

Paleogene Ants of the Genus *Archimymex* Cockerell, 1923 (Hymenoptera, Formicidae, Myrmeciinae)

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Abstract—The genera *Ameghinoia* Viana et Haedo Rossi and *Polanskiella* Rossi de Garcia are synonymized under *Archimymex* Cockerell, which now includes three species, *A. rostratus* (Middle Eocene, United States), *A. piatnitzkyi* (Upper Paleocene–Lower Oligocene, Argentina), and *A. smekali* (Upper Paleocene–Lower Oligocene, Argentina). These species are redescribed, and their assignment to the subfamily Myrmeciinae is argued.

INTRODUCTION

Representatives of the subfamily Myrmeciinae are considered by the majority of authors to be among the most primitive ants with respect to both their morphology and the biology. Thus, they are usually placed at the base of the phylogenetic tree of ants, being considered as the ancestors of the myrmecioid group of subfamilies. Currently, this subfamily is represented by a single genus, *Myrmecia* Fabricius, 1804, which includes 89 species, inhabiting exclusively Australia and allied islands (Ogata and Taylor, 1991). Therefore, its paleontological history is of substantial interest.

To date, five extinct genera have been described that have been assigned to the Myrmeciinae at different times. In 1868, *Prionomyrmex longiceps* was described from Baltic amber of the Late Eocene (Mayr, 1868). Mayr provided an extended description, but his drawings (Mayr, 1868, pl. IV, figs. 74, 75) are a reconstruction rather than a representation of a concrete specimen. Later, this species was redescribed by Wheeler (1915), who examined a series of nine individuals deposited in the Geological Institute in Königsberg, including one male. A description of a worker was supplied with a superb drawing of the best-preserved specimen. Regrettably, the male was not figured by Wheeler, and he simply noted that the venation was similar to that of *Myrmecia* when he characterized it in the description. The assignment of *Prionomyrmex* to the Myrmeciinae is beyond doubt, since all key diagnostic characters of the subfamily are visible in the inclusions. At the same time, this species differs from *Myrmecia* in a number of essential apomorphic characters; therefore, it has been included in the separate tribe Prionomyrmecini (Bolton, 1994, 1995).

Recently, Baroni Urbani (2000) described the second species of *Prionomyrmex*, *P. janzeni*, from Baltic amber. In his paper, he removed *Prionomyrmex* from the subfamily Myrmeciinae, synonymized *Nothomyrmecia* Clark, 1934 and *Prionomyrmex* Mayr, 1868 and respectively, the subfamilies Nothomyrmeciinae Clark, 1951 and Prionomyrmecinae Wheeler, 1915. He did

this on the basis of a cladogram calculated from the analysis of 34 characters of six taxa (*Myrmecia*, Myrmicinae, *Nothomyrmecia*, Pseudomyrmecinae, *Prionomyrmex*, and Vespidae). Uniting *Prionomyrmex* and *Nothomyrmecia* was supported by a unique synapomorphy, the presence of the lateral clypeal carina. At the same time, such an important character as separation of the third abdominal segment in the worker was not taken into account. In this feature, *Prionomyrmex* is similar to *Myrmecia* and members of the subfamilies Myrmicinae, Pseudomyrmecinae, Ponerinae, Cera-pachyinae, and others, but differs from the *Nothomyrmecia*. Thus, there are two incompatible synapomorphies, the lateral clypeal carina in both the worker and the female of *Nothomyrmecia* + *Prionomyrmex* and the formation of the postpetiole between the third and fourth abdominal segments in *Myrmecia* + *Prionomyrmex* (as in the Myrmicinae, Pseudomyrmecinae, Ponerinae, and others). Baroni Urbani considers the first synapomorphy as true, since the degree of constriction between the third and fourth abdominal segments in ants is highly variable.

At the same time, as was shown earlier (Taylor, 1978), it is not the constriction between the segments *per se* that is significant, but the fusion between the anterior parts of the tergite and sternite of the fourth abdominal segment to form a tubulation, which is always present in the Ponerinae, Myrmeciinae, Myrmicinae, and Pseudomyrmicinae and always absent from the Formicinae, Dolichoderinae, Aneuretinae, and Nothomyrmeciinae. The secondary loss of the tubulation is unlikely (Dlussky and Fedoseeva, 1988), whereas independent appearance of the clypeal carina is quite possible. The presence of the fused tergite and sternite of the fourth abdominal segment in *P. janzeni* is clearly seen in the figure provided (Baroni Urbani 2000, fig. 6); thus, it is evident that *Prionomyrmex* is similar to *Myrmecia* and differs from *Nothomyrmecia*. Therefore, it makes sense to retain *Prionomyrmex* in the subfamily Myrmeciinae and consider *Nothomyrmecia* and *Prionomyrmex* to be separate and relatively remote genera.

The other species were described based on variously preserved imprints. Many key characters of the Myrmeciinae are either absent or poorly pronounced in the imprints; therefore, they were missed by the authors of descriptions. As a result, the taxonomic position of these finds has been controversial.

Cockerell (1923) described *Archimyrmex rostratus* based on a single poorly preserved imprint from the Green River Formation, United States (Middle Eocene, Lutetian) and noted in the description the resemblance of this species with *Myrmecia* and *Prionomyrmex*. However, Wheeler (1928), on the basis of a drawing by Cockerell, later came to a conclusion that this ant is more similar to representatives of the subfamily Myrmicinae. Carpenter (1930), who examined and redescribed the holotype of *A. rostratus*, agreed with this opinion. Bolton (1995), in his catalog, included *Archimyrmex* in the subfamily Myrmicinae without assignment to any tribe.

In 1957, *Ameghinoia piatnitzkyi* Viana et Haedo Rossi, 1957 was described from Argentina. The authors allocated the new genus to the subfamily Ponerinae; however, later, Wilson (1971) transferred it to the Mymeciinae without giving any grounds for this action. On the basis of photos, drawings, and the original descriptions, Dlussky and Fedoseeva (1988) proposed that this genus should rather be assigned to a particular group of the Myrmicinae; however, later, Naumann (1991) and Bolton (1994, 1995) agreed with the opinion of Wilson. Also from Argentina, *Polanskiella smekali* (Rossi de Garcia, 1983) was described, which is similar to *Ameghinoia*. The description was rather unprofessional; in addition, it was published in an obscure periodical, so it was missed in Bolton's catalog. Judging from the description, *Polanskiella* and *Ameghinoia* differ from each other in size and nonessential variations in forewing venation; therefore, Dlussky and Fedoseeva (1988) proposed that *Polanskiella* be considered as a junior synonym of *Ameghinoia*.

Originally, *A. piatnitzkyi* was aged as the Late Oligocene or Early Miocene (Viana and Haedo Rossi, 1957); and *Polanskiella smekali* was aged as the Middle Eocene (Rossi de Garcia, 1983). Later, it was shown that both records were of approximately the same age and referred to the Ventana Formation (Petrulevicius, 1999). There are greatly divergent opinions regarding the age of this formation. Initially, it was identified as the Late Paleocene–Middle Eocene on the grounds of paleobotanical data. Later, these beds were dated radiometrically as the Early Oligocene, but this dating is still somewhat doubtful (Petrulevicius, 1999).

Finally, a sensational find was made in Brazil in 1989. In the Lower Cretaceous (Aptian) deposits of the Santana Formation, an insect was discovered that was named *Cariridris bipetiolata* and assigned to the subfamily Myrmeciinae (Brandão *et al.*, 1989). However, the correctness of the reconstruction of this insect is doubtful. Bolton (1995) placed this species in the subfamily Myrmeciinae without ascribing it to any tribe,

Grimaldi *et al.* (1997) classified it as Formicoidea incertae sedis, and Rasnitsyn (1990) concluded that the insect in question belongs to the subfamily Ampulicinae of the family Sphecidae. The latter conclusion seems to be rather well grounded, especially taking into account the fact that finding a true ant in such ancient deposits is in poor agreement with other data on the paleontological history of the Formicoidea (Dlussky, 1998, 1999).

While working in the collection of the Natural History Museum in Vienna (NMW), A.G. Ponomarenko discovered an imprint of a large ant, which was provisionally identified by him as *Ameghinoia* sp. Due to the courtesy of the curator of fossil hymenopterans in this museum, O. Schultz, we were able to obtain this specimen for examination. It turned to be the counterpart of the *P. smekali* syntype figured in photo 3 in the original description (Rossi de Garcia, 1983). Additionally, owing to the efforts of Rasnitsyn, we obtained and examined a large series of ant imprints collected by D. Kohls and C. Labandeira from the Green River Formation and stored at the Department of Paleobiology of the National Museum of Natural History in Washington, DC (USNM, coll. no. 7/97). This series includes ten specimens of *A. rostratus*. One more specimen of this species was collected by Rasnitsyn in 1997 in the same locality and deposited in the collection of the Paleontological Institute of the Russian Academy of Sciences (PIN). Examination of these imprints and their comparison with the description, figures, and photographs of *A. piatnitzkyi* showed that these three species differ only in minor characters and should be assigned to the same genus and included in the subfamily Myrmeciinae. Below, redescrptions of these species are provided and their taxonomic status is considered in detail.

The nomenclature of the forewing venation adopted in this paper is after Rasnitsyn (1980); the cells and veins are shown in Fig. 1a. The measurements are referred to as follows: (AL) alitrunk (mesosoma) length from the junction with the head to that with the petiole; (AH) alitrunk height; (AW) maximum alitrunk width; (HL) length of the head, excluding the mandibles; (MdL) mandible length; (HW) maximum head width; (F2) middle femur length; (F3) hind femur length; (PtL) petiole length, (PtH) petiole height; (PtW) maximum petiole width; (PptL) postpetiole length; (PptH) postpetiole height; and (PptW) maximum postpetiole width.

SYSTEMATIC PALEONTOLOGY

Subfamily Myrmeciinae Emery, 1877

Genus *Archimyrmex* Cockerell, 1923

Archimyrmex: Cockerell, 1923, p. 52.

Ameghinoia: Viana et Haedo Rossi, 1957, p. 109 (syn. nov.).

Polanskiella: Rossi de Garcia, 1983, p. 19 (syn. nov.).

Type species. *A. rostratus* Cockerell, 1923, by monotypy.

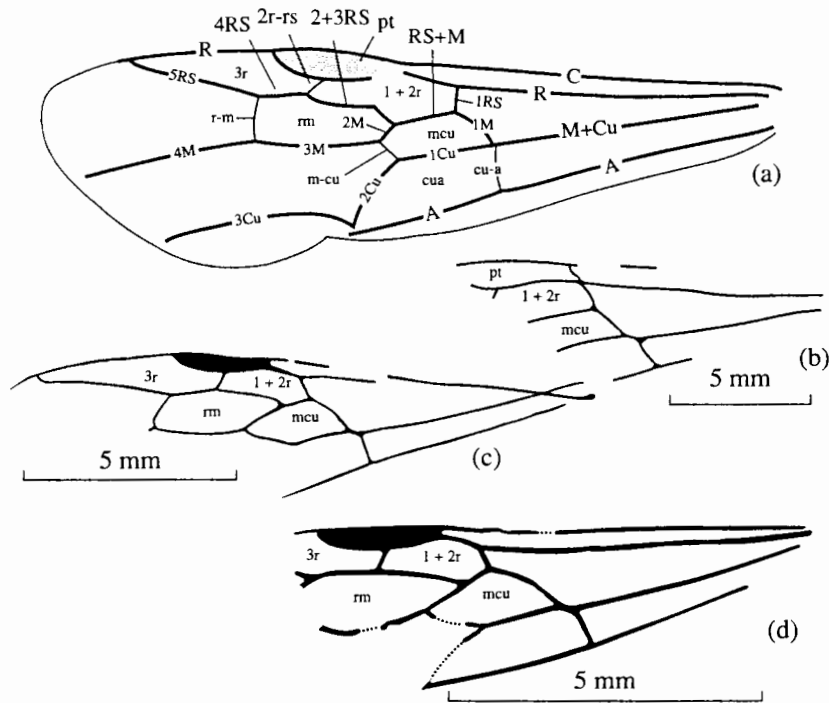


Fig. 1. Forewing venation of *Myrmecia* and venation of preserved fragments of *Archimyrme*x wings: (a) forewing of male *Myrmecia* sp.; (b) fragment of *A. rostratus* forewing, specimen USNM, no. 495989; (c) forewing of *A. smekali*, lectotype NMW, no. 1972/1574/9; and (d) reconstruction of wing of *A. piatnitzkyi*, based on the original drawing and photographs (Viana and Haedo Rossi, 1957). Longitudinal veins are designated by uppercase letters; transverse veins, by lowercase hyphenated letters; and cells, by lowercase italics.

Diagnosis. Female. Large and slender ants with elongate alitrunk and long appendages. Head rounded or short oval, without distinct occipital corners. Mandibles long and linear, masticatory margin with rare coarse obtuse teeth and small denticles between them. Eyes large, oval, somewhat displaced forward. Antennae geniculate, most probably 12-segmented. Scape extends beyond occipital margin of head; funiculus thin, filiform, without distinct clava. Alitrunk elongate. Scutum small and weakly convex, length greater than width, propodeum unconcealed. Propodeum evenly rounded or slightly angled in side view, without spines or teeth. Hind tibia with two spurs; larger spur pectinate, smaller spur simple. Waist two-segmented. Petiole elongate, without node or with poorly pronounced low node, with upper face rounded in side view. Postpetiole bell-shaped and broadly attached to gaster, constriction between postpetiole and gaster poorly expressed. Pygidium evenly convex, without flat plate and denticles. Specialized pygidium with denticles absent. Sting present.

Forewing with closed cells *1 + 2r*, *3r*, *rm*, and *mcu*. Vein *2r-rs* extending from middle of pterostigma at acute angle. Section *1RS* runs into *R* at acute angle near proximal margin of pterostigma. Section *2 + 3RS* evenly curved. Cell *rm* pentagonal and large, its distal corner leveled with at least first basal third of pterostigma. Crossvein *m-cu* parallel to *1M*,

oblique towards wing base in its lower part. Cell *cua* present. Vein *2Cu* smooth, *cua* height subequal to *mcu* height. Vein *cu-a* runs into *M + Cu* near cell *mcu* proximal to section *1M* at distance that two to three times longer than vein thickness.

Species composition. *A. rostratus*, *A. smekali*, and *A. piatnitzkyi*.

Comparison. From other known fossil genera of ants with a two-segmented waist, except for *Prionomyrmex* from Baltic amber, it differs in the broad bell-shaped postpetiole, broadly attached to the gaster. From *Prionomyrmex*, it differs in the shape of the head and petiole.

Remarks. The spurs of the hind tibiae are clearly visible in the lectotype *A. smekali* and in the photograph of *A. piatnitzkyi* paratype no. 3. Regrettably, neither the antennal funiculus nor the hind tibial spurs are preserved in any of the *A. rostratus* imprints. However, on the basis of the general similarity of it with the two other species, we surmise that they were similar in these characters as well.

*Archimyrme*x *rostratus* Cockerell, 1923

*Archimyrme*x *rostratus*: Cockerell, 1923, p. 52, figs. a and b; Wheeler, 1928, p. 117; Carpenter, 1930, pp. 16–17, pl. 2, fig. 5; Bolton, 1995, p. 75.

Holotype. University of Colorado, no. 15174, lateral imprint of worker (counterpart USNM, no. 69617);

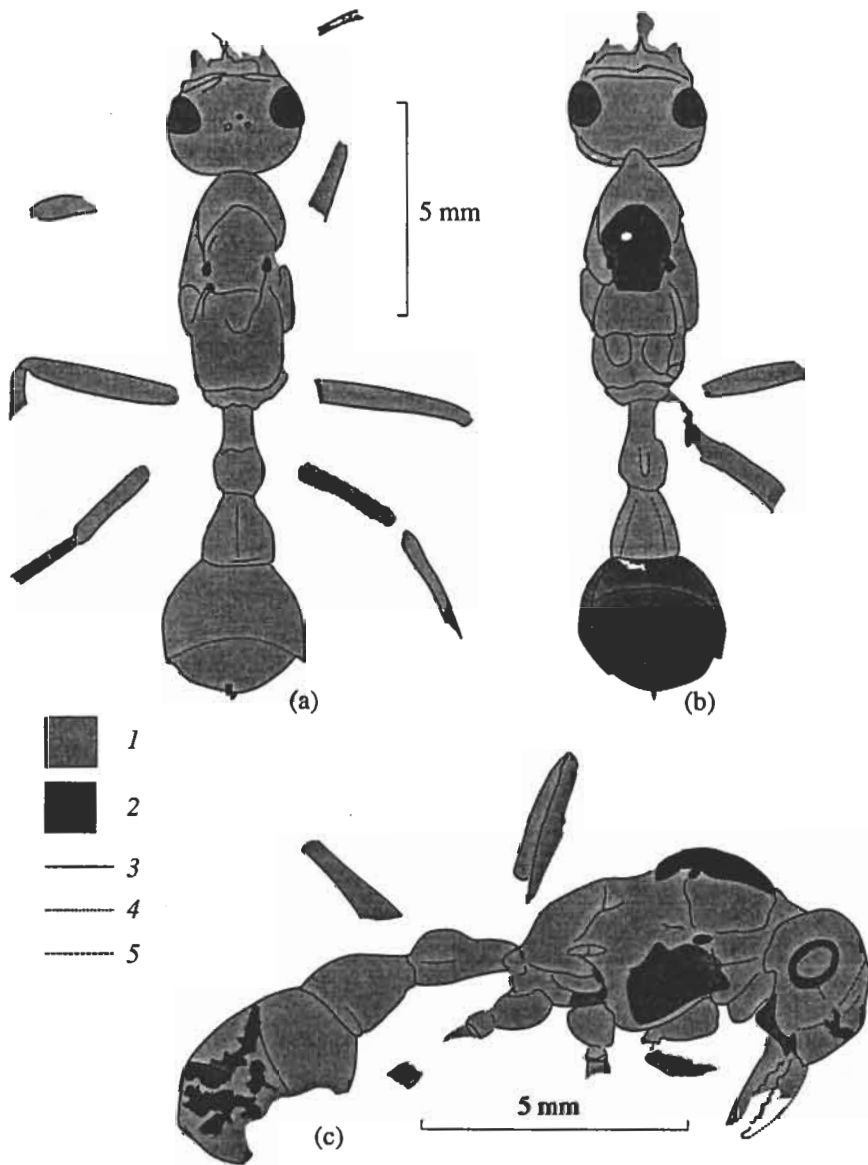


Fig. 2. *Archimymex rostratus* Cockerell: (a, b) imprint and counterpart of specimen USNM, no. 496002; (c) imprint of specimen USNM, no. 496004. Designations: (1) areas differing in color from the host rock, (2) coalified chitin remains, (3) visible boundaries of sclerites, (4) presumable boundaries of sclerites, and (5) folds and ridges.

United States, Colorado, Roan Mountain Ute Trail; Middle Eocene (Lutetian), Green River Formation.

Description (Figs. 1b, 2). Female. The body is 13.2–15.8 mm long. The head is rounded, 1.2–1.3 times broader than it is long. The mandibles are somewhat shorter than the head, with several large coarse teeth and smaller denticles between them. Judging from the preserved fragment of an antenna in imprint no. 496002a, the scape is most likely long and thin. The alitrunk is narrow and long, more than two times greater in length than in width or height. The scutum is clearly longer than it is wide. The legs are long and thin. The posterior coxae are slightly disposed and not touching. The propodeum is slightly and evenly convex in side view. The petiole has a weakly pronounced node in its rear portion

and is 2–2.2 times greater in length than in width or height. The length of the postpetiole is approximately equal to its width and height. The gaster is compact and short elliptical. The sting is short and thick.

In the forewing, the 1RS section runs into R immediately near the proximal margin of the pterostigma; it is 1.6 times shorter than the 1M section. The 1RS and 1M sections form an angle of about 180°. The 1M section is not curved. The RS + M section is apparently longer than the 2M section.

Measurements, mm: holotype (after Cockerell, 1923): (AL) 5.3, (HL + MdL) 4.0, (F2) 3.7; specimen USNM, no. 495 602: (AL) 5.5, (AH) 2.3, (F2) 3.6, (F3) 4.1, (PtL) 1.7, (PtH) 0.9, (PptL) 1.6, (PptH) 1.4;

specimen USNM, no. 495894: (AL) 5.8, (AW) 2.1, (HW) 2.5, (PtL) 2.0, (PtW) 0.9, (PptL) 1.6, (PptW) 1.3; specimen USNM, no. 495985: (AL) 4.4, (AW) 1.9, (HL) 1.95, (HW) 2.3; specimen USNM, no. 495986: (AL) 5.3, (AW) 2.5, (HL) 2.2, (HW) 2.8, (PtL) 2.0, (PtW) 1.0, (PptL) 1.5, (PptW) 1.5; specimen USNM, no. 495989: (AL) 5.5, (AW) 2.3, (HW) 2.7, (PtL) 1.8; specimen USNM, no. 496001: (PtL) 2.0, (PtW) 1.0, (PptL) 1.4, (PptW) 1.5; specimen USNM, no. 496002: (AL) 5.3, (AW) 2.4, (HL) 2.3, (HW) 3.1, (PtL) 2.2, (PtW) 1.1, (PptL) 1.5, (PptW) 1.6; specimen USNM, no. 496003: (AL) 4.2, (PtL) 1.5, (PptL) 1.1; specimen USNM, no. 496004: (AL) 5.4, (PtL) 2.2, (PtH) 1.1, (PptL) 1.7; and specimen USNM, no. 496004: (AL) 4.4, (AW) 2.0, (HW) 2.2, (PtL) 1.7.

Remarks. All specimens with a preserved head or gaster tip are undoubtedly females. They are very similar to the description and the photograph of the *A. rostratus* holotype in their size and proportions and in the form of the petiole and postpetiole. On this basis, we assume that the holotype is also a female, rather than a worker as was proposed by both Cockerell and Carpenter. The only essential difference is that, according to Cockerell, the holotype has an elevation, on the propodeum which was interpreted as the base of one of the paired propodeal spines, whereas in all specimens studied by us the propodeum is evenly convex and not armed with spines or teeth. Carpenter (1930), who examined the holotype, concluded that only a part of the propodeum was visible and that the adjoining parts of the dorsal side of the propodeum were covered by the host rock. However, he did not attempt to prepare the holotype being afraid of damaging it. Relying on Carpenter's expertise in ant imprints, we dare not describe a new species, but assign the examined specimens to *A. rostratus*, which is supported by their record in the same deposits of the Green River Formation.

As a rule, only the body is preserved in imprints from the Green River Formation, whereas the antennae, legs, and wings are completely or partially missing. Apparently, the water in the bodies water where the insects were buried was alkaline; this resulted in partial dissolution of the chitin. Specimens nos. 495602, 496004, and 2-98 are lateral imprints, while the others are all dorsal imprints of females. In all specimens except for nos. 495986 and 496002, the head was strongly downturned upon burial (the normal situation for ants with long mandibles); thus, it is visible from behind in dorsal imprints. Specimen no. 495602 has completely preserved middle and hind femurs and tibiae; specimens nos. 495986 and 496004 retained fragmentary mandibles; and specimen no. 495989, a fragmentary forewing.

Material. Specimens USNM, nos. 495602, 495894, 495985, 495986, 495989, and 496001–496005 from Anvil Points, site no. 40193, Colorado, United State; specimen PIN, no. 4621/634 from the same locality; Middle Eocene (Lutetian), Green River Formation.

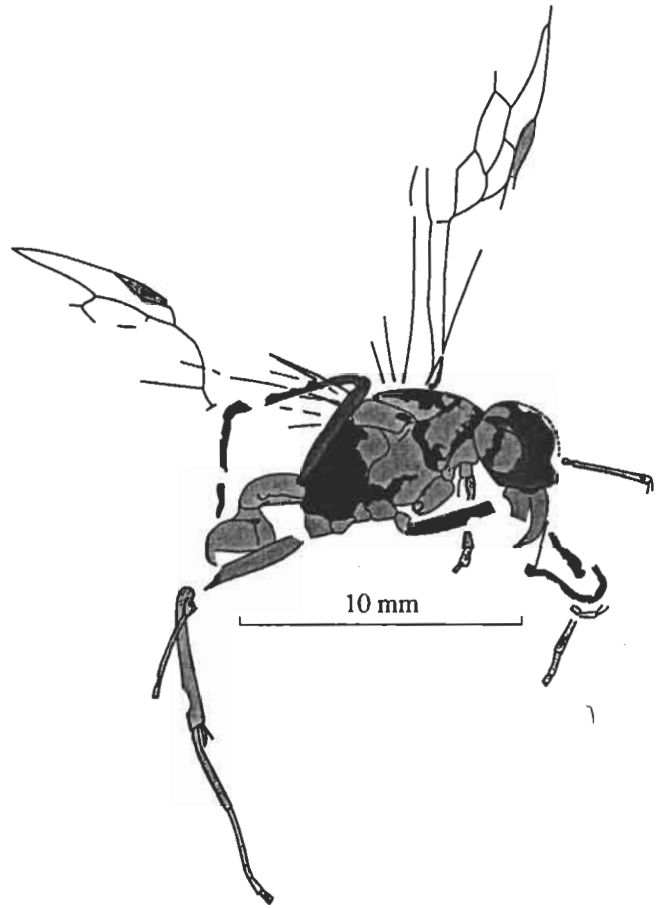


Fig. 3. *Archimyrmex smekali* (Rossi de Garcia), lectotype NMW, no. 1972/1574/9. For designations, see Fig. 2.

Archimyrmex smekali (Rossi de Garcia, 1983) comb. nov.

Polanskiella smekali: Rossi de Garcia, 1983, pp. 19–20, figs. 1–3 and 5 (syn. nov.).

Ameghinoia smekali: Dlussky and Fedoseeva, 1988, p. 133 (syn. nov.).

Lectotype (designated here to maintain the stability of nomenclature). NMW, no. 1972/1574/9, specimen labeled "Patagonien, Argentinien am Rio Limay, 71° Wv. Greenwich, zwischen 40° und 41° sudl. Breite. Leg. H. Smekal"; Late Paleocene–Early Oligocene, Ventana Formation.

Description (Figs. 1c, 3). Female. The body length is ca. 3 cm. The head is rounded. The mandibles bear four to five large teeth,¹ which are long and similar to the head in length. The scape is long and thin and extends beyond the occipital margin of the head. The flagellomeres are more than two times as long as they are broad. The alitrunk is relatively massive, 1.7–1.9 times as long as it is high. The legs are long and thin. The propodeum is weakly and evenly convex in side view. The petiole lacks a node and looks like an arched cylinder; in side view, its dorsal surface is weakly convex and its

¹ The teeth are not visible in the lectotype, but are preserved in other imprints, judging from the original description.

ventral surface is weakly concave; in the lectotype, it is 2.2 times as long as it is high. The postpetiole has an abruptly narrowed anterior portion, and its length is approximately equal to its height and width. The gaster is oval.

In the forewing, section 1RS runs into R proximad of the posterior margin of the pterostigma at a distance approximately equal to the length 1RS. 1RS is half as long as 1M. Section 1M is curved proximally and forms an angle of less than 180° with 1RS. Section 2M is noticeably longer than RS + M. Cell *rm* is greater in area than either of the cells *mcu* or $1 + 2r$.

Measurements, mm: (AL) 6.7, (HL) 2.9, (MdL) 2.2, (F3) 4.5, (PtL) 2.2.

Comparison. Differs from other species by its large size, by the absence of the node of the petiole, and by the abrupt constriction in the anterior part of the postpetiole.

Remarks. In the original description, it was erroneously indicated that this species possesses 8-segmented antennae. In the lectotype, the preserved fragment of the funiculus clearly consists of seven segments. Comparing this fragment with the length of the complete funiculus of the specimen figured in photo 2, one may postulate that the number of antennomeres do not differ from that in the majority of ants, 12 in the female and in the worker. The reconstruction of the forewing venation made in the original publication has nothing in common with the real situation, and, therefore, its comparison with the wing venation of other ants performed by Rossi de Garcia may be rejected.

Material. Lectotype.

This species was described based on ten specimens stored at the Asociacion Paleontologica Bariloche, San Carlos de Bariloche, Rio Negro, Argentina. Since the author did not indicate the collection numbers of the specimens and did not fix the holotype, to clarify the application of the species epithet, we propose to designate the specimen from the Natural History Museum in Vienna, which is a counterpart of the specimen figured in photo 3 of the original description, as the lectotype.

Archimyrmex piatnitzkyi (Viana et Rossi, 1957) comb. nov.

Ameghinoia piatnitzkyi: Viana et Haedo Rossi, 1957, pp. 109–113, figs. 1–3, photos 1–3; Dlussky and Fedoseeva, 1988, p. 133; Bolton, 1995, p. 63.

Holotype. Paleontological collection of the Entomology Division, Bernardino Rivadaria Museum of Natural History, Argentina, no. 1, lateral imprint of female figured in photo 1 of original description; Rio Pichileufu, San Carlos de Bariloche, Argentina; Late Paleocene–Early Oligocene, Ventana Formation.

Description (Figs. 1d, 4e–4g). Female. The length of the body is 16–18 mm. The head is oval, and the length of the head capsule is slightly greater than its width. The mandibles are elongated, but noticeably shorter than the head. The alitrunk is relatively massive,

and its length is 1.7–1.8 times greater than its height. The legs are long and narrow. The propodeum is weakly and evenly convex in side view. The petiole has a small but distinct node and a distinct cylindrical anterior portion; it is 1.7 times longer than the maximum height and 1.5 times as long as it is broad. The anterior portion of the postpetiole lacks constriction, the length and width of the postpetiole are approximately equal, and its height is noticeably greater than its length. The abdomen is oval.

In the forewing, section 1RS runs into R proximad of the pterostigma at a distance roughly equal to its length. Section 1M is 2.6–2.9 times as long as 1RS. Section 1M is proximally curved and forms an angle of less than 180° with 1RS. Section 2M is a little longer than RS + M. Cell *rm* is greater in area than either of the cells *mcu* or $1 + 2r$.

Measurements, mm (based on photos): specimen no. 2: (AL) 6.5 and (HL) 3.3; specimen no. 3: (AL) 6.0, (HL) 3.5, (F2) 4.4, and (F3) 5.2.

Comparison. It differs from other species of the genus by the well-pronounced node of the petiole. Additionally, it differs from *A. smekali* by a smaller size and the absence of an abrupt constriction in the anterior portion of the postpetiole.

Material. Holotype, as well as paratypes: specimen nos. 2 and 3, lateral and dorsal imprints of females, from the same locality. All are studied on the basis of photographs.

TAXONOMIC POSITION OF *ARCHIMYRMEX*

The most detailed description of the subfamily Myrmeciinae based on characters of workers of the single recent genus *Myrmecia* is provided by Bolton (1994). Some characters pointed out by him are not visible in *Prionomyrmex* or not mentioned in the descriptions; however, those that are observable well suffice for its inclusion in this subfamily. Workers and females of *Myrmecia* (Figs. 4a, 4b) and *Prionomyrmex* (Figs. 4c, 4d) are characterized by the following set of shared features, which appears to be principal for the assignment of a genus to the subfamily Myrmeciinae (only those features that may be seen in imprints are listed):

(1) The ocelli are present in workers. However, in *Myrmecia*, this character is present in all members, whereas, in *Prionomyrmex*, it is seen only in some specimens.

(2) The antennae are geniculate and 12-segmented, with a long scape and a filiform funiculus, which lacks a distinct clava.

(3) The maxillary palps are long and six-segmented, while the labial palps are four-segmented.

(4) The hind tibiae have two spurs, one of which is simple and the other of which is longer and pectinate.

(5) The claws have an additional tooth.

(6) The promesonotal and mesopropodeal sutures are well-pronounced in the worker.

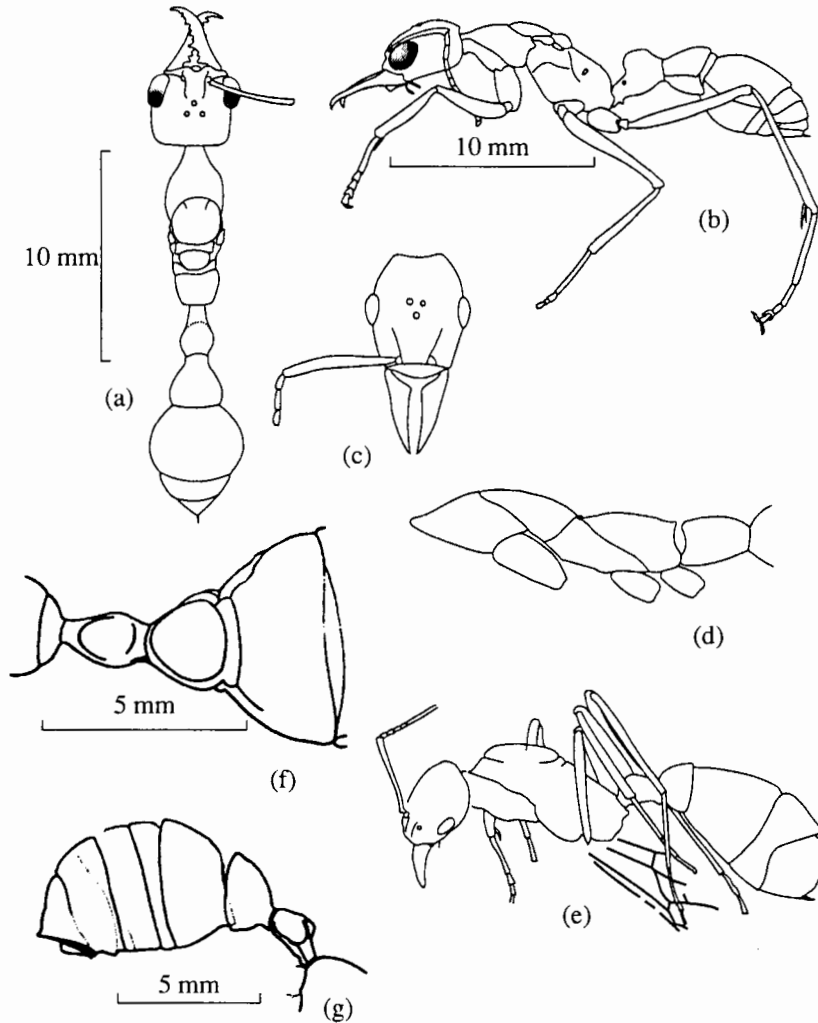


Fig. 4. Extant and extinct Myrmeciinae: (a, b) *Myrmecia pyriformis* F. Smith; (c, d) *Prionomyrmex longiceps* Mayr (after Mayr, 1868): (c) head, from above and (d) alitrunk and petiole, side view; and (e–g) *Archimyrmea piatnitzkyi* (after Viana and Haedo Rossi, 1957): (e) holotype (drawing based on photograph), (f) petiole of specimen no. 3, from above; and (g) petiole and gaster of specimen no. 2, side view.

(7) The petiole is two-segmented, the postpetiole is broadly attached to the gaster.

(8) The pygidium is simple, with neither denticles nor a flattened area.

(9) The sting is well-developed.

To these, some details of forewing venation of the gyne and male *Myrmecia*² may be added (Fig. 1a):

(10) The closed cells 1 + 2r, 3r, rm, and m-cu are present; rm and m-cu are pentagonal.

(11) The vein cu-a runs into M + Cu near the cell m-cu somewhat proximad of the branching of 1M and 1Cu.

(12) The transverse vein m-cu is parallel to 1M and inclined to the wing base in its lower part.

(13) The cell cua is present.

²Wheeler (1915) gave a brief description of the male of *Prionomyrmex*, but did not provide a drawing and only indicated that its wing venation is similar to that of *Myrmecia*.

At the same time, distinct differences between these genera are present.

In *Myrmecia*, the head is quadrangular, rectangular, or trapezoidal; widened anteriorly; and has well-separated occipital corners, whereas, in *Prionomyrmex*, it is elongated and has strongly convex sides and a concave occipital margin, and the eyes are situated at the midlength of the sides of the head, unlike in *Myrmecia*, whose eyes are shifted anteriorly.

In *Myrmecia*, the anterior edge of the clypeus is emarginated so that the labrum is well visible, whereas it is angled anteriorly in *Prionomyrmex*.

In *Myrmecia*, the mandibles are long and linear, with sparse large rough teeth and smaller denticles between them, whereas, in *Prionomyrmex*, although the mandibles are long, they are not linear, but rather triangular, with approximately equal teeth along the entire masticatory margin.

In *Prionomyrmex*, the propodeum has small blunt teeth, whereas in *Myrmecia*, it is rounded or slightly angled in profile and has neither spines nor teeth.

In both *Myrmecia* and *Prionomyrmex*, the petiole has a well-developed node, whose transverse section is quadrangular or rounded in *Myrmecia* and triangular in *Prionomyrmex*.

Characters 1, 3–6, and 8–13 are undoubtedly plesiomorphic, since they are present in the most ancient and primitive Formicoidea of the subfamilies Armaniinae and Sphecomyrminae. Characters 4–6 and 8–13 are also typical of primitive representatives of the subfamily Ponerinae. Characters 2 and 7 are apomorphic with reference to the Armaniinae and Sphecomyrminae and plesiomorphic with reference to other subfamilies with a two-segmented petiole. Long linear mandibles with occasional large teeth have been considered by many authors as a plesiomorphic character, although this is unlikely to be the case. Gynes of the Armaniinae and Sphecomyrminae have relatively short sphecooid mandibles with two teeth. Short triangular mandibles with several teeth, as, for example, in the Leptanillinae, should be considered to be the most primitive ant mandibles (Dlussky and Fedoseeva, 1988). The unusual structure of the clypeus of *Myrmecia*, the presence of teeth on the propodeum of *Prionomyrmex*, and the structure of the head capsule and the presence of a well-developed node of the petiole in both genera are unquestionable apomorphies.

Comparing the above descriptions of the species of *Archimyrmex*, it is clear that they are distinguished by only minor details of the wing venation, body size (*A. smekali* is about 3 cm long, while the other two species are 14–16 mm long), and proportions (slender body in *A. rostratus* and more robust and massive body in *A. smekali* and *A. piatnitzkyi*) and substantially differ in the structure of the petiole. Thus, their assignment to the same genus is beyond doubt.

The more ambiguous task is the assignment of *Archimyrmex* to a certain subfamily, since all representatives of this genus are known as fossil imprints and many characters that are observable in Recent species and amber inclusions are not visible. Even if one assumes that the characters that are not preserved in one species but present in others are shared by all species of the genus, they are insufficient for a confident assignment to any subfamily. In the *A. smekali* imprints, characters 2, 4, and 7–13 are present and the mandibles are similar in structure to those of *Myrmecia*; *A. piatnitzkyi* shows characters 2, 4, 7–9, and 11–13, and *A. rostratus* shows characters 7–9, 11, and 12 and is similar in mandibular structure to *Myrmecia*. The wing apex is not preserved in the latter two species; nevertheless, it is highly probable that closed cells 1 + 2r, 3r, rm, and mcu were present in them, especially as the position of vein cu-a preserved in the imprint in relation to the cell mcu usually correlates with a complete set of cells (Dlussky, 1981). None of the *A. rostratus* imprints retained tibial spurs and antennae; therefore, the presence of two spurs and of geniculate antennae may be only hypothesized,

based on the similarity of the rest of the characters of the three species and a preserved fragment of an antenna in one imprint. Even assuming this, the absence of information about the structure of the palps and claws and about the presence of the ocelli in workers does not allow straightforward postulation that *Archimyrmex* should be assigned to the subfamily Myrmeciinae.

There is, however, indirect evidence for the assignment of this genus to the subfamily Myrmeciinae. The two-segmented petiole is present in members of the subfamilies Myrmeciinae, Pseudomyrmecinae, Ecitoninae (*Cheliomyrmex* Mayr), Aenictinae, Leptanillinae, and Myrmicinae. Additionally, in some Cerapachyinae, the constriction between the third and fourth abdominal segments is so deep that the third segment looks like the postpetiole.

We should reject at once the assignment of *Archimyrmex* to the Ecitoninae, Aenictinae, and Leptanillinae, since the gynes of these subfamilies are primarily wingless. Similarly, this genus cannot be assigned to the Pseudomyrmecinae, since these ants have an entirely different habitus associated with habitation in narrow mines in wood, i.e., a long narrow body with short thick legs and antennae and short, massive, triangular mandibles. The presence of a specialized pygidium with a flat area, which is often surrounded by teeth, is characteristic of the Cerapachyinae, whereas in *Archimyrmex*, the pygidium is evenly convex. In addition, Cerapachyinae having a similar habitus and elongated mandibles are not known.

Some Myrmicinae have a similar habitus, so there were grounds for the inclusion of *Archimyrmex* (Wheeler, 1928) and *Ameghinoia* (Dlussky and Fedoseeva, 1988) in the Myrmicinae. However, the venation of the forewing of these ants differs greatly. First, in all Myrmicinae, the cu-a vein runs into M + Cu approximately at the midlength between the wing base and the point of deviation of 1M from 1Cu, which is much closer to the base of the wing than in the Myrmeciinae and other primitive subfamilies (Dlussky, 1981). Second, some cells are reduced in many Myrmicinae. Finally, in those genera with a full set of cells (such as *Anisopheidole* Forel, *Aphaenogaster* Mayr, *Messor* Forel, *Pheidole* Westwood, *Pogonomyrmex* Mayr, etc.), the 2M section is reduced and the rm cell is triangular or petiolate, the transverse m-cu vein does not have plesiomorphic declination as in primitive ants, the 5RS vein is often not fused with R, and the 3r cell is open at its apex. Thus, *Archimyrmex* cannot be assigned to this subfamily either; therefore, the only solution is to include it in the subfamily Myrmeciinae.

The structure of the head and petiole of *Myrmecia* and *Prionomyrmex* are highly specialized in different ways, and thus the former genus cannot be ancestral to the latter or vice versa. At the same time, the shape of the head capsule and the petiole of *Archimyrmex* are clearly plesiomorphic with regard to both these genera. In this genus, the head capsule has a strongly rounded occipital margin without distinct occipital corners, as in

the Armaniinae and Sphecomyrminae; the eyes are shifted anteriorly but the displacement is weaker than in *Myrmecia*.

The petiole of *A. smekali* lacks a node, *A. rostratus* has a poorly expressed thickening in the posterior portion of the petiole, and *A. piatitzkyi* has a small but distinct node. Earlier, Dlussky and Fedoseeva (1988) showed that the development of the node correlates with the elongation of muscles responsible for downward movement of the gaster or, in other words, with intensification of downward movement of the gaster along with sclerotization and a decrease in mobility of gastral segments relative to each other. Thus, in the case of *Archimyrme*, we most probably are observing consequent stages of this process. Archaic characters are visible in the forewing venation (Figs. 1c, 1d). In particular, the mcu cell is large, as in the Armaniinae and Sphecomyrminae, and its distal part is situated at least one-third of the way from the base of the pterostigma, whereas in *Myrmecia* (Fig. 1a), the distal margin of the mcu cell approaches only to the base of the pterostigma. At the same time, in *Archimyrme*, section 2 + 3RS is smoothly curved and any trace of separation of cells 1r and 2r is absent, whereas in *Myrmecia*, this character demonstrates a more primitive state. In species of this genus, 2 + 3RS is angled, and in some individuals a stub of the transverse vein isolating cells 1r and 2r diverges from this angle.

Thus, *Archimyrme* differs from *Myrmecia* and *Prionomyrmex* in a set of plesiomorphic characters and may be considered as an ancestor of *Myrmecia*. At the same time, it is uncertain whether the mandibles of *Myrmecia* are plesiomorphic in relation to those of *Prionomyrmex* or developed independently from triangular mandibles with few teeth. Therefore, we cannot take *Archimyrme* as an ancestor of *Prionomyrmex*.

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REFERENCES

- Baroni Urbani, C., Rediscovery of the Baltic Amber Ant Genus *Prionomyrmex* (Hymenoptera, Formicidae) and Its Taxonomic Consequences, *Ecl. Geol. Helv.*, 2000, vol. 93, pp. 471–480.
- Bolton, B., *Identification Guide to the Ant Genera of the World*, Cambridge: Harvard Univ. Press, 1994.
- Bolton, B., *A New General Catalogue of the Ants of the World*, Cambridge: Harvard Univ. Press, 1995.
- Brandão, C.R., Martins-Neto, R., and Vulcano, V.A., The Earliest Known Fossil Ant (First Southern Hemisphere Mesozoic Record) (Hymenoptera: Formicidae: Myrmeciinae), *Psyche*, 1989, vol. 96, nos. 3–4, pp. 195–208.
- Carpenter, F.M., The Fossil Ants of North America, *Bull. Mus. Compar. Zool. Harvard*, 1930, vol. 70, pp. 1–66.
- Cockerell, T.D.A., The Earliest Known Ponerinae Ant, *Entomologist*, 1923, vol. 56, no. 718, pp. 51–52.
- Dlussky, G.M., Miocene Ants (Hymenoptera: Formicidae) of the USSR, in *Novye iskopaemye nasekomye s territorii SSSR* (New Fossil Insects from the USSR), Moscow: Nauka, 1981, pp. 64–83.
- Dlussky, G.M., Cretaceous Formicoids and the Time of the Formation of Ants, *X Vserossiiskii Simpozium "Murav'i i zashchita lesa"* (X All-Russia Conf. on Ants and Forest Protection), Moscow, 1998, pp. 5–8.
- Dlussky, G.M., The First Finding of a Formicoid (Hymenoptera: Formicoidea) in the Lower Cretaceous Deposits of the Northern Hemisphere, *Paleontol. Zh.*, 1999, no. 3, pp. 62–66.
- Dlussky, G.M. and Fedoseeva, E.B., The Origin and Early Stages of Ant (Hymenoptera, Formicidae) Evolution, in *Melovoi biotensnoticheskii krizis i evolyutsiya nasekomykh* (Cretaceous Biocenotic Crisis and Insect Evolution), Moscow: Nauka, 1988, pp. 70–144.
- Grimaldi, D., Agosti, D., and Carpenter, J.M., New and Rediscovered Primitive Ants (Hymenoptera, Formicidae) in Cretaceous Amber from New Jersey, and Their Phylogenetic Relations, *Am. Mus. Novit.*, 1997, no. 3208, pp. 1–43.
- Mayr, G.L., Die Ameisen des Baltischen Bernstein, *Beitr. Naturk. Preuss., Heraus Gegeben V. D. Phys.-Ökon Ges., Königsberg*, 1868, vol. 1, pp. 1–102.
- Naumann, I.D., Hymenoptera, in *The Insects of Australia*, Carlton: Melbourne Univ. Press, 1991, vol. 1, pp. 916–1000.
- Ogata, K. and Taylor, R.W., Ants of the Genus *Myrmecia* Fabricius: A Preliminary Review and Key to the Named Species (Hymenoptera: Formicidae: Myrmeciinae), *J. Nat. Hist.*, 1991, vol. 25, pp. 1623–1673.
- Petrulevicius, J.F., Insectos del Cenozoico de la Argentina, *Rev. Soc. Entomol. Argentina*, 1999, vol. 85, nos. 1–2, pp. 95–103.
- Rasnitsyn, A.P., The Origin and Evolution of Hymenopterous Insects, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1989, vol. 174, pp. 1–192.
- Rasnitsyn, A.P., Table 1. Known Cretaceous Hymenoptera, in Insects from the Santana Formation, Lower Cretaceous, of Brasil, *Bull. Am. Mus. Nat. Hist.*, 1990, no. 195, pp. 124–129.
- Rossi de Garcia, E., Insectos fosiles en la formation Ventano (Eoceno) provincia de Neuquen, *Rev. Ass. Geol. Argentina*, 1983, vol. 38, no. 1, pp. 17–23.
- Taylor, R.W., *Nothomyrmecia macrops*: A Living-Fossil Ant Rediscovered, *Science*, 1978, vol. 201, pp. 979–985.
- Viana, M.J. and Haedo Rossi, J.A., Primer hallazgo en el Hemisferio Sur de Formicidae extinguidos y catalogo mundial de los Formicidae fosiles, *Ameghiniana*, 1957, vol. 1, nos. 1–2, pp. 108–113.
- Wheeler, W.M., The Ants of the Baltic Amber, *Schrift. Phys.-Ökon. Ges., Königsberg*, 1915, vol. 55, pp. 1–142.
- Wheeler, W.M., *The Social Insects: Their Origin and Evolution*, New York: Harcourt, Brace, and Co, 1928.
- Wilson, E.O., *The Insect Societies*, Cambridge: Harvard Univ. Press, 1971.