The first representative of the trap-jaw ant genus *Anochetus* Mayr, 1861 in Neogene amber from Sumatra (Hymenoptera: Formicidae)

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INTRODUCTION

Ponerinae were estimated to originate about 73 million years ago (Mya) in the most recent molecular analysis of ants (Borowiec et al. 2019). But the two putative fossil records from the Turoanian (~91 Mya) of South Africa and the Campanian (~72 Mya) of Myanmar suggest an older age (Dlussky et al. 2004; Barden 2017; Zheng et al. 2018). Ponerine ants become more and more abundant through the Cenozoic, being known as fossils in the Nearctic, Palearctic and Australian regions, either as compression fossils or inclusions in amber (Barden 2017).

Trap jaws have evolved independently several times in ants, and are found in the subfamilies Formicinae, Myrmicinae, and Ponerinae (review in Larabee & Suarez 2014), as well as in the extinct Sphecomyrminae (Perrichot et al. 2016). Within the Ponerinae, the tribe Ponerini consists of 25 genera, among which both the genus Anochetus Mayr, 1861 and its sister group Odontomachus Latreille, 1804 exclusively contain trap-jaw ants (Brown 1976, 1978; revised by Larabee et al. 2016).

The genus Anochetus is predominantly intertropical and forest-inhabiting (Brown 1978). In the Indomalaya bioregion where Sumatra belongs, there are 4691 ant species, but only 14 of the 1307 Indonesian species belong to Anochetus. To date, 115 Anochetus species have been described worldwide (Antweb at https://www.antweb.org/, accessed September 2019).

Brown (1978) proposed a phylogeny and a key to the Anochetus species from Asia, Melanesia, and the Pacific region. New species of Anochetus from the Philippine Islands were described recently (Nuril Aida & Idris 2011; Zettel 2012). The most recent paper on the genus Anochetus is a revision of the extant Chinese species (Chen et al. 2019).

Going back in time, one subfossil is known from the Holocene Madagascar copal, while eight fossil Anochetus species were described from the Miocene Dominican amber (Baroni-Urbani 1980; MacKay 1991; De Andrade 1994; Vankerkhoven et al. 2010; Antweb).

Here we describe the first fossil Anochetus discovered in the reputedly Miocene Sumatran amber. It is an alate queen that was probably trapped in resin during nuptial flight. Larabee et al. (2016) proposed dates for the different Anochetus species groups. Thus the study of this new fossil may help to test the maximum age of this Sumatran amber currently determined on the basis of stratigraphy.

MATERIAL AND METHODS

The fossil is preserved in a piece of relatively darkened yellow amber, which was carefully ground and polished prior to examination and photography. It is part of a small collection of 53 amber pieces with inclusions bought from a local trader (Starnborn Creations). This material will be deposited by Jean-Marc Pouillon in the near future in an official institution. This fossil resin is assigned to the Glessite group (Narudeesombat et al. 2014; Naglik et al. 2018) and was probably produced by trees of the family Dipterocarpaceae, likely close to Shorea Roxb. ex C.F.Gaertn. (1805). Sumatran amber is a byproduct of coal mining, and different ages ranging from Eocene to Pliocene have been recorded for these coal mines (Belkin & Tewalt 2007; Bak et al. 2016). Previous reports of Sumatran amber, although from different localities, suggested an early Miocene age and a dipterocarp tree source (Durham 1956; Langenheim & Beck 1965; Brackman et al. 1984; Lambert et al. 1999, 2013).
The material comes from the South Sumatra Basin, probably from Sinamar, Dharmasraya Regency, West Sumatra, in a mine supposedly Miocene in age (15-25 Mya) (De Smet & Barber 2005). Many fossils within these amber inclusions are deformed because the amber was probably heated by volcanic activity that occurred in the area during the Miocene (Kosmowska-Ceranowicz et al. 2017). It is especially the case for this fossil ant, thus the body shape was partially deformed rendering the dimensions weakly indicative.

The fossil was studied and measured using incident and transmitted light with stereo microscopes (Olympus SZX9 and Nikon SMZ 1500). Images were digitally compiled using Zerene Stacker software, and arranged using Adobe Photoshop software. Life Science Identifiers (LSIDs) are used as the globally unique identifier for ZooBank registration entries (Pyle & Mitchell 2008). The LSID number of the article was generated by us and appears at the beginning of the article.

Morphological terminology follows Brown (1976, 1978) and Zettel (2012), with a modification of head and pronotum measurements. Due to amber deformation, the fossil was laterally compressed, rendering pronotum width not indicative. We thus transformed pronotal index (PI) into PrH/HH. The following measurements were used for morphological descriptions (Figs 1; 2).

**Measurements and indices**

- **HL**: head length;
- **HW**: head width;
- **MdL**: mandible length;
- **PcH**: petiole height;
- **PeL**: petiole length;
- **PrH**: pronotum height;
- **SI**: scape index;
- **SL**: scape length;
- **TL**: total length;
- **WL**: weber's length.

 private collection

coll. JMP Jean-Marc Pouillon, Nivolas-Vermelle.

**SYSTEMATIC PALEONTOLOGY**

Class INSECTA Linnaeus, 1758
Order HYMENOPTERA Linnaeus, 1758
Family FORMICIDAE Latreille, 1809
Subfamily PONERINAE Lepeletier de Saint-Fargeau, 1835
Tribe PONERININI Lepeletier de Saint-Fargeau, 1835
Genus Anochetus Mayr, 1861

**DESCRIPTION**

**Diagnosis.** — Mandibles very thin in basal part and distinctly broadened at apex; petiolar node much narrow at base; subpetiolar process large with subtriangular ventral margin; deeply U-shaped posterior part of head, rounded anterior margin of gaster from lateral view.

**Body**

Dark, fairly preserved, except for missing apices of mandibles destroyed during preparation, dorso-ventral flattening of head, thorax, and propodeum, and splitting of antennae and legs.

**Head**

Pyriform, much longer than broad (CI: 56), broadened in the anterior third, widest at the level of eyes, eyes on laterally-produced ocular prominences (Fig. 1C) with deeply concave ventral margin in ventral view; posterior head margin deeply emarginate medially, forming diverging, strongly pointed postero-lateral corners; mandible elongate, adjacent, subporrect, lying nearly parallel at full closure, with dorsal margin edentate, each with at least two teeth directed ventrally in an apical group, dorsal margin without distinct teeth; antenna long and slender, with 12 flagellomeres, hardly visible; scape exceeding posterior corner of head; in lateral view of mesosoma; pronotum apparently sculptured over entire disc, with dorsal outline slightly convex from anterior to posterior; posterior corner of propodeum weakly angulate; petiolar node higher than long, petiolar node narrowly rounded at apex, with vertical margins; subpetiolar process developed, with subtriangular ventral margin; forewing with a distinct pterostigma; venation as in Figure 2; gaster oval;

**Anochetus miosumatensis**

Ngô-Muller, Garrouste & Nel, n. sp. (Figs 1-3)

**Holotype.** — Specimen JMP2362 (alate queen), stored in coll. JMP.

**Locality.** — Sinamar, Dharmasraya Regency, West Sumatra, South Sumatra Basin, Miocene.

**Etymology.** — Named after the Miocene period and the Sumatra Island.

**Remarks**

According to the key to Asian species of Anochetus (Brown 1978), combined with data in more recent publications (Nuril Aida & Idris 2011; Zettel 2012; Chen et al. 2019), this fossil Anochetus belongs to the A. risii Brown, 1978 group as defined by Brown (1978). A number of Anochetus species of the risii group are present in Java, Malaysia and Philippines. Altogether, the fossil A. miosumatensis Ngô-Muller, Garrouste & Nel, n. sp. is closer to Anochetus tua Brown, 1978 than to any other species of risii group. However, a unique combination of characters is observed in this fossil queen ant from the Miocene of Sumatra, allowing to consider it as a new species as described below.

**Anochetus miosumatensis**

Ngô-Muller, Garrouste & Nel, n. sp.

(Figs 1-3)

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Fig. 1. — Anochetus miosumatensis Ngô-Muller, Garrouste & Nel, n. sp., holotype JMP2362: A, habitus in left lateral view; B, habitus in right lateral view; C, head and mesosoma in ventral view; metasoma in lateral view. Scale bars: A, B, 2 mm; C, 1 mm; D, 0.5 mm.
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third abdominal tergum sub-trapezoidal with slightly convex anterior margin and straight posterior margin.

DISCUSSION

After (Brown 1976, 1978), this fossil belongs to Anochetus rather than to Odontomachus, because of the following characters: pyriform head, broadened in anterior third, with eyes situated at broadest part on laterally-produced ocular prominences, combined with elongate, adjacent, subporrect trap-jaw mandibles lying nearly parallel at full closure, each with three teeth (at least two are visible in our fossil) in an apical group, with apical tooth ventral at apex; nuchal carina forming a broad uninterrupted curve across posterodorsal extremity of head, with median groove absent.

If we follow the key to species of Asia, Melanesia and Pacific regions (internet site Antwiki at http://www.antwiki.org/wiki/Welcome_to_AntWiki), Anochetus miosumatrensis Ngô-Muller, Garrouste & Nel, n. sp. would fall near A. tua because of the following characters: mesial edge of mandible with two margins up to preapical tooth or angle; dorsal margin edentate; pronotum apparently sculptured over the entire disc; posterior lobes of head very pronounced and acute. The petiolar node narrowly rounded at apex is also shared by A. miosumatrensis Ngô-Muller, Garrouste & Nel, n. sp. and A. tua. The latter is currently recorded from Malaysia and Borneo, but not from Sumatra. Anochetus tua belongs to the risii group of Brown.

Fig. 2. — Anochetus miosumatrensis Ngô-Muller, Garrouste & Nel, n. sp., holotype JMP2362: A, fore wings; B, forewing reconstruction. Scale bars: 1 mm.
This author characterized the risii group as follows: mandibles each with distinct dorsal and ventral margins, the upper edentate (except for preapical angle), the lower one with small, serial, spaced teeth, or crenulate, or smooth (crenulate in *A. miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp.); intercalary tooth of mandibular apex arises from well beyond mid-length of ventral apical tooth (not visible in *A. miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp.); preapical angle usually well marked; mesonotal disc with a blunt anterior rim, or none (not visible in *A. miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp.); petiolar node pointed or narrowly rounded at apex (narrowly rounded in *A. miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp.). It is reasonable to attribute *A. miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp. to this group of species, which otherwise comprises the species *risii, tua, agilis* Emery, 1901, *breviis* Brown, 1978, *incultus* Brown, 1978, *modicus* Brown, 1978, *strigatellus* Brown, 1978, *peracer* Brown, 1978, and *maryatiae* (Nuril Aida & Idris, 2011). This group is centered in SE Asia, and extends to the Philippines and mainland New Guinea. However, only the species *agilis, incultus, risii, modicus, strigatellus,* and *tua* are present in Malaysia, near to Sumatra.

*Anochetus miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp. differs from *A. agilis* and *A. modicus* in thinner mandibles in the basal part, and a petiolar node much narrower at base. *Anochetus miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp. differs from *A. incultus* in the deeply U-shaped posterior part of head and a petiolar node much narrower at base. It differs from *A. risii* in the same characters plus the mandibles broadened at apex. *Anochetus risii* has also a round angle between the proximal and apical parts of the mandible, a subpetiolar process absent, and the anterior margin of gaster rounded (Chen et al. 2019). *Anochetus strigatellus* has the mandibles very broad at base, an acute petiolar lobe and stronger teeth on mesial part of mandible. *Anochetus miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp. shares with *A. tua* a deeply U-shaped posterior part of head, mesonotal disc with a blunt anterior rim, and the petiole thin and narrowly rounded at the apex (petiolar node is often more strongly axially compressed in queen), first segment of gaster large, and separated from second by a distinct constriction. However, *A. miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp. differs from *A. tua* in the mandibles narrow at base but much broader near their apices, and the basal part of the petiolar node much narrower. *Anochetus miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp. also resembles *A. maryatiae* from the Philippines in the shapes of mandibles and of dorsal petiolar lobe, and differs from *A. maryatiae* in the subpetiolar process being larger (Nuril Aida & Idris 2011).

Extant *Anochetus* sp. have small nests in soil, in termite nests, under logs, in humus and leaf litter at the bases of large trees, and in rotten wood. A few species are arboreal. They are predators on small arthropods, caught and killed or incapacitated by the ants. A similar biology can be inferred for *A. miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp. Larabee et al. (2016) estimated the divergence time between *Anochetus* and *Odontomachus* at around 53 Mya, during the Lower Eocene, while separation dates for the main subgroups of *Anochetus* are much more recent, around 40 Mya or less. *A. miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp. belongs to the *risii* group while the species from the Dominican amber belong to the *emarginatus* Fabricius, 1804, *inermis* André, 1889, *cato* Forel, 1901, and *alitissquamis* Mayr, 1887 groups (see De Andrade 1994). Larabee et al. (2016) estimated the *risii* group to have emerged during the Lower Miocene, while the *cato* group would have appeared at the Upper Miocene. The *emarginatus* group would have emerged during the Oligocene. Thus the current discovery of *A. miosumatrensis* Ngo-Muller, Garrouste & Nel, n. sp. and its affinities with the *risii* group supports a Miocene rather than an older age for this Sumatra amber, in accordance with its geological dating.
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No potential conflict of interest was reported by the authors.

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