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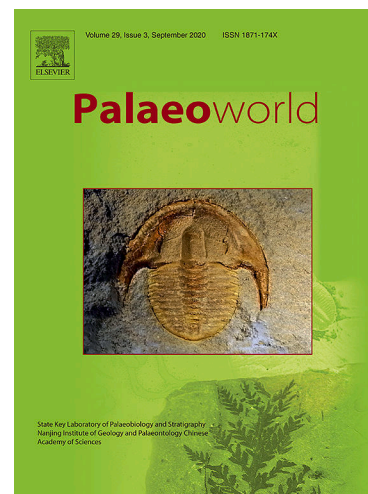
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## The first fossil occurrence of *Odontoponera* (Formicidae: Ponerinae), from Middle Miocene Zhangpu amber

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### Abstract

*Odontoponera pseudotransversa* n. sp. is described from Miocene-aged amber of Zhangpu, Fujian Province, southeastern China. This is the first fossil occurrence of *Odontoponera*, a southeast Asian genus of ponerine ants otherwise known by only two extant species. Although remarkably similar to *Odontoponera transversa*, the new fossil species displays intermingled characters of the two Recent species and a few unique features.

**Keywords:** Hymenoptera; ant; Ponerini; Zhangpu amber; Fotan Group; China

### 1. Introduction

*Odontoponera* Mayr, 1862 is a readily identifiable genus of ponerine ants characterized by a strongly striate head and mesosoma, denticulate anterior clypeal margin, toothed pronotal margins, and emarginate petiolar scale (Schmidt and Shattuck, 2014; Wachkoo et al., 2020). The genus is restricted to Southeast Asia — from Pakistan to New Guinea, and from southern China to the Lesser Sunda Islands of southern Indonesia, and is known by only two species: *O. denticulata* (Smith, 1858) and *O. transversa* (Smith, 1857), the latter with 2 subspecies (Bolton, 2022).

Remarkably, *Odontoponera* is one of the most observed ants in various habitats of southeast Asia (Wheeler and Chapman, 1925; Levy, 1996; Berghoff et al., 2003; Eguchi et al., 2004; Sitthicharoenchai and Chantarasawat, 2006; Zhou et al., 2007; Schmidt and Shattuck, 2014; Wachkoo et al., 2020), albeit apparently with small colonies (ca. 100 individuals), and with epigeic workers individually foraging within only about a meter from their nest entrances (Eguchi et al., 2004; Wachkoo et al., 2020). The genus is thus weakly prone to be caught in resin, unless the nest is located nearby resin-producing trees, and with some fresh resin reaching or approximating the

soil surface. Here, the first fossil occurrence of the genus is reported from Middle Miocene amber of Zhangpu, Fujian Province, southeastern China. It is strikingly similar to *O. transversa*, while the sole species currently recorded from mainland China (Yunnan, Guangxi, Guangdong, Hong Kong, and Macau) and Taiwan (Leong et al., 2017) is *O. denticulata*.

## 2. Material and methods

The present study is based on the single *Odontoponera* worker that was found among over 950 ant individuals from the collection of Zhangpu amber housed in the Nanjing Institute of Geology and Palaeontology (NIGP). Zhangpu amber is dug from two units of blue-gray sandy mudstone interbedded with lignite and diatomite that are part of the Fotan Group, a succession that also includes basalts, arenaceous conglomerates and sandstone and widely occurs throughout Zhangpu County in Fujian Province, southeastern China (Shi et al., 2014; Wang et al., 2021). The age of the amber is estimated to be Middle Miocene (Langhian, ~14.7 Ma) based on  $^{40}\text{Ar}/^{39}\text{Ar}$  radiometric dating of the underlying and overlying basalts (Ho et al., 2003; Zheng et al., 2019; Wang et al., 2021).

The amber piece containing the ant reported here was ground using a water-cooled grinding machine to remove the weathered outer surface, then polished in three flat surfaces near to the ant specimen for optimal dorsal, profile, and full face views, using wet silicon carbide papers (1200 to 4000 grits) on a Buehler MetaServ 3000 polishing machine. Zhangpu amber commonly becomes sticky after polishing, therefore the piece was embedded in a block of epoxy resin (Araldite© 2020) to maintain clean surfaces for the study, imaging of the specimen, and long-term conservation.

The fossil was examined under both incident and transmitted light using a Leica MZ APO stereomicroscope, and imaged with the aid of a Canon 5D Mark II camera attached to it. Stacks of photographs taken at different depths of field were merged using Helicon Focus software (HeliconSoft Ltd.). Measurements were made using the ocular micrometer of the microscope.

The classification follows Schmidt and Shattuck (2014). The morphological terminology follows Keller (2011). The measurements and indices listed below are standard metrics generally used for worker ants, extant or fossil:

BL Body length, the total body length from the anterior margin of the head capsule (excluding mandibles) to the apex of the abdomen, measured in dorsal view.

- HL Head length, the length of the head capsule excluding the mandibles; measured in full-face view in a straight line from a line that spans the anteriormost points of the clypeal lobes to the level of a line that spans the posterior corners of the head capsule.
- HW Maximum head width behind the eyes, measured in dorsal view.
- SL Scape length, maximum straight-line length of the scape, excluding radicle.
- ED Maximum diameter of eye as measured in lateral view of the head to show full surface of eye.
- WL Weber's length, the diagonal length of the mesosoma in profile, from the angle at which the pronotum meets the cervix to the posterior basal angle of the metapleuron.
- PrW Maximum width of pronotum in dorsal view.
- PL Maximum length of petiole in profile view.
- CI Cephalic index ( $HW/HL \times 100$ ).
- SI Scape index ( $SL/HW \times 100$ ).
- OI Ocular index ( $ED/HW \times 100$ ).
- REL Relative eye length index ( $ED/HL \times 100$ ).
- EPI Eye position index. In full-face view, longitudinal length from the anteriormost point of the eye to the anterior clypeal margin, divided by longitudinal length from the posteriormost point of the eye to the posterior head margin  $\times 100$ .

Extensive reference was also made to worker specimens of *O. denticulata* and *O. transversa* illustrated on AntWeb (Version 8.78, <https://www.antweb.org>, accessed 25 July 2022).

This published work and its new nomenclatural act are registered in ZooBank with the following LSID (reference): urn:lsid:zoobank.org:pub:7F7B8D65-D3A9-4901-B894-7187C3374B13.

### 3. Systematic palaeontology

Family Ponerinae Lepeletier de Saint-Fargeau, 1835

Tribe Ponerini Lepeletier de Saint-Fargeau, 1835

Genus *Odontoponera* Mayr, 1862

**Type species:** *O. denticulata* (Smith, 1858).

*Odontoponera pseudotransversa* n. sp.

(Figs. 1–3)

**LSID (species):** urn:lsid:zoobank.org:act:75DA27B8-F2E8-498D-B153-14C9D14D2D24.

**Etymology:** From the Greek ‘pseudo’ (ψευδο) meaning false, in reference to the closely resembling species *transversa*.

**Holotype:** NIGP200658, a nearly complete worker missing the left antennal flagellum, left mandible, and apical portions of the right mid and hind legs; with right lateral side contacting amber surface, altered; integument almost entirely coated by weakly opaque, whitish (bacterial?) film. Deposited in the Nanjing Institute of Geology and Palaeontology, Nanjing, China.

**Type locality:** Zhangpu County, Zhangzhou Prefecture, Fujian Province, China.

**Type horizon:** Amber-bearing mudstone (sedimentary layer II) from the Fotan Group, Middle Miocene, Langhian (~14.7 Ma).

**Diagnosis (worker):** The new species is characterized by the antennal scape moderately long, surpassing the posterior head margin by the length of the first funicular segment; the anterior clypeal margin with seven denticles; the anterodorsal corners of propodeum each with a single, truncated tooth; and the petiolar node with anterior and posterior faces weakly convex, not striate, with dorsal margin broadly and distinctly emarginate between blunt corners.

**Description:**

*Measurements (in mm) and indices:* BL ca. 7.80; HL 2.20; HW 1.75; SL 1.65; ED 0.35; WL 2.95; PrW ca. 1.40; GL 2.50; CI 79.5; SI 94; OI 20; REL 15.9; EPI 34.5.

*Head:* (Figs. 1–2) Head capsule longer than wide; in full-face view, anterior clypeal margin with seven denticles, lateral sides weakly convex, posterior head margin weakly concave. Mandible robust, about half as long as head, triangular, masticatory margin with five large teeth. Eye located anterior to head midlength (EPI 34.5), weakly convex, ovoid, small (OI 20, REL 15.9), its longest diameter only slightly smaller than the minimum distance between anterior eye margin and anterior genal margin. Antenna with 12 segments, with flagellum progressively incrassate toward apex; scape surpassing posterior head margin by length of first funicular segment; flagellomeres 1–5 conical, slightly longer than broad; flagellomeres 6–9

more cylindrical, as long as or slightly shorter than broad; apical flagellomere acute at tip, more than twice as long as broad. Vertex medially with a raised triangular area near posterior head margin, the raised area anteriorly sharply defined.

*Mesosoma*: (Figs. 1, 3A) In profile view, pronotum sharply angled anteriorly, with anterior face nearly vertical, dorsum slightly convex; promesonotal suture and pronotal groove distinct, so that mesonotum well defined. In dorsal view, pronotum with a blunt tooth at each anterodorsal corner; propodeum with a single, sharp, apically truncated tooth at each posterodorsal corner.

*Legs*: (Figs. 1, 3A) Coxae, femora and tibiae of all legs robust, broadest around midlength. Each tibia apically with a pectinate and a simple spur. Pretarsal claws narrow and simple, without additional teeth.

*Petiole*: (Fig. 3B) In profile view, petiole higher than long, with short but distinct anterior and posterior peduncles; petiolar node with anterior and posterior faces slightly convex, with dorsal margin reaching highest level of propodeal dorsum; subpetiolar process not visible, hidden by hindleg. In posterodorsal view, petiolar dorsal margin broadly and distinctly emarginate medially, with blunt corners.

*Metasoma*: (Figs. 1, 3A) Helcium infraaxial. Gaster only weakly constricted between third and fourth abdominal segments. In dorsal view, third abdominal tergite longest, broadest at posterior margin of third abdominal tergite.

*Sculpture*: Head capsule except clypeus with fine, longitudinal to oblique rugae converging medially on frons and vertex. Dorsal mandibular surface finely, longitudinally striate, additionally punctate along basal mandibular margin, and basally with a transverse groove (Fig. 2C). Scape similarly finely, longitudinally striate and with scattered, shallow punctures. Mesosoma except pronotal collar with coarse rugae; in dorsal view, transverse, thick rugae with interspaces deep, 1.5× as thick as rugae; pronotal rugae slightly concave anteriorly, pronotal teeth, increasingly convex posteriorly; mesonotal rugae distinctly concave; propodeal rugae weakly concave. In lateral view, pronotal rugae concentric around pronotal tooth; mesopleuron, metapleuron and propodeum with oblique rugae. Petiolar node and gaster smooth.

*Setation*: Head capsule, antennae, legs, petiole and metasoma densely covered by short, adpressed, fine setae. Vertex, scapes and legs additionally with scattered, slightly longer, semi-erect, thin setae (on scape, inserted in punctate areas). Scattered,

long (as long as or longer than first funicular segment), semi-erect, thicker setae dorsally on mesosoma and petiolar node, dorsally and ventrally on metasoma.

#### 4. Discussion

The fossil displays intermingled characters of the two extant species, as follows:

- a small size – body length 7.8 mm, versus 6.8–10 mm in *O. transversa* (Yamane, 2009; and measurements taken on AntWeb workers CASENT0249126, CASENT0900666, CASENT0907214, and CASENT0911207), 8.75–10.35 mm in *O. denticulata* (Leong et al., 2017; Wachkoo et al., 2020; Hazarika and Kanikor, 2021);
- the relatively large eyes: ratio of minimum distance between anterior margin of eye and anterior margin of gena to maximum eye diameter 1.2 – versus 1.5–2 in *O. transversa*, 1.2–1.4 in *O. denticulata* (Yamane, 2009; Wachkoo et al., 2020);
- the vertexal protuberance distinct, anteriorly sharply defined – as in *O. transversa*, versus less defined and with blunt anterior apex in *O. denticulata* (Yamane, 2009; Leong et al., 2017; and specimen ANTWEB1008558);
- the posterodorsal corners of propodeum each with a single tooth – versus two teeth, rarely one in *O. transversa*, three teeth in *O. denticulata* (Yamane, 2009; Wachkoo et al., 2020);
- the petiolar node with anterior and posterior faces slightly convex and dorsal margin broadly emarginate between blunt corners – versus anterior face straight or concave, dorsal margin deeply emarginate between acute corners in *O. transversa* (Yamane, 2009; and specimen ANTWEB1008558); anterior face straight or slightly convex, dorsal margin weakly emarginate between blunt or rounded corners in *O. denticulata* (Leong et al., 2017; Wachkoo et al., 2020; Hazarika and Kanikor, 2021).

The new species is thus remarkably similar to *O. transversa*, but differs from it (and *O. denticulata*) as follows:

- the antennal scape surpassing posterior head margin by  $1\times$  length of the first funicular segment – versus  $< 1\times$  in *O. denticulata*,  $> 1\times$  in *O. transversa* (Yamane, 2009; Leong et al., 2017; Wachkoo et al., 2020; Hazarika and Kanikor, 2021);



- the petiolar node without distinct rugae – versus posterior face transversely striate in *O. transversa* (Yamane, 2009; and specimen ANTWEB1008558); with or without distinct rugae on *O. denticulata* (subject to variation, see Leong et al., 2017).

## 5. Conclusion

*Odontoponera* is one of the most commonly observed extant ants in Southeast Asia. This contrasts with its scarcity in Zhangpu amber, in which only a single individual was found among over 950 ant specimens (0.1%), while ponerine genera such as *Leptogenys* and *Brachyponera* are distinctly more abundant (3.7% and 1.8% of total ants, respectively; unpublished data). But rather than an actual differential abundance in the Miocene rainforest biome of Zhangpu, this could simply be explained by the distance of *Odontoponera* nests from the resin-producing, dipterocarp trees (Shi et al., 2014). It has been observed that workers of *O. denticulata* only forage within about a meter from their nest entrances (Eguchi et al., 2004), so that a longer distance of the nests from dipterocarp trees may have prevented *Odontoponera* from engulfment in resin.

The Zhangpu biota is extraordinarily rich and it is hoped that further specimens of *Odontoponera pseudotransversa* n. sp. will be discovered in this amber deposit, allowing full assessment of its morphological features.

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**Figures captions**

Fig. 1. *Odontoponera pseudotransversa* n. sp., holotype NIGP200658, worker, photomicrographs of habitus. (A) Left lateral view, head in slightly dorsal oblique orientation. (B) Dorsal view, head in slightly right lateral oblique orientation. Scale bar = 1 mm.

Fig. 2. *Odontoponera pseudotransversa* n. sp., holotype NIGP200658, worker, photomicrographs. (A) Dorsal view of head, slightly left lateral oblique orientation. (B) Dorsal view of anterior clypeal margin, right lateral orientation. (C) Right mandible in dorsal view, with indication of poorly visible, apical and subapical teeth. Black arrows indicate the clypeal denticles (md, medial denticle; <sup>1</sup>ld, first left lateral denticle; <sup>1</sup>rd, first right lateral denticle, ...); white arrow indicates the anterior apex of vertexal protuberance. Scale bar = 0.5 mm.

Fig. 3. *Odontoponera pseudotransversa* n. sp., holotype NIGP200658, worker, photomicrographs. (A) Mesosoma, petiole, and anterior part of first gastral segment in left lateral view. (B) Petiole in posterodorsal oblique view; arrows indicate the blunt lateral corners of petiolar dorsal margin. Scale bar = 0.5 mm.

