

The first fossil record of *Polyrhachis* (Hymenoptera: Formicidae: Formicinae) from the Upper Miocene of Crete (Greece)

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Abstract *Polyrhachis annosus* n. sp., based on part and counterpart of a unique ant worker specimen from Late Miocene deposits of the island of Crete (Greece), is figured and described here. Features of *P. annosus* unique for the large recent genus *Polyrhachis* include a large first gastral segment, a scapus attached at some distance from the clypeus, and an alitrunk (mesosoma) and petiole each with a pair of teeth or spines. The new taxon represents the first occurrence of the genus in the fossil record. The origin and rise of one of the world's largest and most distinct ant genera are still a puzzle, and closely related genera are quite diverse in Tertiary amber deposits. Interestingly, the abundance of *Polyrhachis* in Indonesian copal confirms the statement that their absence in Baltic amber is not casual.

Keywords Hymenoptera · Formicinae · *Polyrhachis* ·
New species · Miocene · Fossil ant

Kurzfassung Aus dem Obermiozän von Kreta (Griechenland) wird erstmals ein Exemplar der Ameisen-Gattung *Polyrhachis* beschrieben und abgebildet. Obwohl

nicht vollständig überliefert, sprechen vor allem die Erhaltung von Stacheln am Mesosoma und Petiolus sowie das deutlich vergrößerte erste Gastral-Segment für eine Zugehörigkeit zur Gattung *Polyrhachis*. *Polyrhachis annosus* n. sp. stellt den fossilen Erstnachweis der Gattung dar. Rezent ist *Polyrhachis* eine der größten und auffälligsten Ameisengattungen weltweit und nahe verwandte Taxa sind in tertiären Bernsteinvorkommen bereits relativ divers und gut dokumentiert. Darum gibt der mangelnde Fossilbericht von *Polyrhachis* Rätsel auf. Interessanterweise bestätigt die Überlieferung von *Polyrhachis*-Arten im holozänen Kopal von Sulawesi (Indonesien), dass ihre Abwesenheit im Baltischen Bernstein nicht zufällig ist. Um den Ursprung von *Polyrhachis* zu klären sind allerdings weitere Fossilfunde notwendig.

Schlüsselwörter Hymenoptera · Formicinae ·
Polyrhachis · Neue Art · Miozän · Fossile Ameise

Introduction

Ants are one of the most studied insects in the world, and they are the most successful and widespread eukaryotic organisms on Earth. They have a crucial role in many ecosystems through their interactions with other arthropods, plants, or fungi (Hölldobler and Wilson 1990; Jolivet 1996). Their fossil record is extensive, and the main subfamilies are well known since Cretaceous times. The oldest known definitive ants are currently reported from contemporaneous Albian–Cenomanian ambers of France and Myanmar and are either considered as incertae sedis within the formicid subfamilies or belong to the extinct Sphecomyrminae (Dlussky 1996; Nel et al. 2004; Engel and Grimaldi 2005; Perrichot et al. 2008a, b).

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So it is surprising that representatives of the genus *Polyrhachis*, one of the world's largest and most distinct genera of ants, are completely unknown from the fossil record.

In this paper we describe the first fossil *Polyrhachis* species belonging to the ant subfamily Formicinae from late Miocene deposits of the island of Crete (Greece). *Polyrhachis* are characteristic ants because of their spines or ridges on the mesosoma and spines on the top of the petiole, and the first upper plate of the gaster being elongated and comprising more than one-half of the total length of the gaster. The new fossil is moderately preserved but yields characters that can be used to place it in one of the taxonomically and ecologically most diverse ant genera, with over 500 described species organised into 12 subgenera (Robson and Kohout 2005). *Polyrhachis* occurs mostly in the tropics and subtropics of the Old World. These ants are closely related to the cosmopolitan genus *Camponotus*, but are often ornamented with paired spines on the alitrunk and petiole. *Polyrhachis* is found in many different habitat types and shows a wide variety of nesting behaviours. Species in the subgenus *Cyrtomyrma* are weaver ants, nesting in folded leaves held together with larval silk. Others nest in the soil, in rotting wood, or arboreally. One species even inhabits intertidal mud flats and can swim (Nielsen 1997).

The record of fossil insects from Greece is very sparse, and there have been only few records of Miocene insects. Unger (1867) provided a brief description of a Neogene fossil flora from the island Euboea and recorded some insects, including mostly beetle elytra, but also a purported '*Bombus*' forewing. Later, Bachmayer et al. (1971) reported on additional Neogene fossil insects from Euboea. However, there are undoubtedly additional specimens collected during geological campaigns in Greece, but none of the insects have been seriously treated in detail by entomologists (*vide* Bürgin 1994).

Geological setting and sedimentary environment

During the Neogene the palaeogeography of the circum-Mediterranean region was strongly influenced by the collision of the Afro–Arabian and Eurasian plates. As consequences of plate movements, the Alpidic mountain chains were upfolded, the marine connections to the Indo-Pacific and Paratethys were interrupted, and the marine passage to the Atlantic Ocean became continuously restricted. Hence, in the Late Miocene nearly the present-day configuration of the Mediterranean had formed (Rögl and Steininger 1984). An important driver for the changes in landscapes and environments in the eastern Mediterranean during the Neogene was the rollback of the Hellenic Subduction Zone

since the late Oligocene. Until this time Crete was part of the Aegean Landmass and connected with the European continent (Rögl and Steininger 1984). Then the rollback of the Hellenic Subduction Zone caused rapid extension and drowning of the Aegean Landmass, and, related to this process, Crete split off and complex half graben systems subsided all over the island (ten Veen and Postma 1999; Fassoulas 2001).

The studied outcrop is located in the northern Messara Basin, 0.6 km southwest of the village of Apomarma in central Crete (Fig. 1). Together with the northerly adjacent Iraklion Basin, it forms the largest Neogene basin of the island (45 km in N–S extension, 30–50 km in E–W extension). To the west, it is framed by the Ida Mountains that formed a larger landmass (Central Cretan Landmass) during the Late Miocene (Reuter et al. 2006); towards the south and east it borders on the Asteroussia and Dicti mountains. The topography of this basin was shaped by a mosaic of tilted blocks that controlled patterns of facies distribution and subsidence. Some of these blocks were partly elevated above the sea level and formed islands in the basin (Reuter et al. 2006; Reuter and Brachert 2007).

The sedimentary succession of the Messara Basin starts with non-marine and marginally marine siliciclastics of Serravallian to early Tortonian age. During the Tortonian the basin became continuously inundated by the sea, and siliciclastic deposits of the Ambelousos Formation formed in open marine environments (Meulenkamp et al. 1979; Ten Veen and Postma 1999; Reuter and Brachert 2007). Subsequently, the basin drowned rapidly during a pulse of relative basin subsidence and hinterland uplift around the Tortonian–Messinian transition. Hence, shallow water environments along the basin margins became restricted to narrow rims, but offshore isolated carbonate platforms developed on higher situated areas of drowned tilt blocks (Reuter et al. 2006). Sedimentary successions that were deposited between these carbonate platforms in deeper regions of the basin are characterised by rhythmic alternations of decimetric packages of homogeneous and laminated mudstones of the late Tortonian to Messinian Varvara Formation. Towards the top, the sediments of the Varvara Formation become increasingly calcareous and intercalated within calcareous mudstones is a package of laminated gypsum Messinian in age (Meulenkamp et al. 1979).

The studied outcrop exposes a 5-m-thick succession of laminated and homogeneous calcareous mudstones of the Varvara Formation (Fig. 2). The high carbonate content in the sediments and their stratigraphic and spatial vicinity to gypsum deposits (Fig. 2) indicate an early Messinian age. A slumped horizon as well as two intercalated beds of laminated intraclast grainstone (calciturbidites), the lower with imported fragments of shallow water biota (faviid

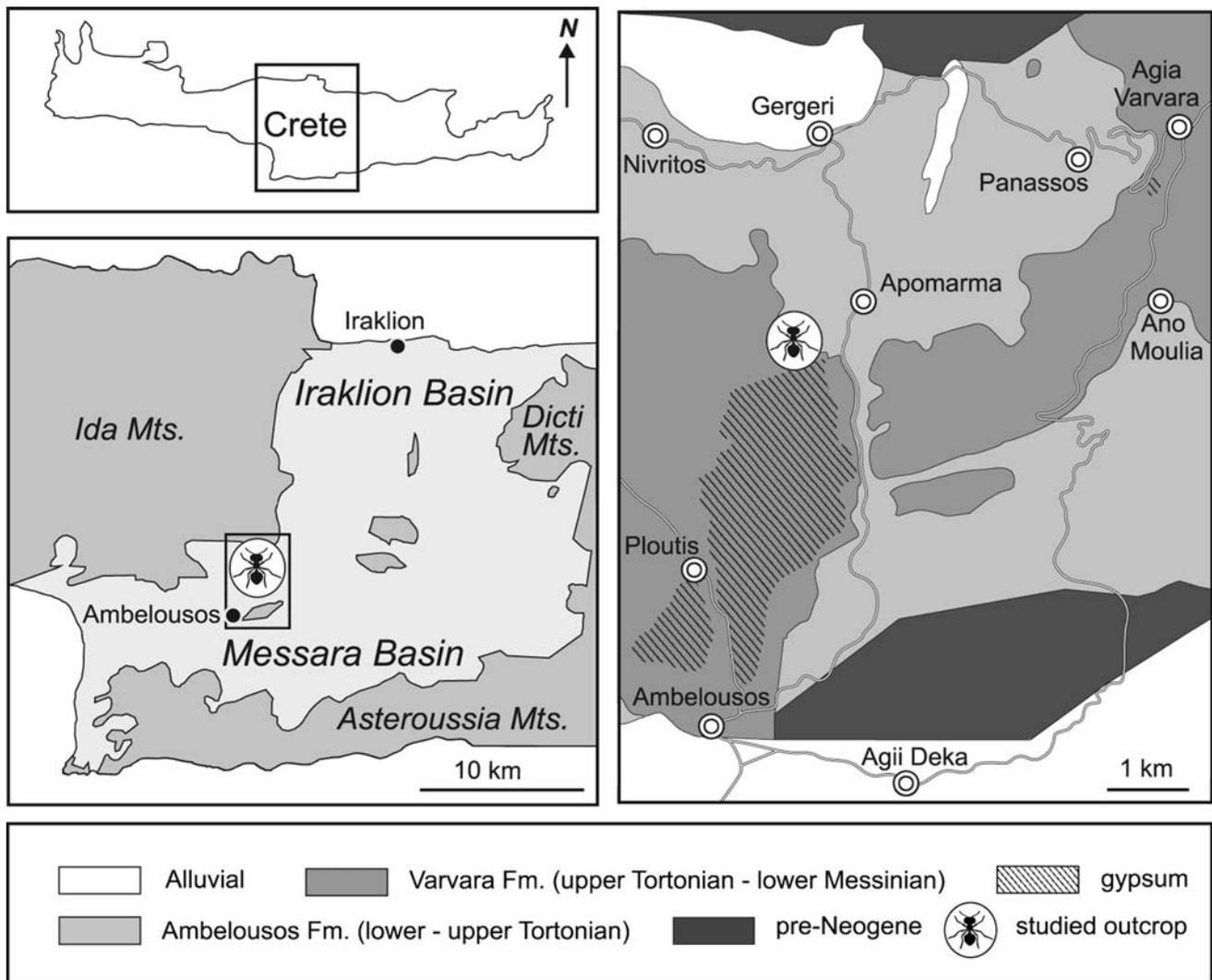


Fig. 1 Geological map of the northwest Messara Basin in central Crete (modified from Meulenkaamp et al. 1979) with location of the studied outcrop (N 35°06'37", E 24°56'47")

corals), point to a deeper position on an unstable slope. The ant fossil described in this study was discovered within a package of laminated calcareous mudstone in the upper part of the section (Fig. 2). Associated with the insect are leaves, seeds, and blossoms of terrestrial plants, partly articulated fish remains, siliceous sponge spicules, and small planktic foraminifers. Such laminated sediments document episodes when water exchange was interrupted in deeper parts of the basin and anoxic bottom water had formed in response to salinity stratification of the water column during periods of wet climate at times of precession minima (Ten Veen and Postma 1996). This milieu was hostile for benthic organisms that fed on organic waste and burrowed through the sediment, but promoted the spread of microbial communities. The latter are documented by two stromatolith horizons interbedded with laminated calcareous mudstones from the lower part of the logged section

(Fig. 2). In contrast, the homogeneous sediments that are sandwiched between the laminated units refer to a better aerated bottom water by the occurrence of *Aphorrais* gastropods and bioturbation textures.

Materials and methods

Ant impression fossils are significantly deformed. Consequently, the calculated measurements and their ratios are more variable than would be expected in three-dimensionally preserved ants. This obscures real differences of taxa, and yet their discrimination is found possible in many cases. Worth mentioning are some measurements that are found to be less affected by deformation than the others, e.g., the length of the alitrunk in comparison to its width and height.

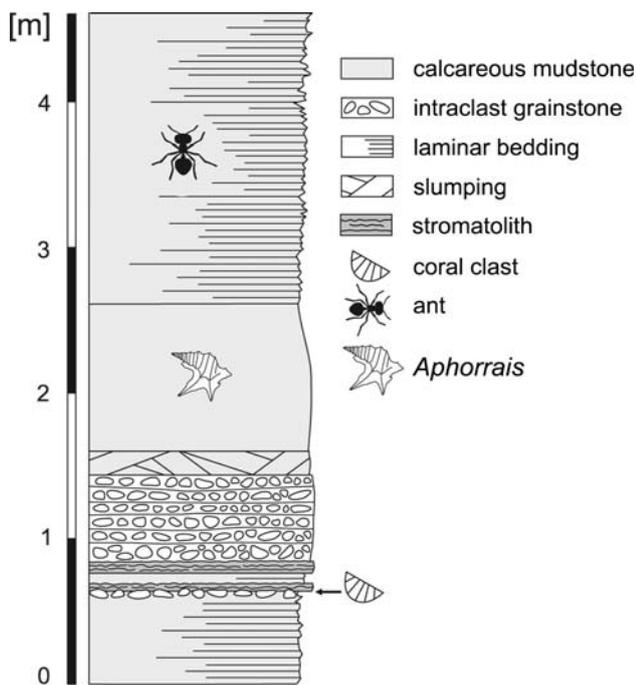


Fig. 2 Measured lithological section in the Varvara Formation southwest of Apomarma

All measurements were made using an ocular micrometer and are given in millimetres; structures were measured as preserved.

Terminology of ant morphology is according to Bolton (1994). The specimens were examined using a Leica MZ 9.5 Stereomicroscope. Photographs were made with a Leica MZ 16 Stereomicroscope and either JVC (model KY-F70B) or Nikon Coolpix 4500 digital cameras and processed using image-editing software (Adobe CS®).

Systematic palaeontology

Formicidae Latreille 1809.

Formicinae Latreille 1809.

Polyrhachis Smith 1857.

Type species: *Formica bihamata* Drury 1773, by original designation.

Comments: Based on the following combination of features, the fossil ants presented here can be affiliated to Formicinae: *Polyrhachis*. Characters of worker Formicinae are as follows: Propodeal lobes absent; waist consisting of one segment (petiole); gaster without constriction between first and second segments. Characters of *Polyrhachis*: Scape inserted at some distance from clypeus; tergite of first gastral segment large, accounting for at least half the length of the gaster; propodeum (posterior segment of alitrunk (= mesosoma) and petiole armed with paired teeth or spines.

Polyrhachis annosus n. sp.

Figs. 3, 4a, b, d.

Derivatio nominis: *Annosus* is the Latin expression for “many years old”.

Holotype: Worker; IPB-WAPPLER-1a, b. The material is deposited in the collections of the Steinmann Institute for Geology, Mineralogy, Palaeontology, University of Bonn.

Type locality: Varvara Formation southwest of Apomarma, Messara Basin, Crete, Greece.

Measurements (in mm): Head length 1.8; length of preserved part of scape 1.8; maximum eye diameter 0.3; alitrunk length 3.5; hind femur length 2.0; petiole length 0.7; maximum petiole width (including spines) 1.55.

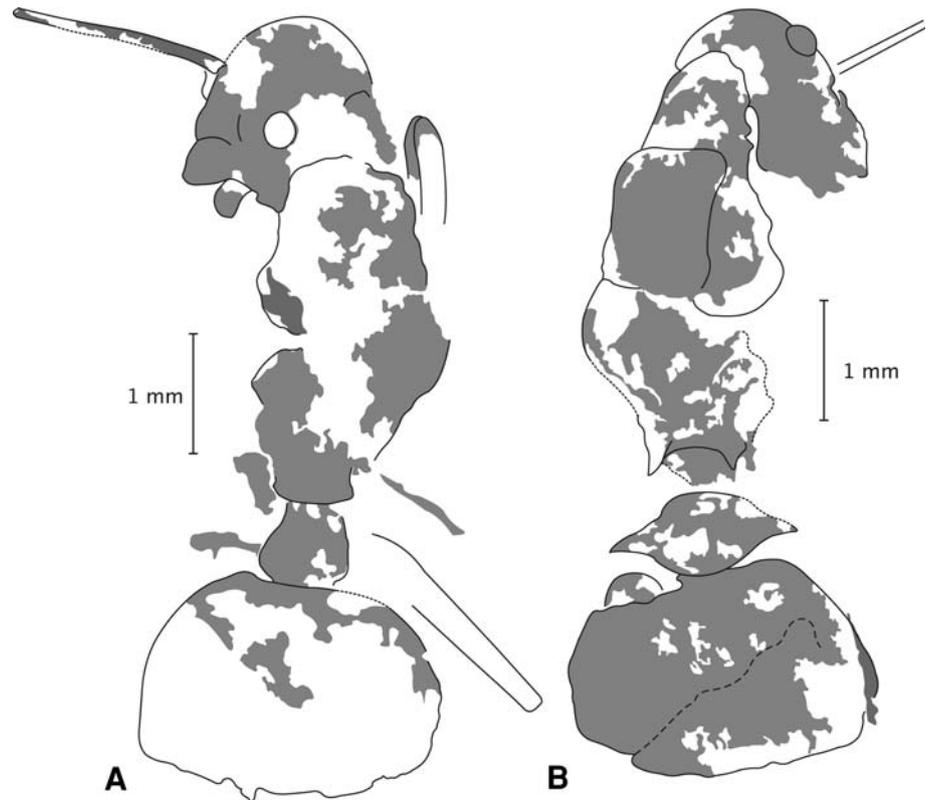
Diagnosis: The new species is noteworthy for the combination of a petiole with two pitchfork-like spines; a pronotum without margination; a propodeum with two teeth; and its distinct meso-propodeal furrows as described below (*vide etiam* Figs. 3, 4a, b).

Description: Worker. Imprint length 6.5 mm. Putative total body length about 7–7.5 mm. Head with rounded occipital margin. Eyes positioned posteriorly, small, round, strongly convex. Scape long, extending beyond the occipital margin of the head. Anterior clypeal margin convex and rounded (Fig. 4b). Alitrunk (mesosoma) elongate, about 2.5 times longer than wide. Pronotum not marginate, without teeth or spines. Promesonotal and mesopropodeal furrows present. Mesonotum marginated laterally, rectangular, longer than wide, without teeth or spines. Propodeum seems to be marginated, with a pair of short blunt teeth directed backward. Petiole with an anterior pair of thick, acute spines directed laterally. Petiole between spines with a nearly horizontal plateau. Legs largely missing by preservation, hind femur apparently rather long. First gastral segment is large, and its form is typical for *Polyrhachis*, so undoubtedly it accounted for at least half the length of the gaster. Anterior part of second gastral segment not preserved in detail, but smaller than first tergite (Fig. 3b).

Comments: The specific assignment of this specimen is still of some doubt, and its placement in the subgenus *Myrmatopa* should be considered tentative. Emery (1925) distinguished the *Polyrhachis schang* group (with *P. elii*, *P. fruhstorferi*, and *P. wallacei*) (comp. Dorow 1995). However, despite the poor preservation of the holotype imprint of *P. annosus*, it more readily agrees with *Myrmatopa* Forel 1915, particularly with its type species *Polyrhachis schang* Forel 1879, in its propodeum not marginated and unarmed, and its petiole bispinous (Emery 1925; Hung 1967; Dorow 1995). At the same time, by its unique combination of characters, *P. annosus* is not similar to any recent species.

Myrmatopa include 43 extant species and subspecies (Bolton et al. 2006) distributed from southern China to Australia with maximum diversity in Indonesia (Dorow

Fig. 3 Worker of *Polyrhachis annosus* n. sp. **a, b** Habitus drawing of part and counterpart of *P. annosus* n. sp., Messara Basin, Late Miocene, holotype IPB-WAPPLER-1a, b. Scale bar 1 mm



1995). All species of the subgenus are arboreal and construct carton nests on or under leaves (Hung 1967).

Discussion

The evolutionary history of ants began in the early Mesozoic. The oldest members of true ants are of late Early Cretaceous age and belong to the structurally least modified subfamily Sphecomyrminae. But they are not the only known ants from the Cretaceous; others include extinct genera belonging to the modern subfamilies Formicinae, Dolichoderinae, Myrmicinae, Ponerinae, Ectatomminae, Aneuretinae, and the extinct subfamily Brownimeciinae (Bolton et al. 2006; Dlussky and Rasnitsyn 2007).

With the beginning of the Tertiary, the fossil record of most modern lineages is excellent and documents an explosive radiation of the group that could be attributed to the rise of diverse ant genera that live in huge colonies today. Already the Eocene Baltic amber has an extremely diverse and abundant ant fauna comprising about 5% of the total insect fossils. This reaches about 35% in Miocene Dominican amber. Mayr (1868), Andre (1895), and Wheeler (1915) studied over 11,000 inclusions of ants in Baltic amber. Prolific descriptions of the ant fauna from the Baltic amber have been provided most recently by Dlussky (1997). Virtually all Baltic amber ants belong to modern

subfamilies and even modern genera like *Formica*, *Lasius*, *Oecophylla*, *Gesomyrmex*, *Dolichoderus*, *Tetraponera*, etc. (Wheeler 1915; Dlussky 1997), which are dominant entomofaunistic elements in tropical forests in the Indo-Australian region, as is *Polyrhachis* as well. Interestingly, Wheeler (1915) already noticed the absence of *Polyrhachis* and the rarity of *Camponotus* in Baltic amber. *Polyrhachis* is also absent in the Miocene Sicilian amber, an entomofauna very different from faunas of other European deposits that seems to be Afrotropical (Emery 1891). Surprisingly, half of the species (14 from 29), which Vieh Meyer (1913) found in copal deposits from Celebes, belong to *Polyrhachis*, and one of them (*P. excitata* Vieh Meyer) even belongs to the subgenus *Myrmatopa*. So, if *Polyrhachis* were present in the Tertiary amber forests they should be fossilized in resin. The abundance of *Polyrhachis* in copal confirms the statement that their absence in the Baltic amber is likely not casual.

Furthermore, *Polyrhachis* lack in the ant-rich Miocene Dominican amber as in all discovered European fossil ant faunas related to lake deposits from Middle Eocene to Early Miocene [e.g. Messel and Eckfeld maar lakes (Eocene, Germany); Bembridge marl (Oligocene, Isle of Wright, UK)], which again include other arboreal ant genera known from the Baltic amber (*Oecophylla*, *Gesomyrmex*, *Dolichoderus*, and *Tetraponera*) (Dlussky 2002, 2009; Dlussky et al. 2009).

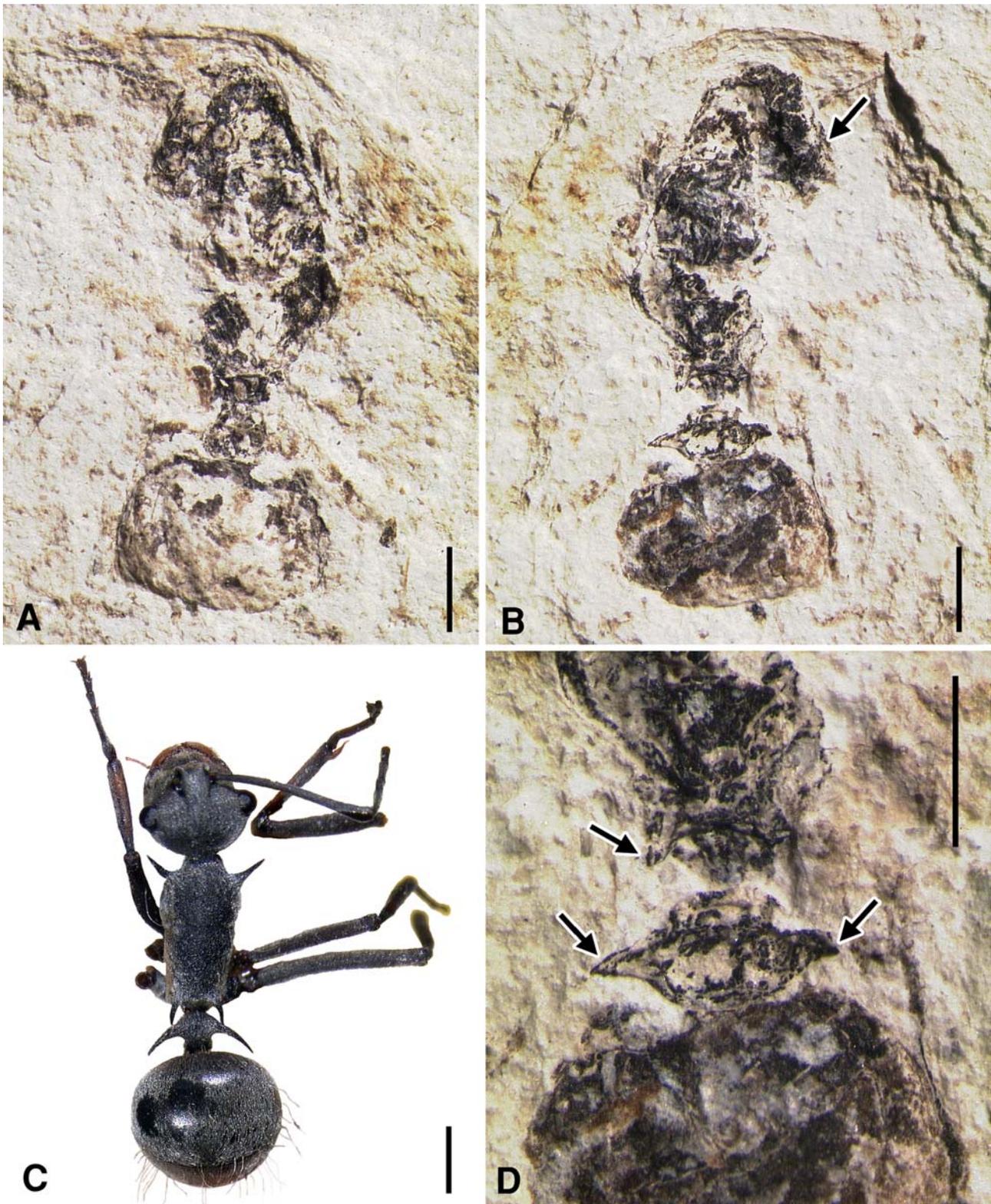


Fig. 4 Worker of *Polyrhachis annosus* n. sp. **a, b** Part and counterpart of *P. annosus* n. sp., Messara Basin, Late Miocene, holotype IPB-WAPPLER-1a, b. *Black arrow* indicates the convex and rounded anterior clypeal margin. **c** Worker of *Polyrhachis subfossa* Viehmeier 1913, Celebes (Sulawesi) copal (gum copal), Holocene,

holotype GBIF/FoCol-ID 0459 (specimen isolated by chemical extraction method described in Viehmeier 1913). **d** Detail of the Propodeum and Petiole of *P. annosus* n. sp. *Black arrows* indicate the position of propodeal and petiole spines. *Scale bar* 1 mm

The most surprising is the absence of *Polyrhachis* in Miocene deposits of Shanwang in southern China (Zhang 1989). Zhang described many species, particularly 11 species of *Camponotus*, but did not report *Polyrhachis*. At the same time there is no doubt that the Shanwang fauna is a typically Oriental tropic fauna. For this reason, their recorded absence from this locality is more likely to reflect their true absence or rarity rather than their being overlooked.

Within the context of cladistic biogeography, the geographical distribution of fossil species may provide information not available from the distribution of extant taxa or support hypotheses based exclusively on the latter. In case of the new species described herein, the fossil locality is inside the distributional range of extant clade members and confirms that the distributional area of the taxon has persisted since the Late Miocene. Anyway, the origin and rise of one of the world's largest and most distinct ant genera is still a puzzle. Clearly, additional fossils of *Polyrhachis* await discovery, and these will undoubtedly provide significant insights into the geological history of this genus and biogeographic pathways of insects during the Neogene.

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