2009

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Michael S. Engel

Jaime Ortega-Blanco

Daniel J. Bennett
Stephen F Austin State University, bennettdj@sfasu.edu

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Author(s): Michael S. Engel, Jaime Ortega-Blanco, and Daniel J. Bennett
Source: Transactions of the Kansas Academy of Science, 112(1/2):1-6.
Published By: Kansas Academy of Science
DOI: http://dx.doi.org/10.1660/062.112.0201
URL: http://www.bioone.org/doi/full/10.1660/062.112.0201

TRANSACTIONS OF THE KANSAS ACADEMY OF SCIENCE
Vol. 112, no. 1/2
p. 1-6 (2009)

A remarkable tiphiiform wasp in mid-Cretaceous amber from Myanmar (Hymenoptera: Tiphiidae)

MICHAEL S. ENGEL[1], JAIME ORTEGA-BLANCO[2], AND DANIEL J. BENNETT[1]

1. Division of Entomology (Paleoentomology), Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive, Suite 140, University of Kansas, Lawrence, Kansas 66049-2811 - msengel@ku.edu; danben@ku.edu

2. Department d'Estratigrafia, Paleontologia i Geociències Marines, Facultat de Geologia, Universitat de Barcelona, 08028 Barcelona, Spain (geoortega@yahoo.es)

The first tiphiid wasp (Aculeata: Euaculeata: Vespoidea: Tiphiiformes) in Cretaceous amber is described and figured. *Thanatotiphia nyx*, new genus and species, is represented by a male entombed in mid-Cretaceous (latest Albian) amber from Myanmar. *Thanatotiphia* possesses remarkable apomorphies in wing venation, lacks key traits of modern subfamilies, and is thus classified in a new subfamily, Thanatotiphiinae. The fossil is further shown to be nested well within the family, indicating that major lineages of Tiphiidae diverged by the mid-Cretaceous. The new taxon is compared with modern tiphiid subfamilies and the sparse fossil history of the family briefly overviewed.

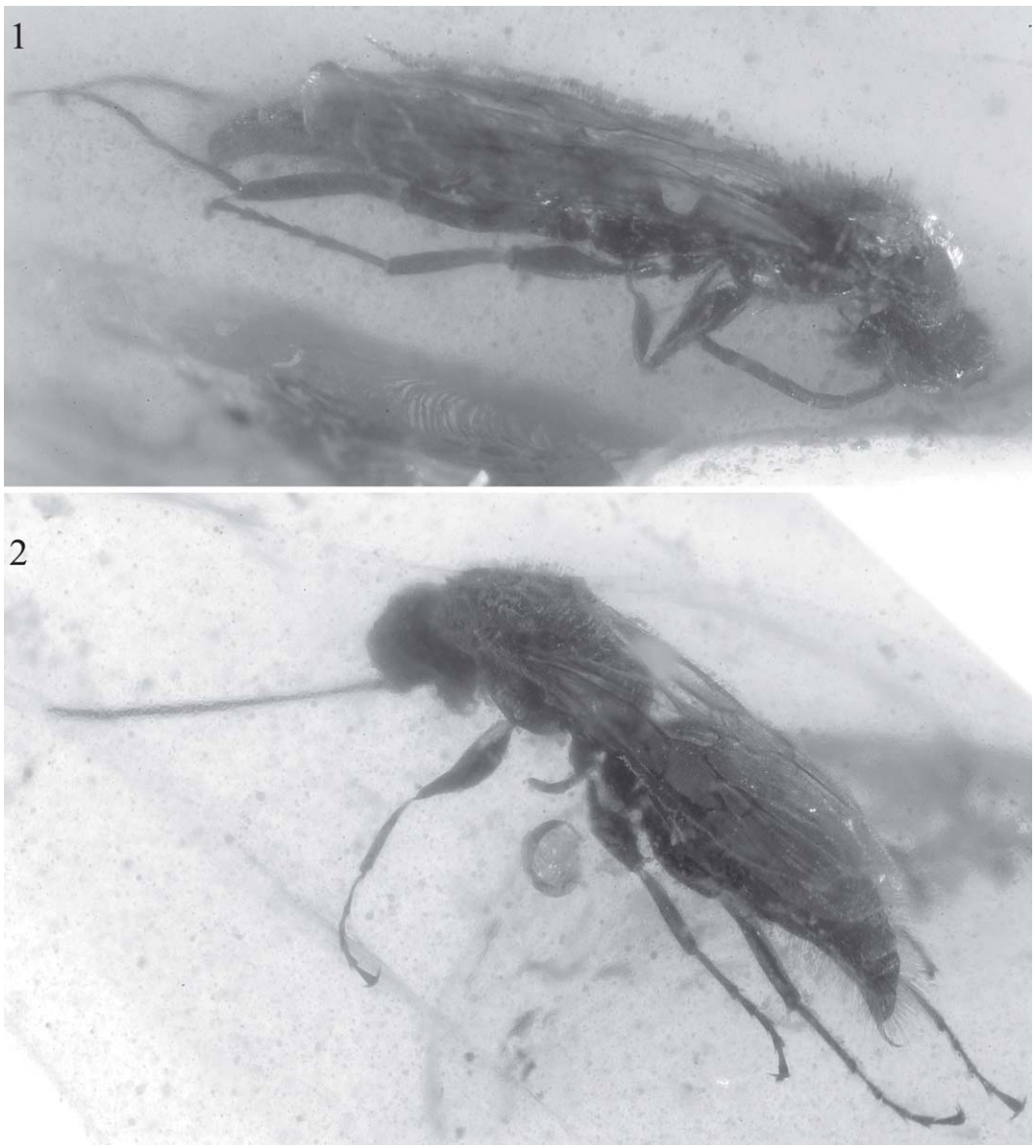
Keywords: Tiphiiformes, paleontology, Mesozoic, amber, Vespoidea, Aculeata, Albian.

INTRODUCTION

The vespoid wasp family Tiphiidae comprises approximately 2000 species of cosmopolitan distribution. Species range in size from 3–25 mm and are presently segregated into seven relatively disparate subfamilies (Kimsey, 1991). While most studies have confirmed tiphiid monophyly (e.g., Brothers and Carpenter, 1993; Brothers, 1999), recent molecular studies have suggested the group to be polyphyletic (Pilgrim *et al*., 2008). However, given that the same molecular analyses failed to recover a monophyletic Vespoidea or other well established groupings within the superfamily, these results should be taken with caution until substantiated. Where known, tiphiids are ectoparasitoids on the larvae of ground-dwelling Coleoptera such as Scarabaeidae and Carabidae (Cicindelinae), and perhaps also some Curculionidae. The only known deviation from this biology is the southern Australian subfamily Diamminae which are ectoparasitoids of mole crickets.

The family is putatively of significant antiquity as evidenced by Anthoboscinae in Early Cretaceous (Aptian) deposits from Brazil. However, further Mesozoic evidence of the family has hitherto been lacking and Tertiary records are confined to compressions with little or no relief, thereby providing little insight into their phylogenetic placement. Although Brischke (1886) recorded in Baltic amber a specimen as "*Tiphia* (?)", no material assignable to Tiphiidae has subsequently surfaced and the collection (Menge Collection) in which this specimen was deposited is apparently lost (Heie, 1967).

Herein we describe a new fossil tiphiid, the second from the Mesozoic and the first in Cretaceous amber. The specimen is a well preserved male in mid-Cretaceous amber from Myanmar (Figs. 1–2). The age and fauna of Burmese amber has been overviewed by Zherikhin and Ross (2000), Grimaldi *et al*. (2002), and Cruickshank and Ko (2003).



Figs. 1–2. Photomicrographs of holotype male of *Thanatotiphia nyx*, new genus and species (AMNH Bu-1573). 1. Right lateral, dorsal oblique view of holotype. 2. Left dorsal oblique view of holotype.

Systematic Paleontology

Family Tiphiidae Leach
Thanatotiphiinae, new subfamily

Type genus - *Thanatotiphia*, new genus.

Diagnosis – Male. Head apparently with frontal lobes dorsally positioned over toruli; toruli positioned low on face; clypeus short; ocelli not enlarged; compound eye inner margin not emarginate. Mesosoma with pronotum not shortened, with both dorsal, horizontal and anterior, vertical sides; mesosternal lamellae,

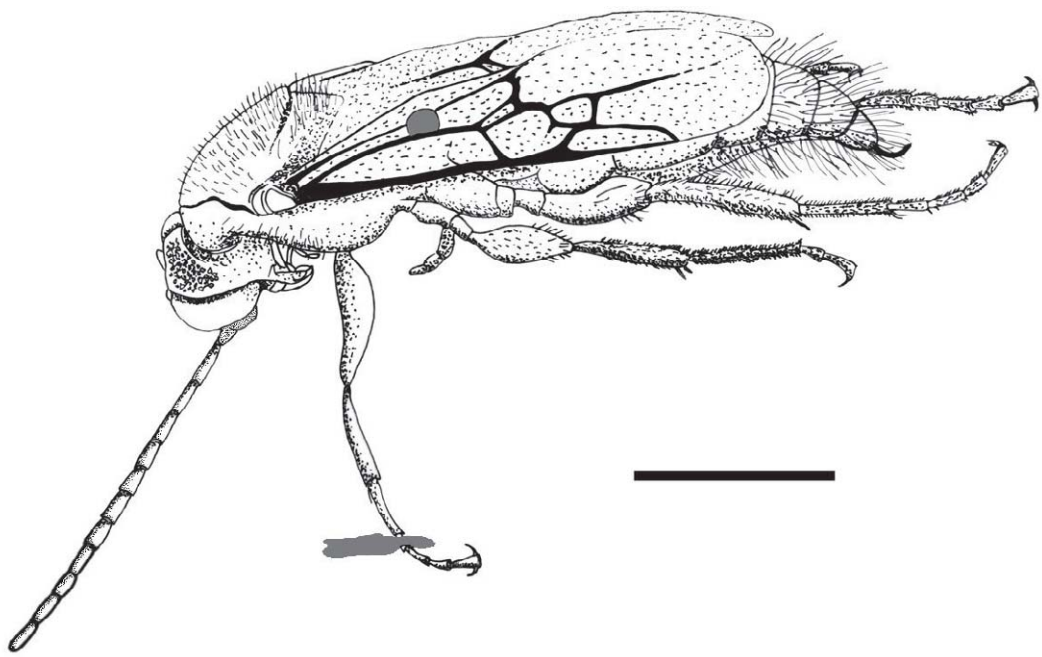


Fig. 3. Habitus of holotype male of *Thanatotiphia nyx*, new genus and species (AMNH Bu-1573). Scale bar = 1 mm.

metasternal platform, and hind coxal cavities hidden by fractures. Forewing (Fig. 4) with tegula short, semicircular, not covering humeral and median plates of forewing base, not extending beyond transscutal sulcus; venation rather reduced, with seven closed cells in total; last segment of Rs oblique upwards closing marginal cell well before forewing apex; two closed submarginal cells, the first enlarged; discoidal cell reduced, narrowly rectangular; second abscissa of Rs (after Rs+M divergence) sinuate, with sclerotized, medial spur midway (remnant of 1r-rs) extending into apical border of first submarginal cell; 2rs-m absent; 2m-cu absent; M not extending much past 1rs-m; Cu not extending much past 1cu-a; 1m-cu exceedingly short, parallel with dramatically shortened basal vein. Legs slender and long; mesotibia with two short spurs; inner metatibial spur straight (not sinuate or modified). Metasoma with sixth sternum not enlarged relative to fifth, exposing basal part of seventh metasomal sternum and hypopygial hook, seventh metasomal sternum simple, not bilobed; eighth sternum modified as a single, strong, acute, upcurved hook (Figs. 2–3), hook not flattened or sculptured and without lateral teeth; apparently lacking cerci.

Thanatotiphia, new genus

Type species - *Thanatotiphia nyx*, new species.

Diagnosis – As for the subfamily (*vide supra*).

Etymology – The new genus-group name is a combination of *Thanatos* [Greek, Θανατος, god of non-violent death, son of the Protogenoi (*i.e.*, the elemental gods) Erebos (darkness) and Nyx (night)] and *Tiphia*, type genus of the family. The name is feminine.

Thanatotiphia nyx, new species
(Figs. 1–4)

Diagnosis – As for the genus (*vide supra*).

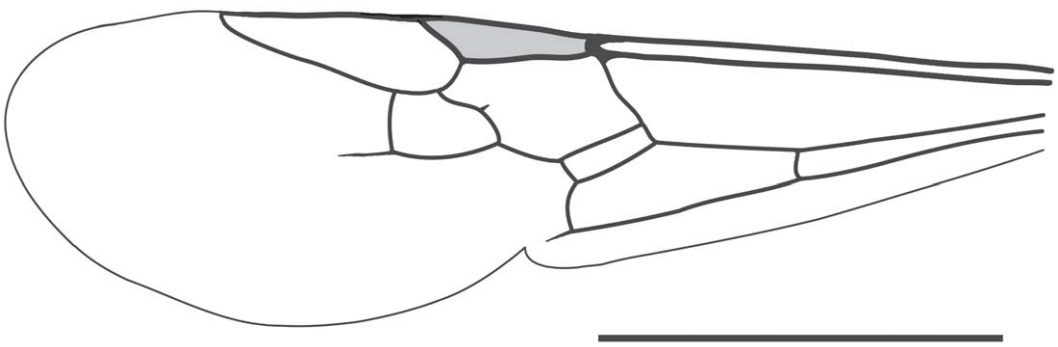


Fig. 4. Forewing venation of *Thanatotiphia nyx*, new genus and species (AMNH Bu-1573). Scale bar = 1 mm.

Description – Male. Body length 4.16 mm; forewing length 2.5 mm. Body relatively slender (Figs. 1–2), integument apparently dark brown; compound eyes bulging, bare; malar space crushed; mandibles with apparently only one long, acute tooth; maxillary palpus with 4 segments visible; labial palpus short, three palpomeres visible, with very short and thin setae; occipital area reticulate, somewhat flattened. Antennae nearly as long as mesosoma + metasoma, 13-segmented; flagellomeres cylindrical, longer than wide, progressively decreasing in length except apical segment longer and rounded. Mesosoma moderately densely setose, setae relatively elongate; mesoscutum apparently with a faint notaulus; medial sulcus not evident; scutellum wider than long, sloping vertically to metanotum. Forewing with very long and narrow costal cell; pterostigma parallel sided; 2r-rs arising from apical two-thirds of pterostigma. Legs flattened laterally with femora inflated medially; mid and hind legs densely covered by short setae; basitarsus as long as tarsomeres 2–4 combined; pretarsal ungues (claws) with minute medial tooth. Metasoma moderately setose proximally, with at least four posterior metasomal segments with abundant, erect, long, and fine setae (Fig. 2).

Holotype – Bu-1573 (Figs. 1–2); Cretaceous (Albian) amber; Myanmar, Kachin, Tanai Village (on Ledo Road, 105 km NW Myitkyna); deposited in the Amber Fossil Collection, Division of Invertebrate Zoology, American Museum of Natural History, New York.

Etymology – The specific epithet is the name of the Protogenos Nyx (Greek, Νυξ), goddess of night.

Discussion

Thanatotiphia's ventrally curved, hook-like sternum VIII readily identifies it as a tiphiid and further reveals its nested position within the family outside of Anthoboscinae and Diamminae, basal subfamilies which lack this feature (Kimsey, 1991). Erection of a new subfamily to receive the fossil is warranted by its exclusion from the remaining tiphiid subfamilies as suggested by its lack of the following synapomorphies: enlarged tegula (Tiphiinae); enlarged ocelli and emarginate eyes (Brachycistidinae); a modified metatibial spur (Methochinae); lobed, sculptured sternum VIII (all but one genus of Thynninae); and emarginate eyes and bilobed sternum VII (Myzininae). Furthermore, the shortened forewing venation, much reduced discoidal cell, and loss of 2m-cu are notable derived features. The fossil may represent a sister taxon to a clade of multiple tiphiid subfamilies but its exact placement is unclear. Kimsey (1991) found a clade consisting of Tiphiinae + Brachycistidinae supported in part by the loss

Table 1. Described fossil Tiphiidae.

Taxon	Locality	Age	References
Architiphia rasnitsyni Darling	Crato Formation, Brazil	Cretaceous (Aptian)	Darling & Sharkey, 1990
Thanatotiphia nyx **n.gen., n.sp.**	Burmese amber	Cretaceous (Albian)	herein
Geotiphia foxiana Cockerell	Florissant shale, Colorado	Eocene (Priabonian)	Cockerell, 1906; Rasnitsyn, 1986
Geotiphia halictina Cockerell	Florissant shale, Colorado	Eocene (Priabonian)	Cockerell, 1910; Rasnitsyn, 1986
Geotiphia pachysoma Cockerell	Florissant shale, Colorado	Eocene (Priabonian)	Cockerell, 1927; Rasnitsyn, 1986
Geotiphia sternbergi Cockerell	Florissant shale, Colorado	Eocene (Priabonian)	Cockerell, 1910; Rasnitsyn, 1986
Lithotiphia scudderi Cockerell	Florissant shale, Colorado	Eocene (Priabonian)	Cockerell, 1906; Rasnitsyn, 1986
Geotiphia orientalis Rasnitsyn	Sikhote-Alin, Russia	Oligocene	Rasnitsyn, 1986
Brachymethoca gigantea Zhang	Shanwang, China	Miocene	Zhang, 1989
Elis pyrula Zhang	Shanwang, China	Miocene	Zhang, 1989
Tiphia brevala Zhang	Shanwang, China	Miocene	Zhang, 1989
Tiphia dimidiata Zhang *et al.*	Shanwang, China	Miocene	Zhang *et al.*, 1994
Tiphia dolichogaster Zhang	Shanwang, China	Miocene	Zhang, 1989
Tiphia mediovena Zhang	Shanwang, China	Miocene	Zhang, 1989
Tiphia rara Zhang *et al.*	Shanwang, China	Miocene	Zhang *et al.*, 1994
Tiphia shanwangensis (Hong)	Shanwang, China	Miocene	Hong, 1983; Zhang, 1989
Tiphia varia Zhang	Shanwang, China	Miocene	Zhang, 1989

of cerci, which seems to be the condition of the fossil. However, the fossil also possesses frontal lobes over the antennal toruli, which was found in Kimsey's (1991) analysis to support the clade Methochinae + (Thynninae + Myzininae). Clearly a reanalysis of the family incorporating fossils and additional character data is needed.

The fossil record of Tiphiidae is exceptionally sparse and, indeed, so is that generally of the non-formicid Vespoidea. While a moderately diverse sampling of vespoid wasps have been recorded from the Cretaceous (e.g., Grimaldi and Engel, 2005; Bennett and Engel, 2005; Engel and Grimaldi, 2006; Engel, 2008), the group as a whole is poorly sampled from this period. The lineage is more abundant in the Tertiary record, but again largely dominated by ants (Formicidae). Among the Tiphiidae only 16 species have been recorded (Table 1), largely as compression fossils from Tertiary deposits in North America and Asia, although those records from the Miocene of China are dubiously assigned as to genus, subfamily, and in some instances even to family and should be critically reviewed.

Acknowledgements

We are grateful to Z. Liu and an anonymous reviewer for comments on the manuscript.

Support for this work was provided by National Science Foundation grants EF-0341724 [HymAToL: Hymenoptera Tree of Life] and DEB-0542909 (both to M.S. Engel). This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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