125% as long as the head. In all recent Ponerinae (168 specimens belonging to 77 species from 19 genera were measured) and Ectatomminae (106 specimens belonging to 30 species from four genera were measured) the author has studied, abdominal segment III is invariably over 75% as long, over 86% as high, and over 84% as wide as segment IV. Some Ponerinae have long linear or narrowly triangular mandibles (over 75% as long as the head), but in all these ants abdominal segment III is approximately as long or longer than segment IV. Among the recent Poneromorpha, only *Paraponera clavata*, the only member of the subfamily Paraponerinae (19 specimens were measured), the size ratio between abdominal segments III and IV partly overlaps with that of Myrmeciinae: segment III is 82–92% as long, 77–85% as high, and 77–88% as wide as segment IV. These ants, however, have wide triangular mandibles.

Thus, a combination of these two characters allows distinguishing reliably between recent Poneromorpha and Myrmeciinae. The ranges of these characters in the fossil genera *Archimyrmex* and *Prionomyrmex* fall fully within the limits of variation found in recent Myrmeciinae and differ from recent Poneromorpha. In *Archimyrmex rostratus*, segment III is 61–75% as long, 51–55% as high, and 50–52% as long as segment IV. In *Prionomyrmex* these parameters are 66–81%, 75–81%, and 72–82%, respectively. Members of both genera have long linear or narrowly triangular mandibles. However, the place of *Avitomyrmex, Macabeemyrma*, and *Ypresiomyrma* in the subfamily Myrmeciinae raises some doubts. In these ants, the constriction between abdominal segments III and IV is not pronounced. The ratios between abdominal segments III and IV and relative mandible length in these ants is intermediate between the recent Myrmeciinae and Poneromorpha.

The author has received from D. Archibald high quality digital photographs of the type specimens of members of these genera, which allowed making the measurements. In *Avitomyrmex*, abdominal segment III varies in size between 60–100% as long and 69–81% as high as abdominal segment IV, and the mandibles are 52–59% as long as the head. In *Macabeemyrma*, these parameters 72%, 78%, and 55%, respectively, and in *Ypresiomyrma*, 69–96%, 69–82%, and 65–80%, respectively. In the opinion of K.S. Perfilieva (pers. comm.), the wing venation of these ants is also intermediate between Myrmeciinae and Poneromorpha. It should be noted that in the Cretaceous *Canapone dentata* Dlussky, 1999 (Canadian amber, Campanian) and *Afropone oculata* Dlussky, Brothers et Rasnitsyn, 2004 (Orapa, Botswana, Turonian) abdominal segment III is shorter than segment IV (60% in *C. dentata* and 68% in *A. oculata*). Yet, at the same time, they have short mandibles (41% and 48% as long as the head, respectively) and doubtlessly belong to Poneromorpha.

Genus *Archimyrmex* Cockerell, 1923

Archimyrmex: Cockerell, 1923, p. 52.

Ameghinoia: Viana, Haedo Rossi, 1957, p. 109 (syn. by Dlussky and Perfilieva, 2003, p. 44).

Polanskiella: Rossi de Garcia, 1983, p. 17 (syn. by Dlussky and Perfilieva, 2003, p. 43).

Type species. *Archimyrmex rostratus* Cockerell, 1923, Middle Eocene, United States.

Diagnosis. Gyne. Large, slender ants with elongate mesosoma and long appendages. Mandibles long, linear or narrowly triangular; masticatory margin with sparse, coarse, blunt teeth and small denticles between them. Petiole elongate, without node or with barely protruding low node with upper surface rounded in profile. Abdominal segment III (first gastral segment) bell-shaped, broadly attached to segment IV. Constriction between these segments barely developed. Segment 1RS in forewing branching off R at acute angle near proximal margin of pterostigma. Segment 2+3RS evenly curved. Transverse vein m-cu parallel to 1M. Transverse vein cu-a branching off M+Cu near cell mcu proximal of segment 1M to distance two or three times greater than width of this vein.

Species composition. *Archimyrmex rostratus* Cockerell, 1923 (Middle Eocene, Green River Formation, United States), *A. piatnitzkii* (Viana et Haedo Rossi, 1957) (Middle Eocene, Ventana Formation, Rio Pichileufu, Argentina), *A. smekali* (Rossi de Garcia, 1983) (Middle Eocene, Ventana Formation, Rio Limay, Argentina), and *A. wedmannae*, sp. nov., described below.

Comparison. The genus differs from the other genera of the subfamily Myrmeciinae in the following combination of characters: the petiole is elongate, without a node or with a barely protruding low node with upper surface rounded in profile; the constriction between abdominal segments III and IV is poorly developed.

Archimyrmex wedmannae Dlussky, sp. nov.

Etymology. In honor of the paleoentomologist S. Wedmann.

Holotype. Forschungsinstitut Senkenberg, Aussenstelle Messel. SMF, Mel. 2016, lateral impression of winged gyne; Germany, Messel Pit; Middle Eocene, Early Lutetian, 47 million years before present (Mertz and Renne 2005).

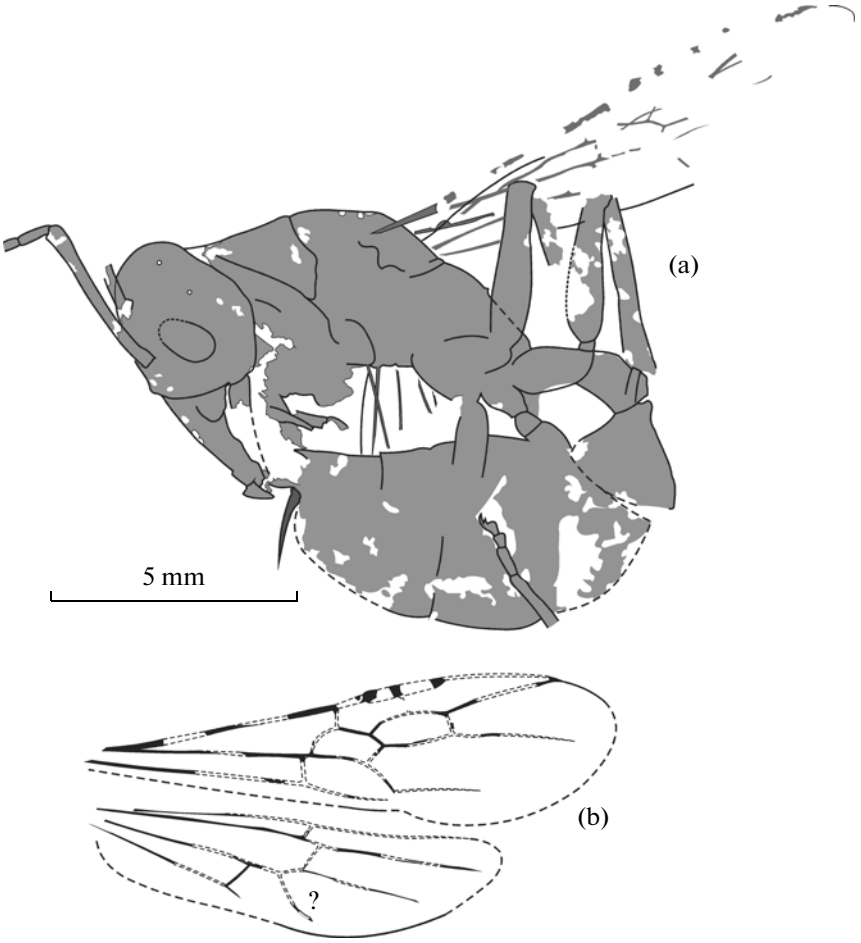

Fig. 1. *Archimyrmex wedmannae*, sp. nov., gyne, holotype, SMF, Mel. 2016: (a) total view of the impression; (b) reconstruction of wing venation. Dashed lines indicate reconstructed veins; position of the transverse vein r-rs (indicated with a question mark, "?") is shown provisionally, since its traces have not been preserved in the impression.

Description (Fig. 1). Gyne. Body length is around 23 mm. The head is short and wide. The eyes are large, oval. The scape is long, more than 1/3 of it is protruding beyond the occipital margin of the head. The mandibles are narrowly triangular, approximately as long as the head. The pronotum is elongate, with dorsal surface straight or weakly concave in profile. The scutum is short. The propodeum in profile is weakly convex, with small denticles. The legs are relatively long. The metatarsal claws have a preapical tooth. The petiole has no node; its dorsal surface in profile is weakly convex, and its ventral surface is weakly concave. Abdominal segment III is slightly higher than long, 68% as long as segment IV, 70% as high as segment IV. The sting is long, well developed. The forewing has closed cells 1+2r, 3r, rm, and mcu; cell cua is not closed. The transverse vein rs-m is positioned distal of r-rs. Cell rm is pentagonal. Fragment 1RS is shorter than fragment 1M. The distal angle of rm is positioned level with the distal angle of the pterostigma. Cell mcu is pentagonal.

Measurements, mm. Mesosoma length 7.4; head length about 2.8; scape length 3.4; maximum eye diameter 1.2; forewing length 10.6.

Comparison. The new species is distinguished from the previously known members of the genus, in which the mandibles are at most 70% as long as the head, by the longer mandibles. The shape of the petiole is similar to that of *A. smekali*, but in this species, in addition to the shorter mandibles, the mesosoma is more compact, and the dorsal surface of the propodeum is more convex.

Remarks. The new species fully complies with the diagnosis of the genus (Dlussky and Perfilieva, 2003) in most characters (metasome shape, wing venation), except the shape of the mandibles. In the previously known secies, the mandibles are shorter (59% as long as the head in *A. rostratus* and 70% as long as the head in *A. smekali*), linear, with large isolated teeth on the chewing margin. Mandibles of the new species are narrowly triangular and approximately as long as the head. However, in our opinion, this difference is not sufficient for describing a new genus.

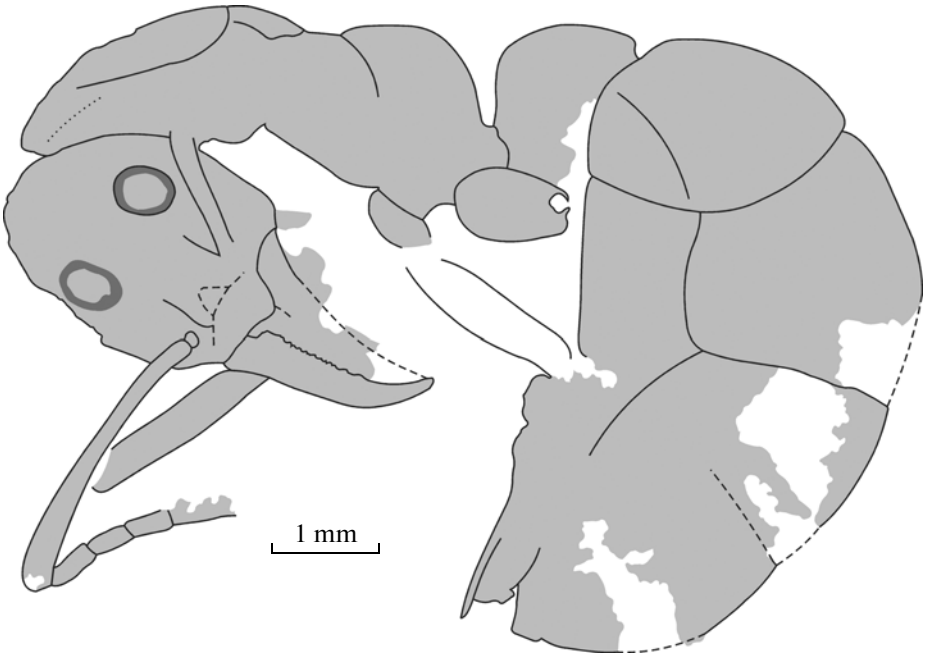

Fig. 2. *Prionomyrmex wappleri*, sp. nov., worker, holotype, Ro A-712.

Members of *Archimyrmex* have been known earlier from the Middle Eocene of the United States and Argentina. The find of *A. wedmannae* shows that the Middle Eocene range of this genus was wider and included also the territory of the modern Europe.

Material. Holotype.

Genus *Prionomyrmex* Mayr, 1868

Prionomyrmex: Mayr, 1868, p. 77.

Type species. *Prionomyrmex longiceps* Mayr, 1868; Late Eocene, Baltic amber.

Diagnosis (for fossil impressions). Worker. Large, slender ants with elongate mesosoma and long appendages. Mandibles long, narrowly triangular, with numerous small denticles on masticatory margin. Anterior margin of clypeus protruding as triangular lobe. Petiole node-shaped, without pronounced anterior cylindrical part. Constriction between abdominal segments III and IV well developed.

Species composition. *Prionomyrmex longiceps* Mayr, 1868, *P. janzeni* Baroni Urbani, 2000 (Late Eocene, Baltic amber) and *P. wappleri*, sp. nov., described below.

Comparison. This genus is distinguished from other genera of the subfamily Myrmecinae by the following combination of characters: the peitole is node-shaped; mandibles are narrowly triangular with numerous small denticles; constriction between abdominal segments III and IV is well developed.

Remarks. Detailed diagnosis of the genus is given by Baroni Urbani (2000). Here only the characters by which fossil impressions of *Prionomyrmex* can be distinguished from those of other described genera of the subfamily Myrmeciinae are provided.

Prionomyrmex wappleri Dlussky, sp. nov.

Etymology. In honor of the paleoentomologist T. Wappler.

Holotype. Institut für Paläontologie, Universität Bonn, Ro A-712, lateral impression of worker; Germany, Rott; Late Oligocene, Aquitanian, 29–30 million years before present (Lutz, 1997).

Description (Fig. 2). Worker. Body length is 14.6 mm. The head is 1.35 times longer than wide. The occipital margin is evenly convex, without pronounced occipital angles. The anterior margin of the clypeus protrudes as a triangular lobe with a rounded apex. The eyes are short oval, almost round, positioned higher than middle of the head. The head is 4.7 times as long as the maximum diameter of the eye. Frontal carinae are parallel, short, not reaching the lower margins of the eyes. The scape is protruding beyond the occipital margin, as long as the head. Segment 1 of the flagellum is approximately as long as segment 2. Segments 1–3 of the flagellum are twice as long as wide. The mandibles are 72% as long as the head. Promesonotum in profile is evenly convex, with a barely visible promesonotal impression. The mesopropodeal impression is wide and rather shallow. The dorsal and declivous surfaces of the propodeum in profile form a strongly rounded blunt angle. The dorsal surface of the petiole in profile is more or less evenly rounded. Abdominal segment III is 76% as long as segment IV.

Measurements, mm. Mesosoma length 4.2; head length 2.7; head width 2.0; scape length 2.7; mandible length 1.95; maximum eye diameter 0.57.

Comparison. *Prionomyrmex longiceps* and *P. janzeni*, described earlier, are very similar to each other and differ only in the degree of development of semi outstanding pilosity. They differ from *P. wappleri* in the following characters: the apex of the clypeal lobe is somewhat pointed, not rounded; segment 1 of the flagellum is half as long as segment 2; petiole in profile is triangular, with a rounded apex.

Remarks. Fossil members of Myrmeciinae were known earlier only from Eocene deposits. The new finding gives evidence that members of this subfamily existed in the territory of the modern Europe at least until the Late Oligocene.

Material. Holotype.

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