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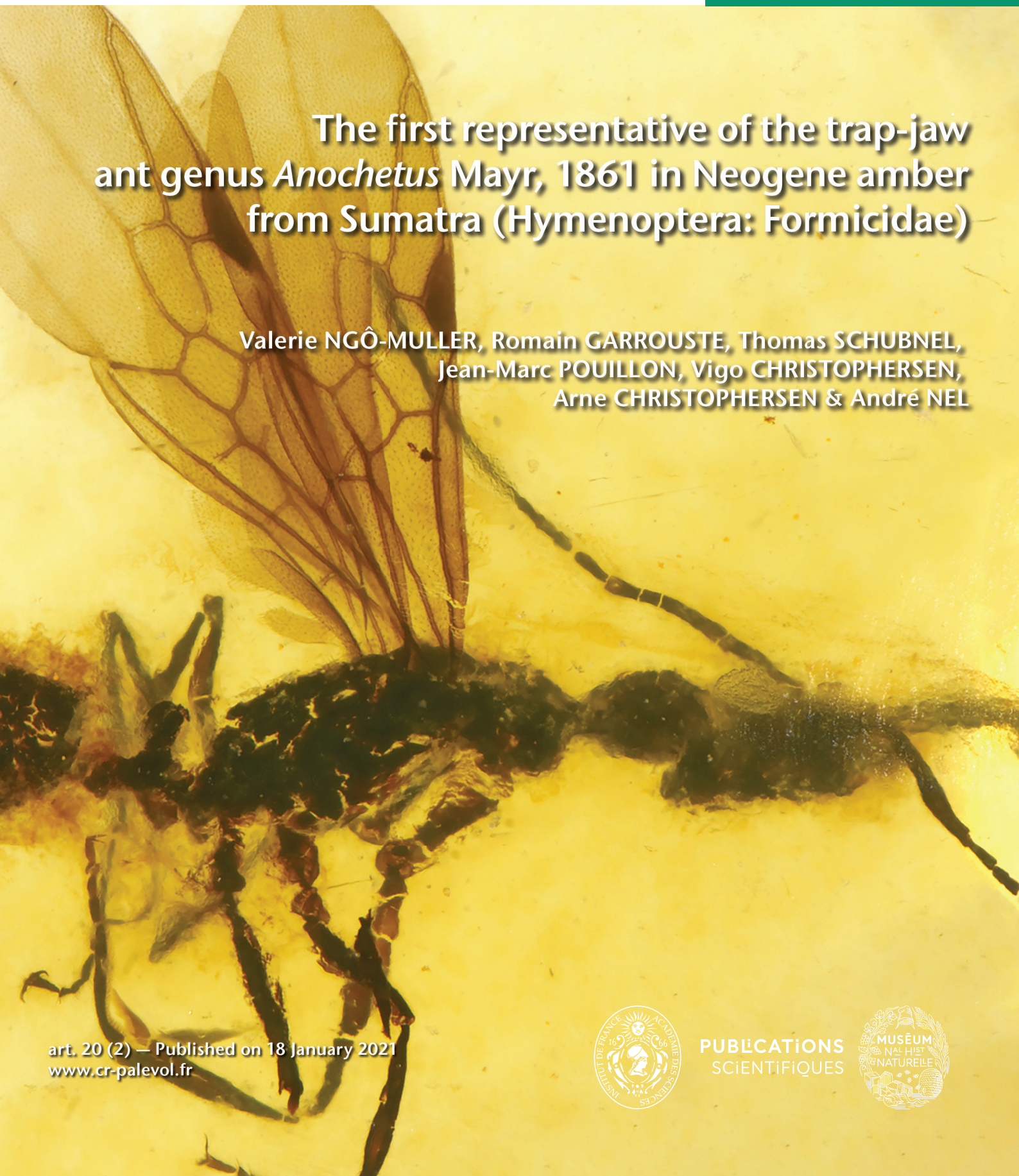

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ABSTRACT
The ponerine ant *Anochetus miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp. is described from a fossil alate female preserved in amber of Sumatra which is reputedly of Miocene age. On the basis of the general morphology, the fossil could be attributed to the extant Sumatran species group *risii* Brown, 1978. By comparing with the living environment of the extant species, this ant probably lived in a warm humid forest where it was trapped in dipterocarpacean resin during nuptial flight. Until now, the known Cenozoic distribution of the genus *Anochetus* was restricted to the Neotropical region. Thus *A. miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp. brings the first record of the genus from Indomalaya biogeographic region.

KEY WORDS
Insecta,
Hymenoptera,
Formicidae,
Ponerinae,
new species,
Sumatran amber.

RÉSUMÉ
La première fourmi du genre Anochetus *Mayr, 1861 de l'ambre néogène de Sumatra (Hymenoptera: Formicidae).*
La fourmi ponérine *Anochetus miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp. est décrite à partir d'une femelle fossile ailée, conservée dans l'ambre de Sumatra, réputée d'âge Miocène. Sur la base de la morphologie, le fossile pourrait être attribué à l'espèce actuelle du groupe *risii* Brown, 1978 de Sumatra. Par comparaison avec l'environnement de vie de l'espèce actuelle, cette fourmi a probablement vécu dans une forêt chaude et humide, où elle a été piégée dans une résine diptérocarpacéenne pendant le vol nuptial. Jusqu'à présent, la distribution cénozoïque connue était restreinte à la zone néotropicale. Ainsi, *A. miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp. fournit le premier enregistrement du genre dans la zone indo-malaisienne.

MOTS CLÉS
Insectes,
Hymenoptera,
Formicidae,
Ponerinae,
espèce nouvelle,
ambre de Sumatra.

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 Turonian (–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 Madagascan 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).

ABBREVIATIONS

Morphological terminology

CI	cephalic index;
FWL	maximum length of forewing;
HH	head height;
HL	head length;
HW	head width;
MdI	mandibular index;
MdL	mandible length;
PI	pronotal index;
PeH	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 PONERINI Lepeletier de Saint-Fargeau, 1835
Genus *Anochetus* Mayr, 1861

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

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ETYMOLOGY. — Named after the Miocene period and the Sumatra Island.

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

LOCUS TYPICUS. — Sinamar, Dharmasraya Regency, West Sumatra, South Sumatra Basin, Miocene.

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.

DESCRIPTION

Measurements and indices

HL 1.25 mm; HW 0.7 mm; HH 0.4 mm; SL 0.8 mm; MdL 1.25 mm; PrH 0.4 mm; FWL 2.7 mm; PeL 0.4 mm; PeH 0.47 mm; WL 1.1 mm; TL 5.0 mm; CI 56; PI 100; MdI 100; SI 114.

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 posterolateral 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; petiole 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;

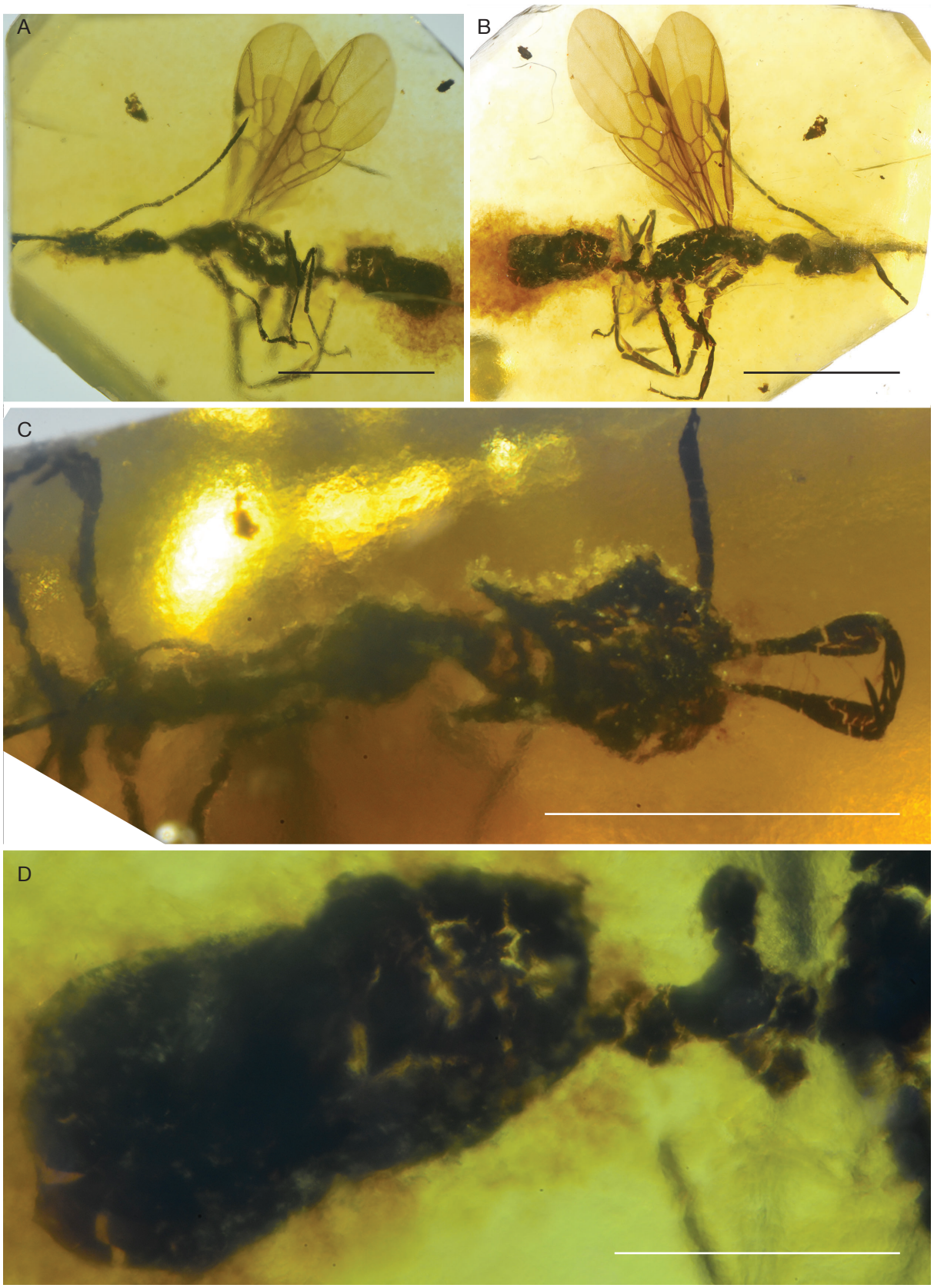

FIG. 1. — *Anochetus miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp., holotype JMP2362: **A**, habitus in left lateral view; **B**, habitus in right lateral view; **C**, head and mesosoma in ventral view; metasoma in lateral view. Scale bars: A, B, 2 mm; C, 1 mm; D, 0.5 mm.

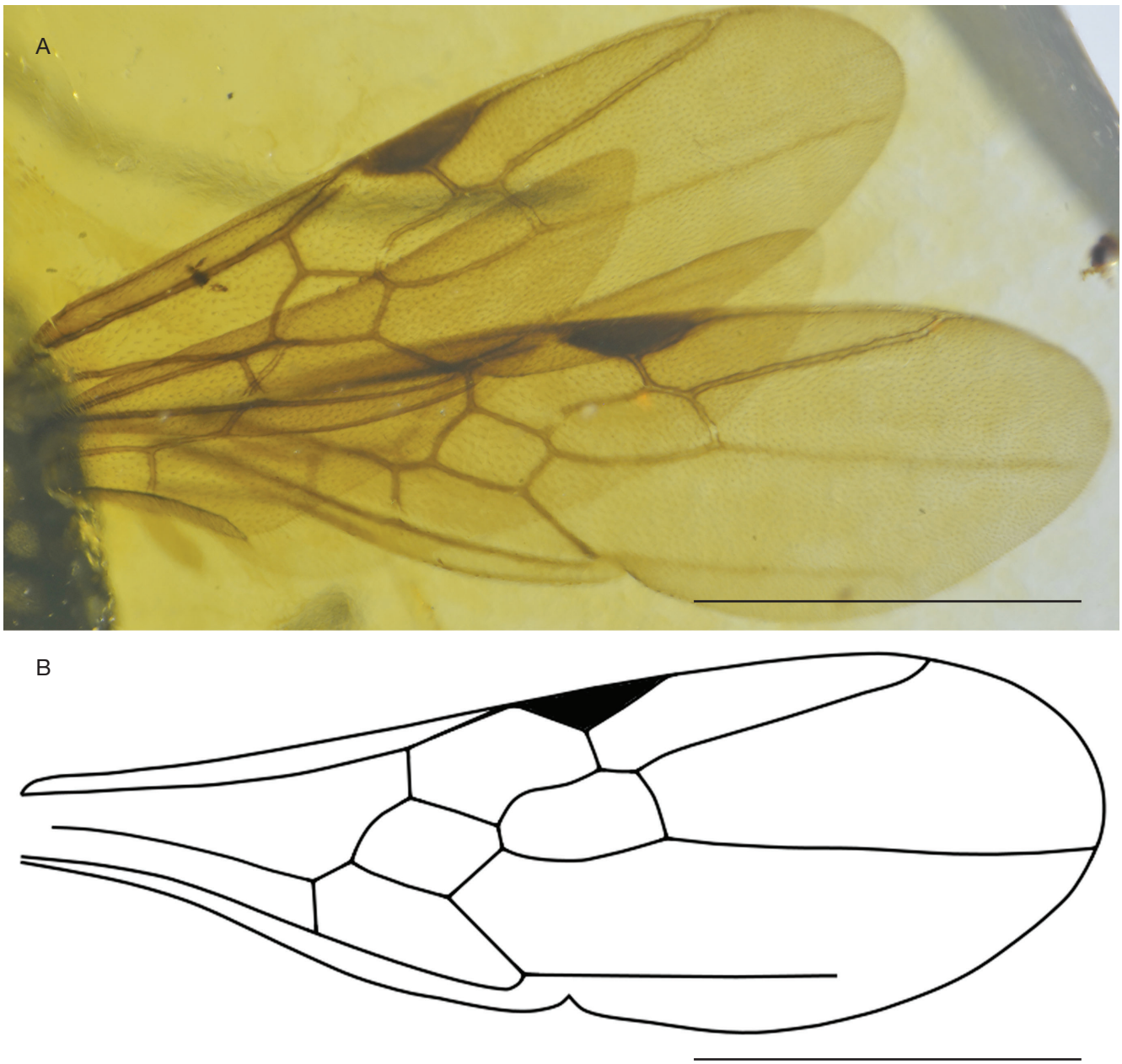

Fig. 2. — *Anochetus miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp., holotype JMP2362: **A**, fore wings; **B**, forewing reconstruction. Scale bars: 1 mm.

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

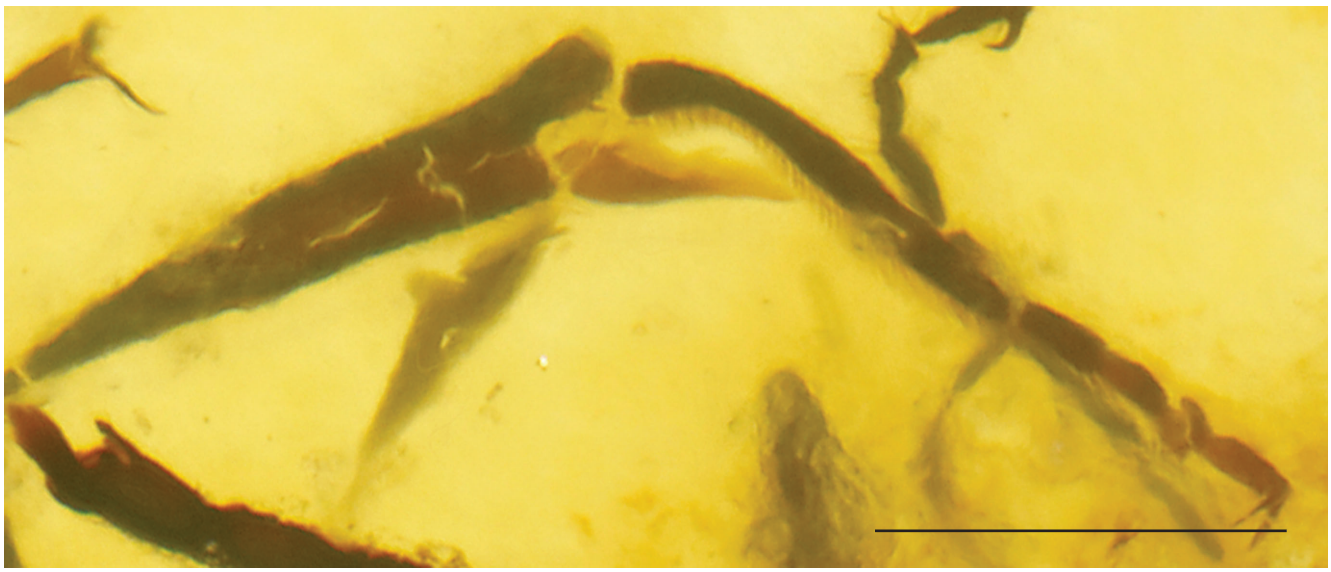

FIG. 3. — *Anochetus miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp., holotype JMP2362. Fore tibia and tarsus. Scale bar: 0.5 mm.

(1978). 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* Ngô-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* Ngô-Muller, Garrouste & Nel, n. sp.); preapical angle usually well marked; mesonotal disc with a blunt anterior rim, or none (not visible in *A. miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp.); petiolar node pointed or narrowly rounded at apex (narrowly rounded in *A. miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp.). It is reasonable to attribute *A. miosumatrensis* Ngô-Muller, Garrouste & Nel, n. sp. to this group of species, which otherwise comprises the species *risii*, *tua*, *agilis* Emery, 1901, *brevis* 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 Ngô-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* Ngô-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* Ngô-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* Ngô-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* Ngô-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* Ngô-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* Ngô-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 *altisquamis* 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* Ngô-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.

REFERENCES

Bąk M., Natkaniec-Nowak L., Drzewicz P., Czapla D., Ivanina A. V. & Bogdasarov M. A. 2016. — *Ambrosiella*-like fungi in fossil resin from Jambi Province in Sumatra Island - possible phoretic organisms interacted with invaded insects. *17th Czech-Slovak-Polish Palaeontological Conference*, Kraków: 1.

Barden P. 2017. — Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. *Myrmecological News* 24: 1-30 (corrected version). https://doi.org/10.25849/myrmecol.news_024:001

Baroni-Urbani C. 1980. — *Anochetus corayi* n. sp., the first fossil Odontomachini ant. *Stuttgarter Beiträge zur Naturkunde* (B) 55: 1-6.

Belkin H. E. & Tewalt S. J. 2007. — Geochemistry of Selected Coal Samples from Sumatra, Kalimantan, Sulawesi, and Papua, Indonesia. United States Department of the Interior, Geological Survey, *Open-File Report* 2007-1202: 1-34. https://pubs.usgs.gov/of/2007/1202/

Borowiec M. L., Rabeling C., Brady S. G., Fisher B. L., Schultz T. R. & Ward P. S. 2019. — Compositional heterogeneity and outgroup choice influence the internal phylogeny of the ants. *Molecular Phylogenetics and Evolution* 134: 111-121. https://doi.org/10.1016/j.ympev.2019.01.024

Brackman W., Spaargaren K., Van Dongen J. P. C. M., Couperus P. A. & Bakker F. 1984. — Origin and structure of the fossil resin from an Indonesian Miocene coal. *Geochimica et Cosmochimica Acta* 48: 2483-2487. https://doi.org/10.1016/0016-7037(84)90299-0

Brown W. L. Jr. 1976. — Contributions towards a reclassification of the Formicidae. 6. Ponerinae tribe Ponerini subtrib. Odontomachini. Section A. Introduction, Subtribal characters. Genus *Odontomachus*. *Studia Entomologica* 19: 67-171. https://doi.org/10.5281/zenodo.27000

Brown W. L. Jr. 1978. — Contributions towards a reclassification of the Formicidae. 6. Ponerinae tribe Ponerini subtrib. Odontomachini. Section B. Genus *Anochetus* and bibliography. *Studia Entomologica* 20: 549-638. https://doi.org/10.5281/zenodo.27003

Chen Z., Yang Z. & Zhou S. 2019. — Review of the ant genus *Anochetus* Mayr 1861 (Hymenoptera: Formicidae) from China, with revival of the valid status of *Anochetus gracilis*. *Journal of Hymenoptera Research* 68: 49-74. https://doi.org/10.3897/jhr.68.30784

De Andrade M. L. 1994. — Fossil Odontomachini ants from the Dominican Republic (amber collection Stuttgart: Hymenoptera, Formicidae. 7. Odontomachiti). *Stuttgarter Beiträge zur Naturkunde* (B) 199: 1-28. https://doi.org/10.5281/zenodo.26365

De Smet M. E. M. & Barber A. J. 2005. — Chapter 7. Tertiary stratigraphy, *in* Barber A. J., Crow M. J. & Milsom J. S. (eds). Sumatra: geology, resources and tectonic evolution. *Memoirs of the Geological Society London* 31: 86-97. https://doi.org/10.1144/GSL.MEM.2005.031.01.07

Dlussky G. M., Brothers D. J. & Rasnitsyn A. P. 2004. — The first Late Cretaceous ants (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the Myrmicinae. *Insect Systematics & Evolution* 35: 1-13. https://antcat.org/references/131125

Durham J. W. 1956. — Insect bearing amber in Indonesia and the Philippine Islands. *The Pan-Pacific Entomologist* 32: 51-53. https://www.biodiversitylibrary.org/page/56382810

Kosmowska-Ceranowicz B., Sachanbiński M. & Łydżba-Kopczyńska B. 2017. — Analytical characterization of "Indonesian amber" deposits: evidence of formation from volcanic activity. *Baltica* 30: 55-60. https://doi.org/10.5200/baltica.2017.30.06

Lambert J. B., Shawl C. E., Johnson S. C. & Poinar G. O. Jr. 1999. — Fossil resin from Asia. *Ancient Biomolecules* 3: 29-35.

Lambert J. B., Levy A. J., Santiago-Blay J. & Wu Y. 2013. — Nuclear Magnetic Resonance characterization of Indonesian amber. *Life: The Excitement of Biology* 1: 136-155. https://doi.org/10.9784/LEB1(3)Lambert.02

Langenheim J. H. & Beck C. W. 1965. — Infrared spectra as a means of determining botanical sources of amber. *Science* 149: 52-55. https://doi.org/10.1126/science.149.3679.52

Larabee F. & Suarez A. 2014. — The evolution and functional morphology of trap-jaw ants (Hymenoptera: Formicidae). *Myrmecological News* 20: 25-36.

Larabee F. J., Fisher B. L., Schmidt C. A., Matos-Maraví P., Milan Janda M. & Suarez A. V. 2016. — Molecular phylogenetics and diversification of trap-jaw ants in the genera *Anochetus* and *Odontomachus* (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution* 103: 143-154. https://doi.org/10.1016/j.ympev.2016.07.024

MacKay W. P. 1991. — *Anochetus brevidentatus*, new species, a second fossil Odontomachiti ant (Hymenoptera). *Journal of the New York Entomological Society* 99: 138-140. https://doi.org/10.5281/zenodo.25883

Naglik B., Kosmowska-Ceranowicz B., Natkaniec-Nowak L., Drzewicz P., Dumanska-Słowik M., Matusik J. M., Milovsky R., Stach P. & Szyszka A. 2018. — Fossilization history of fossil resin from Jambi Province (Sumatra, Indonesia) based on physico-chemical studies. *Minerals* 8: 1-14. https://doi.org/10.3390/min8030095

Narudeesombat N., Ounorn P., Bupparaenoo P., Arne Christopherse A., Pisutha-Arnond V. & Sutthirat C. 2014. — Update on the characteristics of amber from Indonesia. The 4th International Gem and Jewelry Conference: 271-276. https://hal.sorbonne-universite.fr/hal-02374681/document

Nuril Aida I. N. & Idris A. B. 2011. — *Anochetus maryatiae*, new species of Ponerinae (Hymenoptera: Formicidae). *Sains Malaysiana* 40: 301-304.

Perrichot V., Wang Bo & Engel M. S. 2016. — Extreme morphogenesis and ecological specialization among Cretaceous basal ants. *Current Biology* 26: 1468-1472. https://doi.org/10.1016/j.cub.2016.03.075

Pyle R. L. & Michel E. 2008. — ZooBank: Developing a nomenclatural tool for unifying 250 years of biological information. *Zootaxa* 1950: 39-50. https://doi.org/10.11646/zootaxa.1950.1.6

Vankerkhoven F., Henderickx H. & Dekoninck W. 2010. — *Anochetus madagascarensis* Forel 1887 found in Madagascan copal (Hymenoptera: Formicidae). *Bulletin de la Société Royale Belge d'Entomologie* 146: 216-219.

Zettel H. 2012. — New trap-jaw ant species of *Anochetus* MAYR 1861 (Hymenoptera: Formicidae) from the Philippine Islands, a key and notes on other species. *Myrmecological News* 16: 157-167.

Zheng D., Chang S.-C., Perrichot V., Dutta S., Rudra A., Mu L., Kelly R. S., Li S., Zhang Q., Zhang Q., Wong J., Wang J., Wang H., Fang Y., Zhang H. & Wang B. 2018. — A Late Cretaceous amber biota from central Myanmar. *Nature Communications* 9 (3170): 1-6. https://doi.org/10.1038/s41467-018-05650-2

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