

A new trap-jaw ant species of the genus *Odontomachus* (Hymenoptera: Formicidae: Ponerinae) from the Early Miocene (Burdigalian) of the Czech Republic

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Abstract *Odontomachus paleomyagra* sp. nov. is described from the Early Miocene of the Most Basin (Czech Republic) on the basis of a single-winged female, representing one of the rare reports of fossil Odontomachini. The new species is separated easily from other trap-jaw ant species groups by differences in mandibular morphology (without denticles on the inner side) and distributional occurrence. The evolutionary and biogeographic history of the Odontomachini is briefly discussed.

Keywords Ponerinae · *Odontomachus* · New species · Miocene · Most Basin · Czech Republic · Trap-jaw ants

Kurzfassung Aus dem Unter-Miozän im Most Becken (Nord Böhmen; Tschechische Republik) wird erstmals ein Exemplar der Ameisen-Gattung *Odontomachus* beschrieben und abgebildet. Die neue Art, *Odontomachus paleomyagra* sp. nov., unterscheidet sich von anderen

Angehörigen der Schnappkieferameisen, vor allem durch Unterschiede in der Morphologie der Mandibeln (ohne Zähnnchen an der Innenseite) und ihrer ungewöhnliche biogeographischen Verbreitung. Die evolutionäre und biogeographische Geschichte der Odontomachini wird kurz diskutiert.

Schlüsselwörter Ponerinae · *Odontomachus* · Neue Art · Miozän · Most Becken · Tschechien · Schnappkieferameisen

Introduction

Ants are one of the dominant and more conspicuous groups of animals in terrestrial ecosystems (Hölldobler and Wilson 1990), and their ecological diversity is reflected in both their number of species (>12,750 spp., e.g., Agosti and Johnson 2007) and morphological adaptations. Among the 26 subfamilies presently recognized among ants, species of the Ponerinae are notable predators, armed with powerful mandibles and a well-developed sting (Hölldobler and Wilson 1990). The mandibles contain some of the most important diagnostic characters for ponerine taxonomy and provide a wealth of insights into ecological niches and foraging modes, as reflected in their extreme diversity of mandibular forms and associated structures. Most distinctive are the trap-jaw ants of the genus *Odontomachus* Latreille, easily recognized by their elongate mandibles, which are capable of opening more than 180° and, when a trigger seta is tripped, snap closed rapidly. This powerful, snapping mechanism is used during prey capture, disabling fast or dangerous victims, or in defense, including providing the force for escape jumps, nest construction, and manipulation of larvae and pupae (e.g., Gronenberg 1995;

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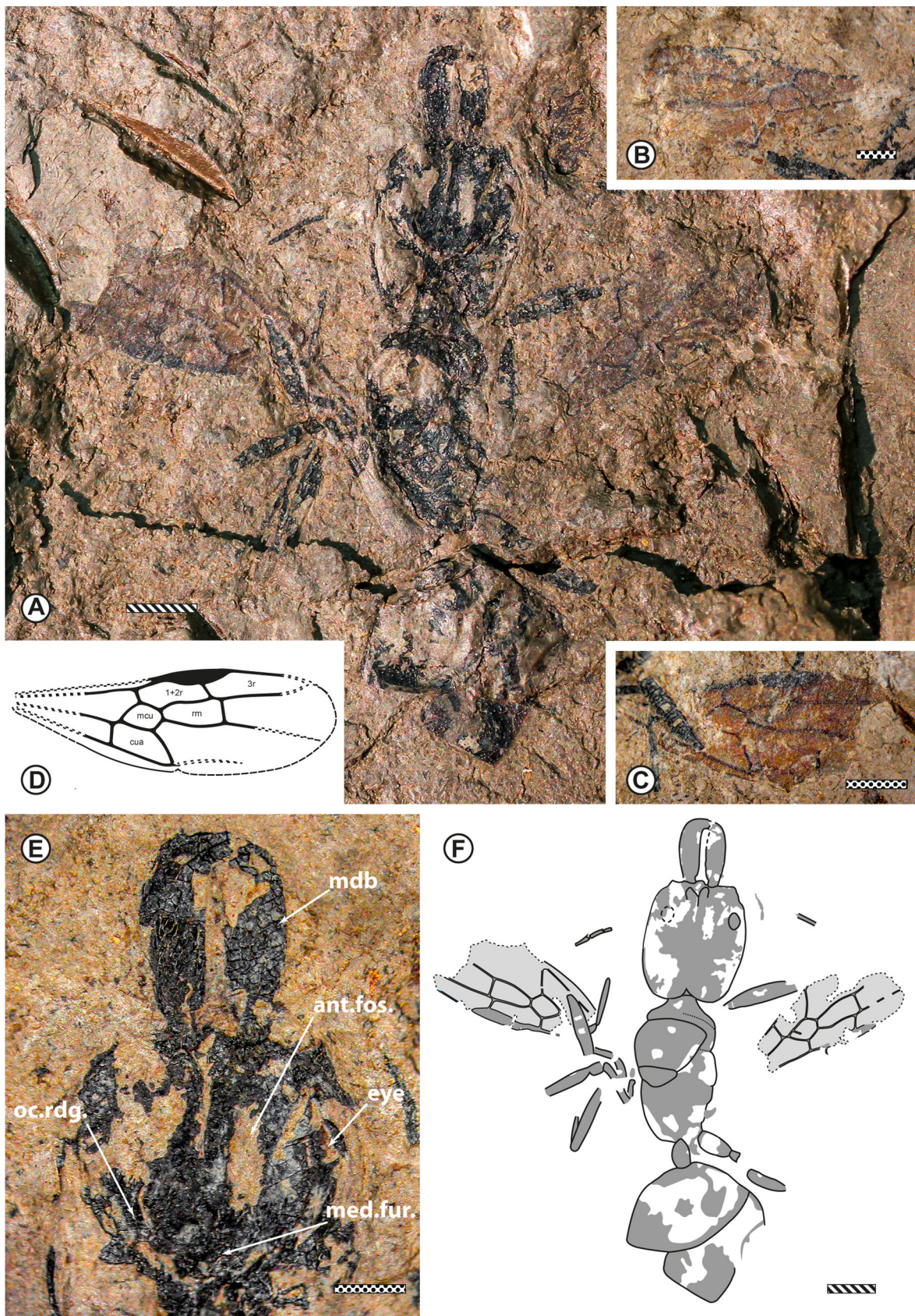


Fig. 1 *Odontomachus paleomyagra* sp. nov. ZD0136 (Bílina Mine Enterprises coll.) from the Early Miocene (Burdigalian), Most Formation, Clayey Superseam Horizon. **a** Gyne, holotype, **b** left forewing, **c** right forewing, **d** Wing reconstruction and nomenclature of venation; cells: *1+2r*, *rm*, *mcu*, *cua*. **e** Detail of the head and pair of large, straight mandibles. *mdb* mandible, *ant.fos.* antennal fossa, *eye* eye, *med.fur.* median furrow, *oc.rdg.* ocular ridge. **f** Habitus drawing of the gyne holotype. Scale bars back slashed 1 mm, dotted 500 μ m

Patek et al. 2006; Spagna et al. 2008). These snapping mandibles make the 69 species of *Odontomachus* among the most specialized of all ponerine ants. Interestingly, such a remarkable specialization is mirrored in the fossil record (LaPolla et al. 2013), as various species in the extinct tribe Haidomyrmecini possess scythe-like mandibles, which appear to have served a similar snapping trap function (Dlussky 1996; Perrichot et al. 2008; Barden and Grimaldi 2012; McKellar et al. 2013). Haidomyrmecines are, however, not related to the Odontomachini and instead are tentatively placed within a different subfamily, the Sphecomyrminae (Perrichot et al. 2008). More importantly, the morphology of their mandibles is distinctively different from that in species of *Odontomachus* (Barden and Grimaldi 2012; McKellar et al. 2013), clearly indicating an independent evolution of snapping trap jaws among the lower ants. Trap jaws are also found independently elsewhere among modern ants, such as *Acanthognathus* Mayr in the Myrmicinae, but those of *Odontomachus* boast the greatest speed of any animal (Patek et al. 2006).

The 69 modern species of *Odontomachus* are widely distributed in tropical regions, with the greatest concentration of species in the Asian and New World tropics (Brown 1976, 1977; Fisher and Smith 2008; Sorger and Zettel 2011; Bolton 2013). Only a few species extend into temperate regions (reviewed in Brown 1976). To date, only two species of *Odontomachus* have been described as fossils, both from the amber mines of the Dominican Republic—*Odontomachus pseudobauri* De Andrade and *Odontomachus spinifer* De Andrade (1994). Species vary considerably in their ecology, including nesting substrates and types of prey, as well as varying morphologically, covering a range of body sizes and mandible lengths (Feitosa et al. 2012). Foraging strategies mainly consist of active hunting for live prey (flies, moths and other ants), gathering of plant and/or insect exudates, and fleshy fruits and seeds (summarized in Schmidt 2011).

Herein, we provide the first description of this peculiar genus of ants from the Early Miocene coal seam deposits of the Most Basin, the third fossil for *Odontomachus* and the first as a compression. Hitherto the composition of this fauna included more than 300 specimens comprising 31 families in 11 insect orders (e.g., Prokop 2003; Kvaček et al. 2004; Fikáček et al. 2008). Ants are the most abundant insect group in the assemblage, comprising nearly

40 % of the recorded specimens, but are mainly represented by isolated wings and disarticulated body structures (personal observation J. Prokop). In addition, we provide some brief comments on the possible affinities of this species relative to species groups within *Odontomachus*.

Materials and methods

The fossil examined in the present work was gathered from the collection of Zdeněk Dvořák deposited in the Bílina Mine Enterprises in Bílina (inventory number prefixed by ZD). The specimen was observed dry and under ethyl-alcohol with an Olympus SZX9 stereomicroscope. All measurements were made using an ocular micrometer and are given in millimeters; anatomical structures were measured as preserved. Line drawings were aided by a camera lucida. All photographs were taken using a Canon EOS 550D digital camera coupled to a MP-E 65-mm macro lens. Morphological terminology used in the descriptions generally follows that employed by Brown (1976); wing vein and cell nomenclature follows Dlussky (2009). The age and stratigraphy of the Bílina Mine coal seam has been summarized briefly in Knor et al. (2013).

Systematic palaeontology

Formicidae Latreille, 1809.

Ponerinae Lepeletier de Saint-Fargeau, 1835.

Odontomachini Emery, 1911.

Odontomachus Latreille, 1804.

Odontomachus Latreille, 1804: 179 (as genus).

Pedetes Bernstein, 1861: 7. Type-species: *Pedetes macro-rhynchus* Bernstein, 1861: 8; by monotypy. Dalla Torre, 1893: 51 (*Pedetes* as junior synonym of *Odontomachus*).

Champsomyrmex Emery, 1892: 558. Type-species: *Odontomachus coquereli* Roger, 1861: 30; by monotypy. Brown, 1973: 179 (*Champsomyrmex* as provisional junior synonym of *Odontomachus*).

Thempsomyrmex Forel, 1893: 163 (incorrect subsequent spelling of *Champsomyrmex*).

Myrtoteras Matsumura, 1912: 191. Type-species: *Myrtoteras kuroiwae* Matsumura, 1912: 192 (junior synonym of *Odontomachus monticola* Emery, 1892). Brown, 1973: 182 (*Myrtoteras* as provisional junior synonym of *Odontomachus*).

Type species: *Formica haematoda* Linnaeus, 1758: 582, by monotypy.

Comments: Based on the following combination of features, the present fossil can be assigned to the trap-jaw ant genus *Odontomachus* (Ponerinae: Odontomachini):

(characters of gyne Ponerinae) waist consisting of one segment (petiole) narrowly attached to first gastral (III abdominal) segment; gaster with constriction between first and second segments; forewing crossvein *cu-a* meeting *M+Cu* near cell *mcu* proximal to section *1M* at distance less than *cu-a* length; (characters of *Odontomachus*) mandibles linear, their bases situated rather close together;

nuchal carina (separating dorsal and posterior surfaces of head) converging in a V at midline.

Odontomachus paleomyagra sp. nov.

Figs. 1, 2

Derivatio nominis: From the Greek *paleomyagra*, ancient mouse-trap (treated as a noun in apposition).



Fig. 2 Reconstruction of the trap-jaw ant *Odontomachus paleomyagra* sp. nov. These predatory insects are noted for their unusual mandibles that are held open at 180° and snap shut on a hair trigger

Holotype: Gyne; specimen No. ZD0136; deposited in the collections of the Bílina Mine Enterprises, Bílina, Czech Republic.

Type locality: Bílina mine near Bílina, Czech Republic.
Age and layer: Early Miocene (Burdigalian), Most Formation, Clayey Superseam Horizon, Holešice Member (No. 30).

Measurements (in mm): Mesosoma length 3.3, head length 2.5, head width 2.0, mandible length 1.4, mandible width 0.4, maximum compound eye diameter 0.26, mesoscutum length 1.0, mesoscutellum length 0.4.

Diagnosis. New species is noteworthy for combination of following characters: mandibles comparatively short, straight, without denticles on inner surface; head rather wide and only slightly narrower across vertex than across compound eyes; petiole without dorsal spine.

Description. Gyne. Imprint length 10.5 mm; putative total body length about 12 mm. Head 1.2 times longer than wide, with feebly concave sides, rounded occipital corners, and concave occipital margin; head width across compound eyes 1.06 times as wide as across vertex; anterior part of head with fine striations; anterior margin of clypeus with small rounded lobe; compound eyes oval, weakly convex, strongly shifted anteriorly, such that gena is nearly 1.5 times as long as maximum compound eye diameter; mandibular bases situated close together, mandibles linear, straight, nearly 0.5 times as long as head, and 3.3 times longer than wide; inner (masticatory) border of mandible without teeth or denticles; mandibular apex evidently consisting of three teeth (as in all known *Odontomachus*; however only two teeth are visible on imprint), one rounded and other with truncate tip. Mesosoma rather elongate; mesoscutum slightly wider than long, flat, not overhanging pronotum; mesoscutellum transverse; propodeum angulate in profile. Petiole with narrowly rounded top, without dorsal spine. Forewing with closed cells *1+2r*, *rm*, *mcu*, *cua*, and perhaps *3r*; section *1M* 1.9 times longer than *1RS*; cell *1+2r* nearly 3 times longer than wide; section *1+2r* S-shaped; cell *rm* pentagonal, 2.2 times longer than wide; crossvein *r-rs* sloping apically and meeting *RS* somewhat basal to junction with *rs-m*, as a result *rs-m* and *r-rs* do not appear as single crossvein; cell *mcu* pentagonal; meeting of crossvein *cu-a* and *M+Cu* proximal to *1M* and *1Cu* fork, separated from it by more than 3 times width of vein.

Comments: De Andrade (1994) described two fossil species of *Odontomachus* from Miocene amber of the Dominican Republic: *O. spinifer* and *O. pseudobauri* (Table 1). These species belong to the Neotropical *haematodus* species group as defined by Brown (1976) and

Table 1 Diversity of Miocene ants of the subtribe Odontomachiti

Subtribe Odontomachiti [§]	References
Genus <i>Odontomachus</i> Latreille	
<i>Odontomachus pseudobauri</i> de Andrade [DA]	de Andrade (1994)
<i>Odontomachus spinifer</i> de Andrade [DA]	de Andrade (1994)
<i>Odontomachus paleomyagra</i> sp. nov. [BM]	This study
Genus <i>Anochetus</i> Mayr	
<i>Anochetus corayi</i> Baroni Urbani [DA]	Baroni Urbani (1980)
<i>Anochetus brevidentatus</i> MacKay [DA]	MacKay (1991)
<i>Anochetus ambiguus</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus conisquamis</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus dubius</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus extinctus</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus intermedius</i> de Andrade [DA]	de Andrade (1994)
<i>Anochetus lucidus</i> de Andrade [DA]	de Andrade (1994)

[§] Comprising ponerine ants with trap-jaws sensu Brown's (1976, 1978) classification of the "subtribe Odontomachiti"

DA Dominican amber (23–19 Ma); The age and origin of Dominican amber is reviewed by Iturralde-Vinent and MacPhee (1996) and Grimaldi and Engel (2005)

BM Bílina mine (~20 Ma)

today include the large majority of New World species in the genus. Taxa of the *haematodus* species group differ from *O. paleomyagra* by the form of the head and longer mandibles with numerous denticles on the inner (masticatory) margins. The construction of the mandibles of the new species is most similar to *O. assiniensis* Emery, 1892, which today occurs in SE Africa, and the Oriental *rixosus* species group, including *O. rixosus* Smith, 1857, *O. monticola* and *O. latidens* Mayr, 1867, mainly occurring today in SE Asia, Sumatra, Borneo and Java (Brown 1976). However, these species have a more elongate head: (1.3–1.5 times longer than wide). The head width across the compound eyes is 1.08–1.16x as wide as across the vertex within the *rixosus* species group, 1.07–1.11x in *O. assiniensis*, whereas this is only 1.06x in *O. paleomyagra*.

Discussion

The subtribe Odontomachiti sensu Brown (1976, 1978) today consists of only the closely related genera *Odontomachus* Latreille and *Anochetus* Mayr. These genera are known only from a handful of fossils from Dominican amber and dating no older than the Early Miocene (summarized in Table 1), but these records and their surprisingly modern character (rather than belonging to stem-group Odontomachiti) serve to demonstrate that this clade is considerably older. Indeed, Ponerinae as a whole extends well into the Mesozoic (e.g., Grimaldi et al. 1997; Engel

and Grimaldi 2005; Grimaldi and Engel 2005; LaPolla et al. 2013) and has experienced a rich history of continuous diversification throughout the Tertiary (e.g., Dlussky and Wedmann 2012; LaPolla et al. 2013). This impressive diversification resulted in a collection of taxa so divergent from one another that some have at times been placed in distinctive tribes (Ouellette et al. 2006; Fisher and Smith 2008; Santos et al. 2010). More recent phylogenetic studies support the sister group relationship between *Odontomachus* and *Anochetus*, and suggest that they may be subdivided into some rare taxa that are present in the Palaearctic Region versus putatively ‘old’ lineages that ‘are predominantly tropical or straddle the temperate-tropical transition zone of East Asia’ (Ouellette et al. 2006; Fisher and Smith 2008; Santos et al. 2010). Certainly, the biogeographic history of this clade is complicated, and, unfortunately, the few fossil records shed relatively little light on the matter, particularly given that the fossils are all well placed within their respective monophyletic genera and, as noted above, emphasize that they are considerably older than the Miocene (Fig. 3). One possible scenario is that the *Odontomachus* group is at least as old as the Paleocene–Eocene with stem members of each genus spreading from Asia into the various parts of the world. These various tropical elements would eventually have become isolated and continued to speciate in those regions after the Eocene–Oligocene transition when considerable climatic cooling and drying took place, whereas the plant assemblage of the lower

Miocene Břilina locality indicates rather moderate to sub-tropical climatic conditions (Kvaček 1998). Such a scenario would account for the modern distribution of the species as well as the few known fossils, but requires considerable testing against future palaeontological discoveries and phylogenetic analyses. Certainly fossils can provide some of the most critical data for illuminating historical biogeographic patterns. For instance, the discovery in northern deposits of otherwise ‘austral’ lineages has greatly revised our interpretations of the evolution of many plant and animals clades, especially among insects (e.g., Grimaldi and Engel 2005). Accordingly, fossils such as *O. paleomyagra* have the potential, when ultimately included in cladistic studies, to transform our understanding of historical patterns.

The present fossil, along with those in amber, also demonstrates the antiquity and relative evolutionary stability of the unique mandibular morphology of these trap-jaw ants. While there are subtle differences in the mandibles among the numerous species groups of *Odontomachus*, the overall groundplan of the odontomachine trap jaw is relatively conserved. This effective prey-capture mechanism as well as its suitability for constructing and manipulating nest elements has apparently persisted for ~20 million years, and likely much longer. It would be interesting to look for morphological or morphometric proxies permitting an estimation of the force and speed potentially produced in the fossil species. This would allow

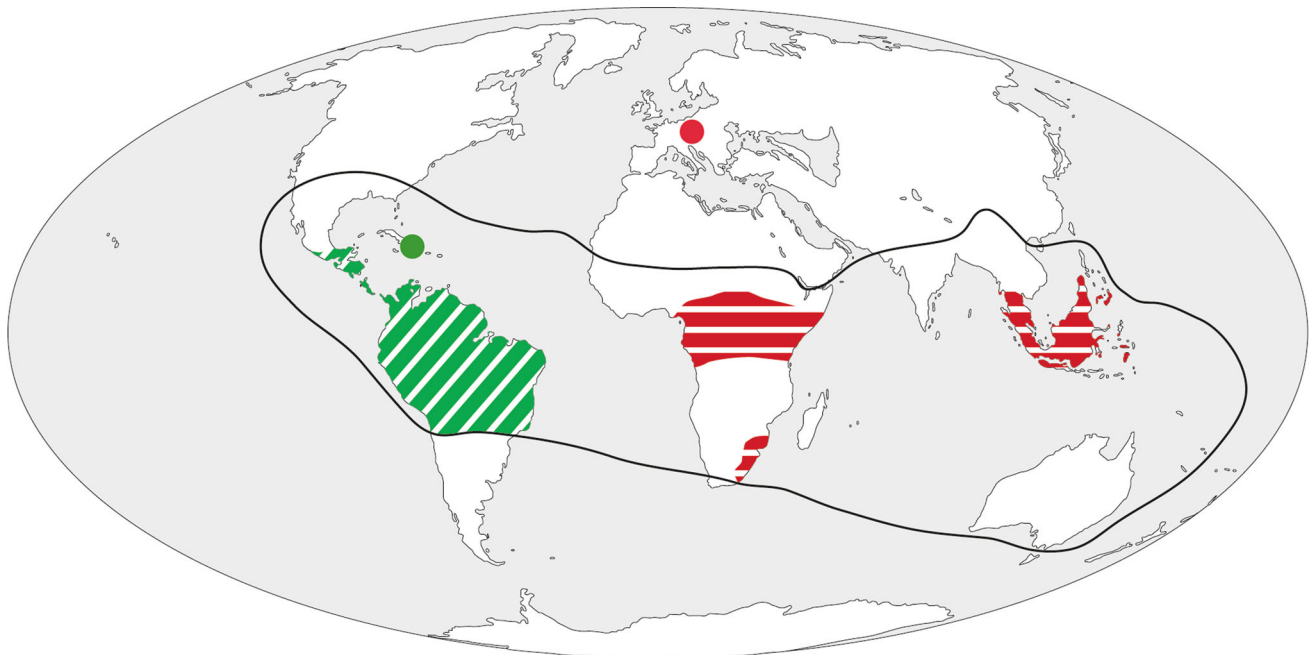


Fig. 3 Present-day distribution of the genus *Odontomachus*. The shaded areas represent the distribution of recent species closely related to the known fossils, both corresponding in color (green dot

amber specimens, red dot compression specimen). Palaeogeographic reconstruction for the Miocene Epoch based on the plate model presented in Blakey (2011)

a quick estimation of these values for all of the living species and, when placed in a phylogenetic framework, would result in a reconstruction of mandibular force evolution across this clade. Perhaps the considerable power produced by the mandibles of *O. bauri* (Patek et al. 2006; Spagna et al. 2008) is shared across additional species of *Odontomachus* and even ancient in origin, a fascinating area for investigation. Eventual discovery of the origins of the genus group temporally and biogeographically will permit placing the common ancestor of odontomachines in its original ecological context and could shed light on those factors resulting in the spectacular evolutionary novelty of their prominent mandibles. Such hypotheses will only be successfully tested and resolved by continued palaeontological work among the ants.

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