

# New Finds of the Fossil Ant Genus *Prionomyrmex* Mayr (Hymenoptera, Formicidae, Myrmeciinae) in Late Eocene European Amber

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**Abstract**—A new species of the fossil genus *Prionomyrmex*, *P. gusakovi* sp. nov., represented by three workers from Baltic amber (Late Eocene, Priabonian, 33.9–37.2 Mya), is described. *Prionomyrmex longiceps* Mayr was first identified in the coeval Rovno amber from Ukraine. The differences between the species described and other known species of the genus are presented. The main problems of evolution and systematics of the extinct representatives of the subfamily Myrmeciinae are discussed.

**Keywords:** ants, Formicidae, *Prionomyrmex gusakovi* sp. nov., paleontology, Baltic, Bitterfeld, and Rovno ambers, systematics, evolution

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## INTRODUCTION

The extinct ant genus *Prionomyrmex* was established by Mayr (1868), based on *P. longiceps* Mayr, 1868, represented by a single worker from Baltic amber. Later, Wheeler (1915) studied nine *Prionomyrmex* workers from the Baltic amber (but not the holotype!), reported additional important diagnostic features of this genus, and first described the male (a single specimen without the abdomen), which he identified as *P. longiceps*. Unfortunately, all the material mentioned above was destroyed during World War II.

The genus was considered monotypic until the end of the 20<sup>th</sup> century, but then Baroni Urbani (2000) described *P. janzeni*, a new species from Baltic amber, which is very close to *P. longiceps* and differing from the latter mainly by the absence of erect setae on the scape. Finally, Dlussky (2012) recently described a new species, *P. wappleri*, represented by an imprint from the Upper Oligocene Rott fossil locality in Germany, and a large (approximately 20 mm long) Myrmeciinae worker, which has not yet been described, was recorded from the Early Eocene Oise amber (France) (Aria et al., 2011; La Polla et al., 2013).

*Prionomyrmex* was first assigned to the subfamily Ponerinae (Mayr, 1868). Wheeler (1915) also regarded this genus as a representative of Ponerinae, but assigned it to a new tribe, Prionomyrmecini (sic!), even though Emery (1877) earlier placed this species into the “group” Myrmeciidae. Brown (1954) transferred

the tribe Prionomyrmecini to the subfamily Myrmeciinae, but Baroni Urbani (2000) raised the tribe Prionomyrmecini to a subfamily level and synonymized the generic name *Nothomyrmecia* Clark, 1934 with *Prionomyrmex*, so that he regarded the name of the subfamily Nothomyrmeciinae as a junior synonym of Prionomyrmecinae. Dlussky and Perfilieva (2003) as well as Ward and Brady (2003) independently transferred *Prionomyrmex* back to Myrmeciinae and resurrected the name *Nothomyrmecia* from synonymy. However, Baroni Urbani (2005) returned to his own earlier opinion on the subfamily status of the Prionomyrmecinae and the synonymy of *Prionomyrmex* and *Nothomyrmecia*. Finally, Archibald et al. (2006), and later, Dlussky (2012), restored the “status quo”, so that *Prionomyrmex* and *Nothomyrmecia* are currently regarded as separate genera of Myrmeciinae; and we fully support this opinion.

To date, thirteen workers and one male of *P. longiceps* have been reported: the holotype, 10 specimens described by Wheeler, and photographs of two specimens are available on the AntWeb website (<https://www.antweb.org/images.do?subfamily=myrmeciinae&genus=prionomyrmex&rank=genus&project=allantwebants>); importantly, they all were found in Baltic amber. In addition, the holotype and the paratype of *P. janzeni*, and the holotype of *P. wappleri* are also available.

We investigated five specimens (workers) in five pieces of amber. We identified two specimens from

Rovno and Bitterfeld amber as *P. longiceps* (see below), and assigned three workers from Baltic amber to the species *P. gusakovi* sp. nov., described below. The specimen from Rovno amber is the first record of a representative of the subfamily Myrmeciinae in Ukraine; thus, the overall number of Rovno hymenopteran species, including *P. longiceps* and another nine chrysidoid and encyrtid species found in Rovno amber (Martynova et al., 2019; Colombo et al., 2020; Perkovsky et al., 2020; Simutnik and Perkovsky, 2020), reached 128. Only 64 hymenopteran species from Rovno (50%) are also known from Baltic amber (Perkovsky, 2018).

## MATERIALS AND METHODS

One *P. longiceps* specimen (worker) from Rovno amber is deposited in the private collection of N.R. Khomich's (Rovno, Ukraine), no. F-125. Beside this, photographs of a specimen (worker without a head) from Bitterfeld amber (Germany) identified as *P. longiceps* by Dlussky were available to use; the photographs were taken by Dlussky in 2003. We also studied three workers of *P. gusakovi* sp. nov. (the holotype and two paratypes) from Yantarnyi, Kaliningrad Region, Russia. Holotype and paratype No. 964/1320 of the species described are deposited at Paleontological Institute, Russian Academy of Sciences (PIN RAS) in Moscow, and the paratype is deposited at the Geologisch-Paläontologisches Institut der Universität Hamburg (GPIH; currently named the Centrum of Natural History, CeNak) (GPIH no. 4993; no. 6762 of C. Gröhn's collection).

## STATE OF THE INCLUSIONS

The holotype of *P. gusakovi* is visible in the right lateral position; it is a whole specimen that lacks antennae; a *Lasius* sp. worker is found in the same piece of amber. The paratype PIN no. 964/1320 is visible from the ventral side; it is a whole specimen largely obscured by fissures in the amber; the antennae, maxillary and labial palps, tibial spurs, tarsal claws, and decumbent pubescence on the ventral surface of the head, coxae, and upper part of the petiole are well visible; a *Dolichoderus* sp. worker is found in the same piece of amber. The paratype GPIH no. 4993 is a whole specimen with most diagnostically significant details visible.

A Leica Z16 APO stereomicroscope connected to a Leica DFC 450 camera was used to take the photographs, which were further processed in LAS Core software.

It was impossible to measure all structural details in all specimens, and therefore we measured as many of them as possible with a 0.01 mm precision: HL, head length from the anterior edge of the clypeus to the middle of the occipital margin; HW, maximal head width behind the eyes; FW, minimal distance between

the frontal carinae; FLW, distance between the external edges of the frontal lobes; SL, scape length from its apex to the articulation with condylar bulb; EL, eye length (maximal diameter); MDL, mandible length; ML, thorax (mesosoma) length in side view measured from the anterior margin of the neck shield to the posterior margin of the metasternal lobes; MH, thorax (mesosoma) height in side view, measured from the uppermost point of the promesonotum perpendicularly to the lowermost point of the mesopleuron; PRW, pronotum width from the top; PL, petiole length; PH, petiole height in side view; PW, petiole width from the top; PPL, postpetiole length; PPH, postpetiole height in side view, from the uppermost to the lowermost point, measured perpendicular to the tergo-sternal suture; PPW, postpetiole width at the top; L-IV, length of abdominal segment IV; H-IV, height of abdominal segment IV; GL, gaster length; HTL, hind tibia length; body length was calculated as the total length of the head, thorax (mesosoma), petiole, and gaster.

Index abbreviations are not given here to facilitate the perception of information, but rather the size ratios of various structures are presented: for example, HL/HW, rather than HI.

## SYSTEMATIC PALEONTOLOGY

### Subfamily Myrmeciinae Emery, 1877

#### Genus *Prionomyrmex* Mayr, 1868

Type species. *P. longiceps* Mayr, 1868, by monotypy; Baltic amber, Late Eocene.

**Diagnosis.** Workers large, polymorphic with regard to size, body length 9.4–14.8 mm. Body slender, elongated, with long legs. Antennae with 12 segments, scape long, somewhat protruding beyond the occipital margin of the head, funiculus filiform, without a club. Mandibles long, narrow triangle-shaped, masticatory margin with a series of small denticles and coarse short bristles. Eyes large, located approximately in the middle of the lateral sides of the head or slightly posterior to them. Maxillary palps of six segments, which is in agreement with the report by Wheeler (1915), labial palps with four segments. It is necessary to note that Baroni Urbani (2000) reported a palp formula of 5, 2 for *P. janzeni* but did not rule out the possibility of the basal segments being poorly visible in the specimen studied. The petiole without the anterior peduncle and with a well-developed node with a narrowly rounded dorsum. The constriction between the abdominal segments III and IV is sharp and deep. Middle and hind tibiae with two spurs (simple and pectinate). Tarsal claws with an additional preapical tooth (see also: Mayr, 1868; Wheeler, 1915; Baroni Urbani, 2000; Dlussky, 2012).

The reader is referred to the study by Wheeler (1915, p. 27) for a characterization of the only male of this genus described so far.

**Species composition.** Two species, *P. longiceps* and *P. janzeni*, from Baltic amber; the former also found in Bitterfeld and Rovno amber, as reported in the present study; *P. wappleri* from Upper Oligocene deposits of Germany; and *P. gusakovi* sp. nov. from Baltic amber. The age of all amber specimens mentioned 33.9–37.2 Ma (Late Eocene, Priabonian).

**Notes.** *Prionomyrmex* is clearly distinct from all fossil and recent ant genera known and is the closest to *Nothomyrmecia*, an endemic Australian genus. Detailed analysis of the taxonomic position and the possible relations of *Prionomyrmex* to other groups of ants has been performed by Ward and Brady (2003).

*Prionomyrmex gusakovi* Radchenko et Perkowsky, sp. nov.

Plate 8, figs. 1 and 2; Plate 9, figs. 1–4

**Etymology.** In honor of V.A. Gusakov, who provided the material (holotype and paratype) for our studies and subsequently donated it to PIN RAS.

**Holotype.** PIN No. 964/1319, worker; labeled by Gusakov: “2011 Collection of Viktor Gusakov CVGM № 33AFMP2011”; AntWeb CASENT 0917648; Yantarnyi, Kaliningrad Region, Russia, Baltic amber, Late Eocene.

**Description** (based on a combination of visible features of the holotype and paratype specimens). The head is elongated, with weakly convex lateral sides, rounded occipital corners, and a straight occipital margin. The anterior edge of the clypeus protrudes as a somewhat pointed triangular lobe, very narrowly rounded at the apex. The frontal carinae are very weakly curved, extend to the level of the lower edge of the eyes, the frontal lobes slightly extended, the frontal triangle distinct. The eyes are oval, located slightly posterior to the middle of the lateral margins of the head. The holotype lacks ocelli (at least, they are not visible), but the paratype GPIH No. 4993 has well-developed ocelli. The maxillary palps of 6 segments, labial palps with four segments. Segments of the antennal funiculus elongated, more than two times as long as wide; the first segment approximately twice shorter than the second; the second is the longest, and the others gradually decrease in length, even though the apical segment is longer than any of the three closest ones.

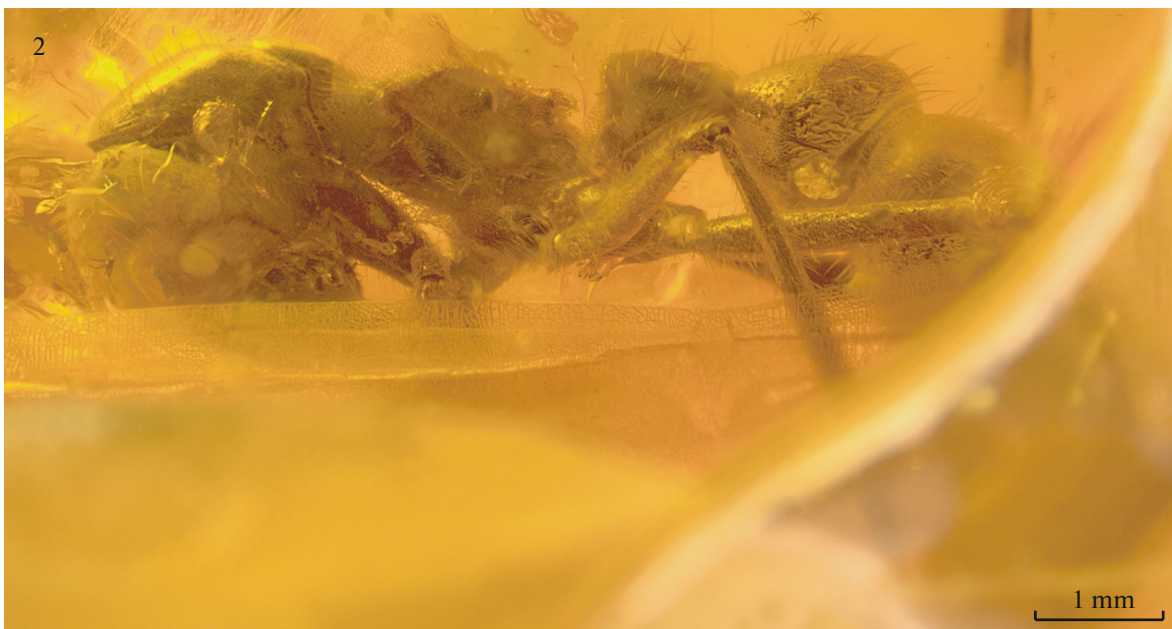
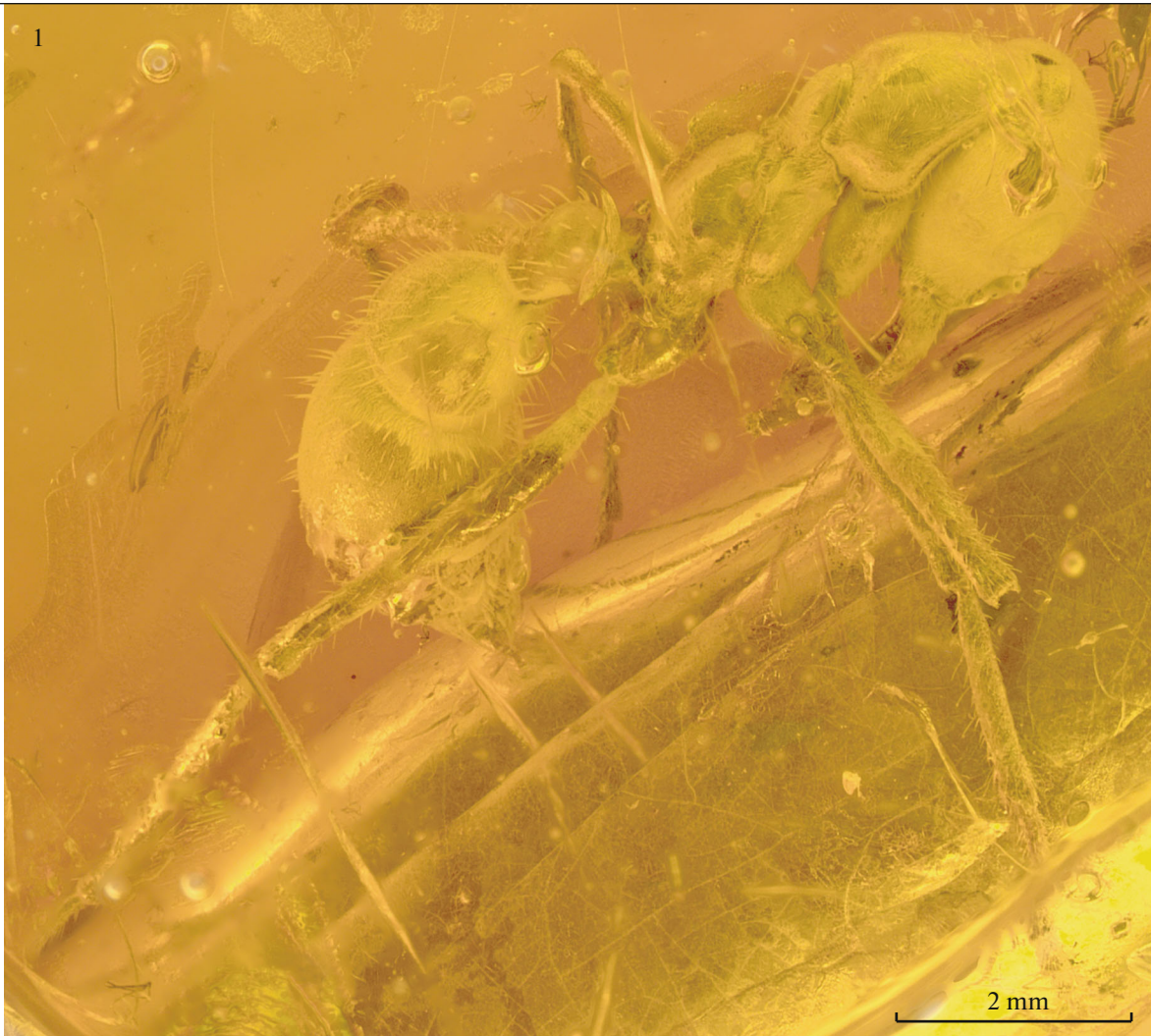
The thorax (mesosoma) is long, slender, pronotum gradually and weakly convex, promesonotal junction apparently mobile, promesonotal and metanotal sutures sharp, rather deeply impressed. The propodeum is gradually arched, without a sharp transition between the upper and posterior surfaces, with small denticles; the upper surface is almost as long as the posterior one. The propodeal spiracles are slit-like. The anterior surface of petiolar node very slightly concave, posterior surface slightly convex, the apex is rather narrowly rounded. The postpetiole (abdominal

segment III) is much more robust than the petiole, convex, expands gradually backwards, bell-shaped, distinctly lower and shorter than the first gastral segment (abdominal segment IV), and sharply separated from the latter by a deep constriction.

The entire body and legs with abundant, rather long, straight or slightly curved erect or semi-erect hairs, scape with short and sparse erect hairs. In addition, the entire body surface with dense, soft, silky decumbent pubescence, so that the sculpture is poorly discernible, but body surface with very weak microsculpture, slightly shiny. The body color of amber inclusions is, as a rule, an artefact, but still, the holotype is brownish-grey, one paratype is somewhat lighter, and the other paratype is blackish-brown.

**Measurements**, mm: holotype: body length 9.4, HL 2.28, MDL 1.86, EL 0.69, ML 4.51, MH 1.33, GL 3.71, PL 1.17, PH 1.01, PPL 1.35, PPH 1.45, L-IV 1.90, H-IV 1.85, HTL 2.86; HL/EL 3.31, MDL/HL 0.81, ML/MH 3.40, PL/PH 1.16, PPL/PPH 0.93, PPL/PL 1.15, PPH/PH 1.43, PPL/L-IV 0.73, PPH/H-IV 0.71. Paratype No. 964/1320: body length 11.5, HL 2.65, HW 1.86, SL 2.39, MDL 2.23, EL 0.80, HTL 3.41, length of antennal funicular segments, first to eleventh: 0.28, 0.56, 0.48, 0.42, 0.38, 0.35, 0.35, 0.35, 0.34, 0.32, 0.42, width of all segments approximately 0.15; HL/HW 1.42, SL/HL 0.90, SL/HW 1.22, MDL/HL 0.84, HL/EL 3.33. Paratype GPIH No. 4993: body length 14.8, HL 2.76, HW 1.91, SL 2.39, MDL 2.23, EL 0.82, FW 0.74, FLL 0.85, ML 4.82, MH 1.48, GL 4.66, PL 1.06, PH 0.90, PW 0.80, PPL 1.48, PPH 1.80, PPW 1.86, L-IV 2.12, H-IV 2.33, HTL 3.55, length of antennal funicular segments, first to eleventh: 0.37, 0.69, 0.58, 0.48, 0.42, 0.42, 0.42, 0.37, 0.32, 0.28, and 0.42, width of all segments approximately 0.15–0.16; HL/HW 1.42, SL/HL 0.86, SL/HW 1.23, HL/EL 3.35, FW/HW 0.38, FLW/FW 1.14, MDL/HL 0.81, ML/MH 3.25, PL/PH 1.18, PPL/PPH 0.82, PPL/PL 1.40, PPW/PW 1.94, PPH/PH 2.00, PPL/L-IV 0.70, PPH/H-IV 0.77.

**Comparison.** The habitus of *P. gusakovi* is similar to those of the known Baltic amber species *P. longiceps* and *P. janzeni*, but the former species can be reliably distinguished from the latter two by the presence of dense decumbent body pubescence. Moreover, the upper surface of the propodeum in the latter two species is clearly longer than the posterior one, whereas they are approximately equal in length in *P. gusakovi*. It is necessary to note that Wheeler (1915) noted that five *P. longiceps* workers studied by him lack decumbent body pubescence, but one specimen (B 259) from the collection of the Geological Institute in Königsberg had abundant pubescence. It appears completely logical to suppose that the specimen discussed should be assigned to *P. gusakovi*. The species described above differs from *P. wappleri* in the length





ratio of the first and second antennal funicular segments and clypeus shape (the anterior edge of the clypeus is rounded, not pointed, in *P. wappleri*). Moreover, it is not very likely, although not impossible, that fossil ant species with an age difference of 10 million years are conspecifics.

**Material.** In addition to the holotype, two paratypes: PIN no. 964/1320, Gusakov's label: 1999 Collection of Viktor Gusakov (Russia: Moscow) CVGM, no. 332AFMPI1999 *Prionomyrmex longiceps* Mayr Eocene Baltic Amber»; AntWeb CASENT no. 0917649 (*Dolichoderus* sp. worker ant in the same piece of amber); GPIH no. 4993, C. Gröhn's collection numbered 6762; AntWeb CASENT no. 0917646; Baltic amber.

#### *Characteristics of Newly Found Prionomyrmex Longiceps Inclusions*

(1) Worker, Rovno amber: Ukraine, Rovno Region, Vladimirets district; from N.R. Khomich's private collection, Rovno, Ukraine. Whole specimen, visible from the upper left side, lacks antennae (pl. 9, fig. 5).

Measurements (mm): body length 12.3, HL 2.85, EL 0.85, MDL 2.25, ML 4.95, PRW 1.20, PL 1.50, PH 1.20, PW 1.20, HTL 3.50; HL/EL 3.35, MDL/EL 0.79, PL/PH 1.25.

(2) Photograph made by Dlussky, worker, Bitterfeld amber; deposited at the Museum für Naturkunde Berlin, Germany (MNKB) (former Zoological Museum of the Humboldt University, no. 12/223). Damaged specimen, visible in the right lateral view, head and greater part of the gaster missing (pl. 9, fig. 6). The head and the antennae are missing, and therefore the attribution of this specimen to *P. longiceps* is somewhat conditional, as it can also be a representative of *P. janzeni*.

## DISCUSSION

Representatives of *Prionomyrmex* are the largest ants found in the Late Eocene European amber: their size ranges from 9.5 to almost 15 mm. Workers of only few species of other genera found in amber have a body length that exceeds, or at most reaches 10 mm: they are, for example, *Paraneuretus tornquisti* Wheeler, 1915 (8–10 mm), *Ponera gracilicornis* Mayr, 1868 (10.5 mm) [currently transferred to the genus *Pachycondyla* F. Smith, 1858 (Bolton, 1995), but the assignment of this species to a genus needs revision], *Cataglyphoides constrictus* (Mayr, 1868) (up to 10 mm), and some *Formica* L., 1758 species (up to 10 mm)

(Wheeler, 1915). The total number of specimens of these species is on the order of 0.5% of the total number of ants found in amber, whereas the number of inclusions of *Prionomyrmex* proper does not exceed 0.1% (Dlussky and Rasnitsyn, 2009). *Prionomyrmex* was previously known only from Baltic and Bitterfeld amber, but we also found it in Rovno amber. Moreover, one species from the same genus is known from much less ancient Oligocene deposits (see below).

There are several potential explanations for the scarcity of *Prionomyrmex* finds in Late Eocene European amber: these species were actually rare, colonies were small, their lifestyle and large size of workers. It is entirely possible that all these factors influenced low representation of the genus in of amber inclusions.

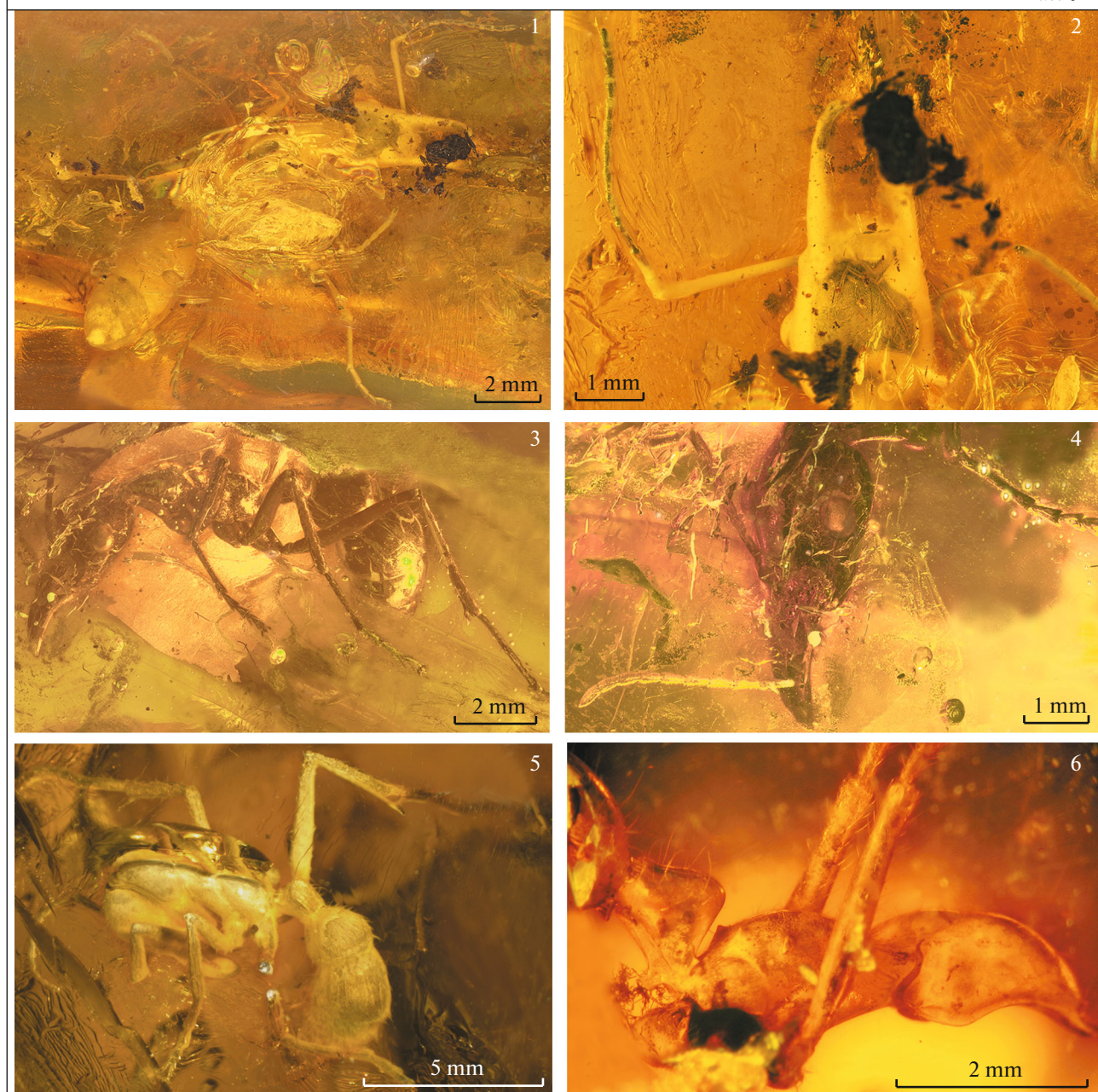
Wheeler (1915) supposed that *Prionomyrmex* could have been arboreal, because they had distinctive morphological traits, such as elongated body, antennae, and legs, large eyes, and long strong mandibles, but the putative phylogenetic relationships of this genus to the modern ants show that Wheeler's hypothesis was most likely erroneous (see also: Archibald et al., 2006).

At present, *Prionomyrmex* are universally assigned to the subfamily Myrmeciinae, which includes two recent genera, *Myrmecia* Fabricius, 1804 and *Nothomyrmecia*, distributed in Australia, Tasmania, and New Caledonia. All known species of these genera are characterized by a rather low level of social organization with several hundred to 1–2 thousand workers per colony; these ants build nests in the soil and forage alone on the soil and in the litter, but they can also climb tree trunks to collect nectar and honeydew and to prey on small invertebrates (Taylor, 1978; Hölldobler and Wilson, 1990). Moreover, a similar body and appendages structure was noted in many representatives of extant genera that build nests in the soil (for example, *Cataglyphis* Foerster, 1859, *Ocymyrmex* Emery, 1886, certain *Aphaenogaster* Mayr, 1853, and others). Therefore, one can assume that *Prionomyrmex* also dwelled on the ground and the colonies in this species were not very large; this, along with their large body size, may have been a reason for the infrequent entrapment of the ants in the resin that was to become amber.

The subfamily Myrmeciinae currently includes the recent genera named above and a number of fossil genera: *Prionomyrmex*, *Archimyrmex* Cockerell, 1923, *Avitomyrmex* Archibald, Cover et Moreau, 2006, *Macabeemyrma* Archibald, Cover et Moreau, 2006, *Ypresiomyrma* Archibald, Cover et Moreau, 2006, and the morphotaxon *Myrmeciites* Archibald, Cover et

#### Explanation of Plate 8

**Figs. 1, 2.** *Prionomyrmex gusakovi* sp. nov., holotype PIN No. 964/1319, worker: 1—body, dorsal-lateral view; 2—mesosoma and petiole, lateral view; Baltic amber.



#### Explanation of Plate 9

**Figs. 1–4.** *Prionomyrmex gusakovi* sp. nov. workers: (1, 2) specimen PIN No. 964/1320: (1) body, ventral view; (2) head and antenna, ventral view; (3, 4) specimen GPIH No. 4993: (3) body, lateral view; (4) head, lateral view; Baltic amber.

**Figs. 5, 6.** *Prionomyrmex longiceps* Mayr, 1868 workers: (5) specimen No. F-125, body, dorso-lateral view, Rovno amber; (6) specimen MNKB No. 12/223, mesosoma and petiole, lateral view, Bitterfeld amber.

Moreau, 2006; moreover, the genus *Propalosoma* Dlussky et Rasnitsyn, 1999, which was initially assigned to the family Rhopalosomatidae, was recently transferred into the subfamily Myrmeciinae (Archibald et al., 2018). All fossil genera listed above (except for *Prionomyrmex* and *Ypresiomyrma*) were

found only in Early and Middle Eocene deposits. It is necessary to note that Dlussky (2012) voiced certain doubts related to the assignment of the latter four taxa to Myrmeciinae and noted that these ants occupied an intermediate position between the recent Myrmeciinae and Poneromorpha with regard to the size ratio of

abdominal segments III and IV, relative length of the mandibles, and wing venation. In our opinion, these conclusions are mostly applicable to Myrmeciinae with a two-segmented waist, but they can be referred to the subfamily Myrmeciinae, along with *Nothomyrmecia*, if the combination of other traits is considered. Continuation of the discussion of this issue is far beyond the scope of the present article, but even if Dlussky was right, the genera listed above may represent an intermediate stage between Poneromorpha and Myrmeciinae.

*Nothomyrmecia* differ from *Myrmecia* in multiple characters, including one trait that is very important from the point of view of evolutionary morphology: the former genus has a one-segmented waist, and the latter, a two-segmented one. Additionally, a one-segmented waist should undoubtedly be considered a plesiomorphic state for all ants, including fossil ones, rather than for *Nothomyrmecia* only.

This fundamental difference is also characteristic of fossil Myrmeciinae: *Archimyrmex* and *Prionomyrmex* have two-segmented waist, whereas *Ypresiomyrma*, *Avitomyrmex*, *Macabeemyrma*, *Propalosoma*, and *Myrmeciites* have one-segmented one.

Four species are currently assigned to the genus *Archimyrmex*: one was found in the United States (Colorado, Green River Formation, middle to late Ypresian, approximately 48.5–53 Ma), two, in Argentina (Ventana Formation, Rupelian–Burdigalian, approximately 20–34 Ma), and one, in Germany (Messel, late Ypresian, 48 Ma).

Argentinean ants merit a focused discussion. First, the list of fossil Myrmeciinae found in South America is limited to these two species (Petrulevičius and Martins-Neto, 2000). Second, an Early Paleocene age was assumed for these ants for a long time (Dlussky and Fedoseeva, 1988; Perfilieva, 2015). However, the age of the Patagonian ants was found to be much younger than Paleocene, like that of ants from the Sakhalinian amber (Radchenko and Perkovsky, 2016).

*Archimyrmex piatnitzkyi* (Viana et Haedo Rossi, 1957) (initially attributed to the genus *Ameghinoia* Viana et Haedo Rossi) was found in the Rio Negro province of Argentina (Ventana Formation), and *A. smekali* (Rossi de Garcia, 1983) (initially attributed to the genus *Polanskiella* Rossi de Garcia) was found in a relatively close Confluencia locality of an unknown age (Petrulevičius and Popov, 2014). The Ventana Formation was dated to the Middle Eocene for a long time, but recent geological studies showed that these deposits are much younger, even though the age estimates vary greatly, from Early Oligocene to Early Miocene (Rupelian–Burdigalian) (Bechis et al., 2014; Encinas et al., 2018).

The subfamily Myrmeciinae was represented by six genera in the Early Eocene of North America

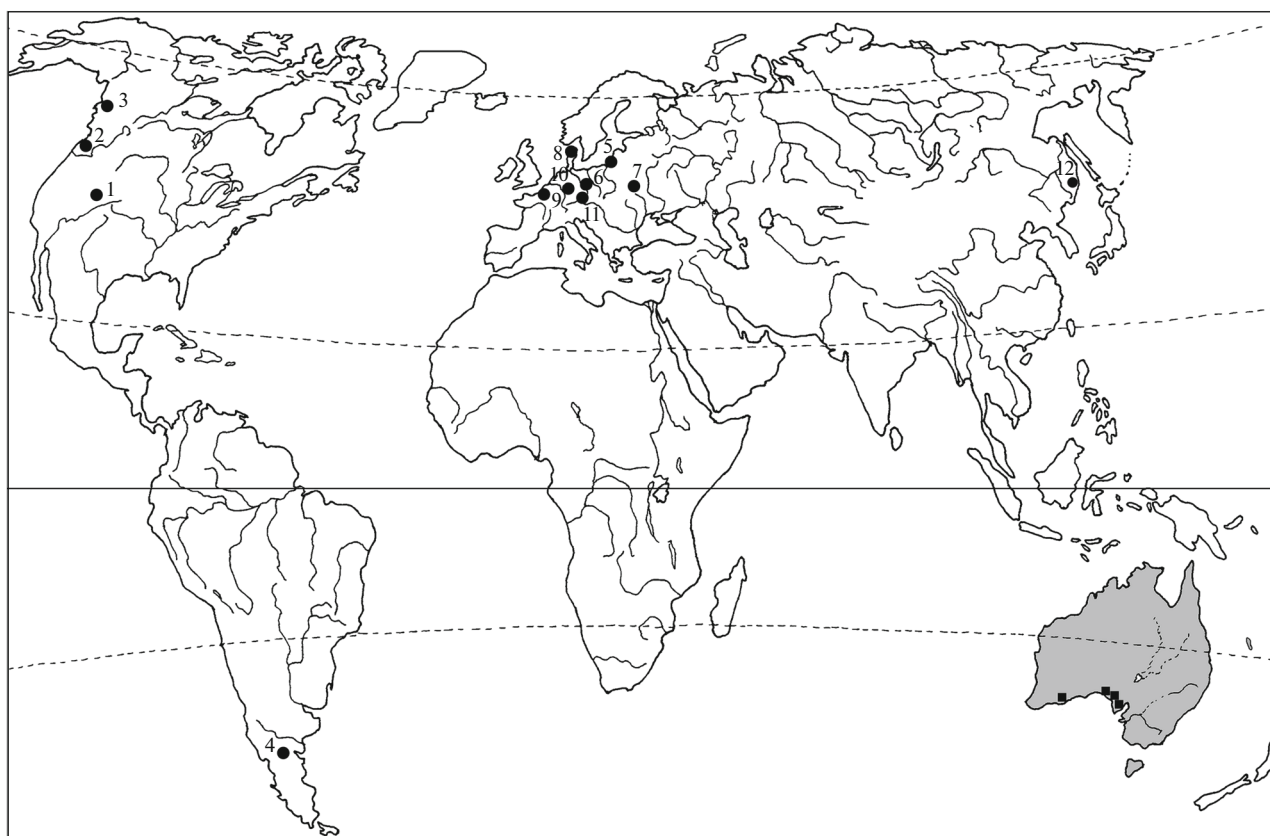
(Archibald et al., 2018), but they all had become extinct by the beginning of the Middle Eocene; at least, no finds from later periods are known at present. However, Patagonian Myrmeciinae are approximately 15 million years younger, and the assignment of these ants to the genus *Archimyrmex* raises certain doubts, especially in the case of *A. piatnitzkyi* with a nodiform petiole, but revision of the type specimens and new finds of these species accumulated during the past few decades is essential for resolving the issue of the systematic position of *A. piatnitzkyi* and *A. smekali*.

*Ypresiomyrma* includes four species: one from Denmark [diatomites of Fur Island (“Mo Clay”), Olst and Fur formations, earliest Ypresian, i.e. close to the Eocene–Paleocene boundary, approximately 54.5–56 Ma], two from Canada (British Columbia, Okanagan Highlands, McAbee; middle Ypresian, 52–53 Ma), and one from Biamo [Primorskiy Region of Russia, Late Eocene, later than Baltic amber and its analogs (Dlussky et al., 2015)]. Representatives of the genera *Avitomyrmex* and *Macabeemyrma* and the morphotaxon *Myrmeciites* include seven species and one imprint of an unidentified species; they were also found in Okanagan Highlands in British Columbia (McAbee, Horsefly River, and Falkland) (Archibald et al., 2006; Dlussky, 2012; the age of the Falkland is 50.5 Ma; Archibald, personal communication); the only *Propalosoma* species and one imprint of an unidentified *Myrmeciites* species were found in another locality in the Okanagan Highlands (north-central Washington, Republic, late Ypresian, approximately 50 Ma; Wolfe et al., 2003) (Fig. 1).

Thus, fossil Myrmeciinae with a one-segmented waist are, in general, somewhat more ancient than those with a two-segmented one: 34–56 Ma versus 23–53 Ma; importantly, only the Green River and Messel species are older than the Priabonian, whereas the age of the *Ypresiomyrma* species found in Primorye is compared to that of *Prionomyrmex* representatives found in Late Eocene European amber (Priabonian, 35–38 Ma) and in Upper Oligocene deposits of Germany (North Rhine-Westphalia, Rott). Dlussky (2012, p. 68) erroneously referred to the statement of Lutz (1997) and believed the age of these deposits to be “Late Oligocene, Aquitanian, 29–30 Mya”, whereas more recent data point at the age of these deposits being 23–24 Ma (Late Oligocene, Chattian) (Böhme, 2003).

Ward and Brady (2003) proposed the following phylogenetic scheme for Myrmeciinae: ((*Archimyrmex* + *Nothomyrmecia*) + *Prionomyrmex*) + *Myrmecia*. It is definitely based on computer cladistic analysis that used multiple traits, but the result still shows that analysis of this type gives rise to some controversy if the evolutionary morphological significance of the traits and the possibility of formation of certain structures





**Fig. 1.** Map of the distribution of extant and extinct Myrmeciinae genera. The range of the genus *Myrmecia* is shaded in gray; *Nothomyrmecia macrops* localities are marked by squares; and fossil genus localities are marked with points: (1) United States, Colorado, Green River, Early Eocene; (2) United States, Washington, Republic, Early Eocene; (3) Canada, British Columbia, McAbee, Early Eocene; (4) Argentina, Patagonia, Ventana Formation, Oligocene–Early Miocene; (5–7) Baltic, Bitterfeld, and Rovno ambers, respectively, Late Eocene; (8) Denmark, Fur Island, Early Eocene; (9) France, Oise amber, Early Eocene; (10) Germany, Hessen, Messel, Early Eocene; (11) Germany, North Rhine-Westphalia, Rott, Late Oligocene; (12) Russia, Primorskiy Region, Bol'shaya Svetlovodnaya (Biamo), Late Eocene.

are not assessed. For instance, the closeness of *Archimymex* and *Nothomyrmecia* is difficult to explain from the evolutionary point of view since the former has a two-segmented waist, but the latter—a one-segmented one (see also Dlussky and Fedoseeva, 1988). The phylogenetic scheme presented by Archibald et al. (2006) appears more appropriate to us: in this scheme *Nothomyrmecia* form a single clade with fossil genera with a one-segmented waist, described by the authors (*Ypresiomyrma*, *Avitomyrmex*, *Macabeemyrma*, and *Myrmeciites*); this clade is a sister one for *Prionomyrmex*, and these two clades together form a sister clade for *Myrmecia*, but *Archimymex* was not included in the analysis.

Ward and Brady (2003) assumed that the subfamily Myrmeciinae arose in the Southern hemisphere (in Gondwana) during the Late Cretaceous and *Nothomyrmecia* and *Myrmecia* subsequently migrated to Australia, whereas *Prionomyrmex* migrated to Europe (Laurasia). However, Archibald et al. (2006) considering the finds of a range of new fossil Myrmeciinae gen-

era in North America and Europe (see above), developed a different, quite substantiated hypothesis, with which we can agree: they assumed that Myrmeciinae emerged in Laurasia. Our finds of *Prionomyrmex* in Late Eocene European amber, and especially the finds of new *Archimymex* and *Prionomyrmex* species in Lower Eocene and Upper Oligocene deposits of Germany (Dlussky, 2012), also support this hypothesis to certain extent.

Detailed analysis of the problem of the possible phylogenetic relationships of fossil and recent representatives of the subfamily Myrmeciinae is far beyond the scope of the present article. Nevertheless, one can assume that taxa with a one-segmented waist were the ancestors of those with two-segmented waist (see also: Archibald et al., 2006).

Dlussky and Perfilieva (2003) provided arguments in favor of *Archimymex* being a putative ancestor of *Myrmecia*, but supposed that *Archimymex* could not have been an ancestor of *Prionomyrmex*, even though insufficient support for the latter hypothesis was pro-



vided. We believe that morphology, timing of the finds, and paleogeographic data allow the assumption of *Archimymex* being a putative ancestor of *Prionomyrmex*. Finally, it is entirely possible to agree with the opinion of Dlussky and Perfilieva (2003) that the different directions in specialization of the head shape, clypeus, mandible, and petiolar structure disprove the hypothesis of *Prionomyrmex* being a putative ancestor of *Myrmecia*.

Thus, *Prionomyrmex* could have emerged on the territory of modern Europe no later than the Middle Eocene, and became extinct without leaving any descendants.

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