Journal *of* Melittology
Bee Biology, Ecology, Evolution, & Systematics *The latest buzz in bee biology*
No. 14, pp. 1–10 29 July 2013

A minute stingless bee in Eocene Fushan amber from northeastern China (Hymenoptera: Apidae)

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Abstract. The first fossil bee in Eocene amber of the Fushan Coalfield, Liaoning, China is described and figured. ***Exebotrigona velteni*** Engel & Michener, new genus and species (Apinae: Meliponini) is based on a stingless bee worker and is remarkably similar in several apomorphic traits to the species of the New World genus *Trigonisca* Moure *s.l.* The diversity of fossil and subfossil Meliponini is briefly summarized, as are the characters and possible affinities of *Exebotrigona*.

INTRODUCTION

The stingless bees (Meliponini) are frequently encountered in the tropics and are particularly abundant and diverse in the Western Hemisphere. Meliponines are highly eusocial, living in often large, perennial colonies and in nests constructed of wax, secreted from dorsal metasomal glands, and resin or propolis that is collected from vegetation (Michener, 2013). Nests are frequently found in tree hollows or among branches, although sometimes they are located in the ground, limestone cliffs, or in the walls of building (Wille & Michener, 1973; Wille, 1983; Roubik, 2006; Michener, 2000, 2007, 2013; Bänziger *et al*., 2011; Engel & Michener, 2013). The most common fossil bee is a meliponine. *Proplebeia dominicana* (Wille & Chandler) is frequently found in pieces of Early Miocene Dominican amber, with thousands of individuals recovered over the last 50 years (Michener, 1982; Camargo *et al*., 2000; Engel & Michener, 2013). Meliponines are also the most common bees found in copal and most of these, if not all, are of living species. Despite this regular occurrence, most fossil species are known only from a single or small series of individuals and the total diversity known from the fossil record is relatively meager (Engel & Michener, 2013). Hitherto 18 species have been recorded as fossils in amber or subfossils in copal, and 12 of these are extinct (Appendix, including a new species described herein) (Engel & Michener, 2013).

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ISSN 2325-4467

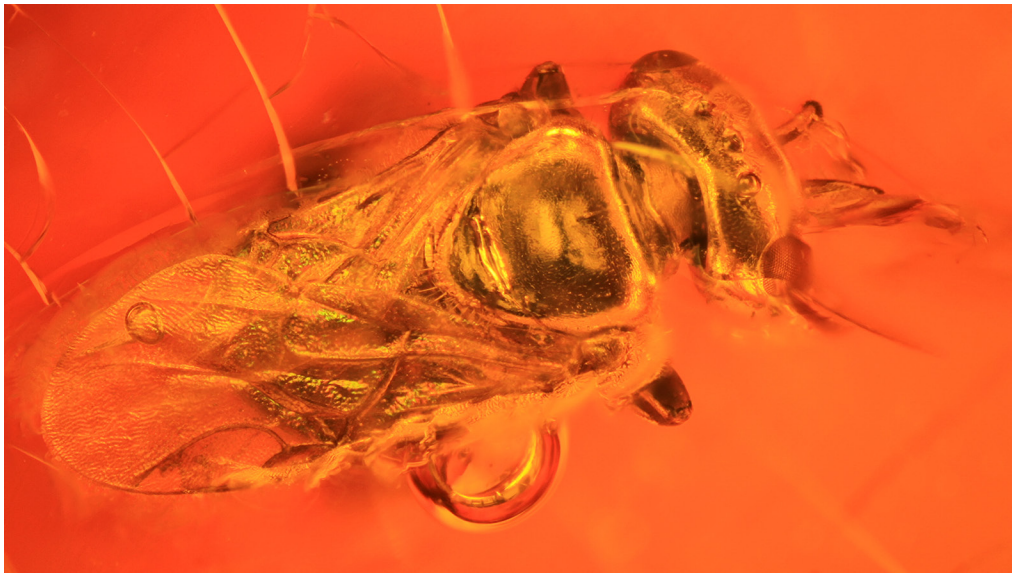


Figure 1. Dorsal photomicrograph of holotype worker of *Exebotrigona velteni*, new genus and species, in Eocene amber from the Fushan Coalfield. Metrics of individual provided in description.

Herein we describe the first fossil stingless bee, and indeed the first fossil bee in general, from the Eocene amber deposits of Liaoning, China (Figs. 1–3). This represents a significant biogeographic and temporal record for fossil Apoidea and we strongly hope that additional specimens and species will be recovered in time.

MATERIAL AND METHODS

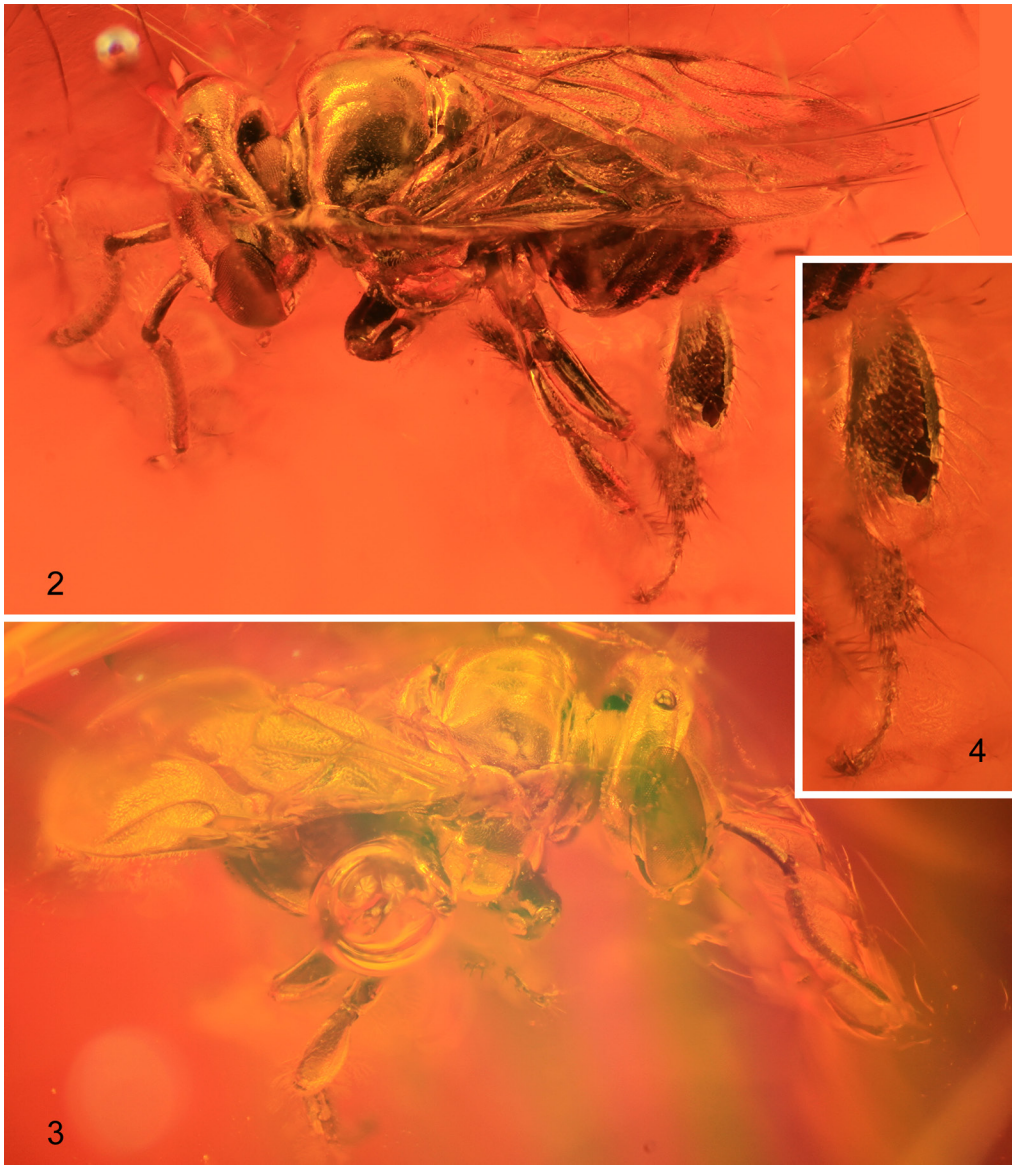
The suprageneric classification followed is that of Engel (2005) and Michener (2007), while the system for genera of Meliponini is based on systems advocated by Moure (1950, 1951, 1961), Rasmussen & Cameron (2007, 2010), Rasmussen (2008), and Michener (1990, 2007). Morphological terminology is adopted from that of Engel (2001) and Michener (2007). Images were prepared using a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscope lens, while for study of fine details an Olympus SZX12 stereomicroscope was used. Information regarding the age, origin, and paleobiota of Fushan amber is summarized by Hong (2002a, 2002b), although considerable caution must be taken when following the identifications provided in these works as many taxa are misplaced even to the level of suborder or superfamily (*e.g.*, see note on cynipoids by Liu *et al.*, 2007).

SYSTEMATIC PALEONTOLOGY

Exebotrigona Engel & Michener, new genus
ZooBank: urn:lsid:zoobank.org:act:FEF5D1E6-D3F7-44D0-B1DD-ADED18B20814

TYPE SPECIES: *Exebotrigona velteni* Engel & Michener, new species.

DIAGNOSIS: Workers minute, forewing length *ca.* 2 mm; integument shining, faintly imbricate to smooth, with minute widely-scattered punctures on head and mesosoma,



Figures 2–4. Photomicrographs of holotype worker of *Exebotrigona velteni*, new genus and species, in Eocene amber from the Fushan Coalfield. **2.** Left lateral habitus. **3.** Right lateral habitus. **4.** Detail of inner surface of metatibia and metatarsus (unclear areas are obscured by internal fractures from this particular view). Metrics of individual provided in description.

apparently without maculations. Head as broad as mesosoma; vertex weakly procurved posterior to ocelli, not produced or ridged; ocelloccipital distance slightly more than one median ocellar diameter; interocellar distance about three times median ocellar diameter, slightly greater than ocellocular distance; scape shorter than alveolocellar distance, not reaching median ocellus (as in *Trigonisca* Moure *s.str.*, not *Dolichotrigona* Moure); ocelli near top of vertex (as in *Trigonisca s.str.*); middle flagellomeres about as long as wide, second and first about as long as wide; distinctly not longer than wide (as in *Trigonisca*, not *Dolichotrigona*). Mesoscutum with notauli faintly evident, not im-

pressed; median line distinctly impressed but not strong; mesoscutellum short, rounded and thick in lateral aspect, slightly overhanging metanotum, shining transverse depression on mesoscuto-mesoscutellar sulcus simple (not extending medioposteriorly into mesoscutellum as V-shaped fovea); propodeum apparently slightly declivitous, basal area apparently short, smooth and shining (not reticulate as in most *Trigonisca*, except smooth in *Leurotrigona* Moure).

Setae on body mostly short and inconspicuous, mesoscutum and disc of mesoscutellum almost bare but posterior margin of mesoscutellum with sparse straight bristles radiating posteriorly, longest ones about two-thirds as long as median length of mesoscutellum (as in *Lisotrigona* Moure).

Forewing extending beyond apex of metasoma, without submarginal crossveins (second abscissa Rs, 1rs-m, 2rs-m), no indication of submarginal cells; pterostigma large, margin in marginal cell slightly convex; marginal cell with base broad, basal angle as measured between pterostigmal vein and r-rs nearly orthogonal; apex of marginal cell acute, open only by one vein width and closed by pigmented membrane or nebulous vein (more extensively open in other genera, except some *Celetrigona* Moure); marginal cell width at pterostigmal apex distinctly greater than distance across submarginal area (as measured from apical abscissa of Rs to M); submarginal angle (as measured between first free abscissa Rs and Rs+M) orthogonal; M terminating without defined bend at position of nebulous 1m-cu, continuing as nebulous vein beyond termination; distal abscissa Cu nebulous [Cu1 and Cu2 *sensu* Engel (2001) nebulous], not defined by tubular and pigmented vein. Hind wing partly visible through forewing, apparently without closed cells.

Metatibia about three times as long as greatest width (an estimate; base of tibia hard to see); outer surface gently concave, glabrous; posterior margin gently convex, not tuberculate (more or less tuberculate in most *Trigonisca s.l.*); distal margin transverse; posterior distal angle distinct, rather sharp, nearly orthogonal; setae along posterior margin dense, elongate, simple (none branched or plumose), and widely spaced (Fig. 4); rastellum apparently represented by slender setae (not a coarse comb as in related genera); inner surface of tibia with broad median zone convex, coarsely punctuate (although partly hidden, almost certainly without finely punctate keirotrichiate area and without smooth bare area); median zone with setae directed posterodistally, probably tapering to pointed apices (but not clearly visible) (not very minute and dense like keirotrichiae of related genera), this zone separated from shining posterior marginal zone by weak slope; marginal zone bare, depressed, shining, medially about one fifth as wide as maximum tibial width but gradually narrower both basally and distally; anterior margin of tibia with distinct narrow, parallel sided, shining, hairless, depressed zone about one sixteenth as wide as tibia; metabasitarsus length about 2x width, about 0.6x as wide as metatibia, inner surface without basal sericeous area, with setae arranged in loosely-defined transverse rows (similar to those of *Trigonisca s.l.* and *Apis* Linnaeus).

ETYMOLOGY: The new genus-group name is a combination of *exebos* (Greek, meaning "past one's youth") and *Trigona*. The gender is feminine.

***Exebotrigona* velteni** Engel & Michener, new species

ZooBank: urn:lsid:zoobank.org:act:A8C24349-5316-4914-9E6C-D1C62016FE84

(Figs. 1–4)

DIAGNOSIS: As for the genus (*vide supra*).

Description: ☿: As for the genus with the following additions: Total body length (as preserved) 2.36 mm. Forewing length 2.08 mm, width 0.76 mm. Head width 1.17 mm; interocellar distance 0.24 mm; ocellocular distance 0.21 mm. Mesoscutal width [measured just anterior to tegulae, *sensu* Brooks & Michener (1988)] 0.78 mm; intertegular distance 0.74 mm. Metatibia apical width 0.25 mm; inner surface with width of median convex zone 0.19 mm, bare anterior marginal zone width 0.06 mm; metabasitarsus width 0.17 mm, length 0.35 mm. Head impossible to see in facial view but the impression is wider than long with short malar areas. Body and legs, including tegulae and tarsi, dark, probably black; wings apparently clear.

♀: Unknown.

♂: Unknown.

Holotype: ☿, Eocene amber; Fushan coalfield, Liaoning, China; deposited in the collection of Jürgen Velten, Idstein, Germany.

Etymology: The specific epithet is a patronym honoring Jürgen Velten for his generosity in permitting us to study this fascinating material from his collections.

Comments: As shown in figure 1, with certain lighting, a pale band of reflection appears on the anterior and lateral margins of the mesoscutum. This is suggestive of integumental color patterns or of bands of pale tomentum of certain other bees. However, careful examination reveals no dense setal bands and probably no pigment pattern forming the marginal 'bands' appearing in figure 1 (*cf.* Figs. 2 and 3). This is merely a matter of reflected light in figure 1.

DISCUSSION

Exebotrigona velteni from the Eocene of China is fascinating in that it exhibits features otherwise considered typical of the Neotropical genus *Trigonisca s.l.* (Moure, 1950, 1951). Both genera have the usual features of minute stingless bees (Michener, 2002) and share the uniquely broad base of the forewing marginal cell, with an angle over 68° and, in many cases, nearly orthogonal as measured between r-rs and the stigmal vein. In addition, as in *Trigonisca*, the width of the marginal cell at the pterostigmal apex is distinctly greater than the distance across the submarginal area from the apical abscissa of Rs to M, and the submarginal angle is orthogonal. The setae on the inner surface of the metabasitarsus are arranged in loose transverse rows, another character typical of *Trigonisca s.l.* (as well as *Apis*). *Exebotrigona* seems to intermingle features among the various subgenera of *Trigonisca s.l.* (*Leurotrigona*, *Celetrigona*, *Dolichotrigona*, and *Trigonisca s.str.*: refer to Description of the genus, *supra*), but lacks some features of all these groups such as the tuberculate posterior margin of the metatibia, perhaps the long propodeum (relatively long dorsal surface in *Trigonisca s.l.*, while this may be relatively short in *Exebotrigona*), and the well-defined rastellum.

From the standpoint of biogeography, one would expect to find *Exebotrigona* more similar to the minute Asiatic genera *Pariotrigona* Moure or *Lisotrigona* than to the New World *Trigonisca*. There is no evidence that this is true although if wing characters were ignored, the similarity to *Trigonisca* would be greatly reduced. A special similarity to *Lisotrigona* is the straight bristles restricted to the posterior margin of the mesoscutellum. In other genera these setae are more curved and less restricted to the marginal part of the mesoscutellum.

Based on an analysis of DNA sequences, Rasmussen & Cameron (2010) recovered *Trigonisca s.l.* at the base of their New World clade of meliponine genera, with an Old World clade comprising as sisters distinct Indomalayan/Australasian and Afrotropi-

cal lineages (with a single Indomalayan/Australasian clade within the Afrotropical group). If the unique form of the wing venation observed in *Trigonisca s.l.* and *Exebotrigona* is apomorphic, then it is possible that the latter falls basal to the *Trigonisca* group, or perhaps even basal to the New World group. Accordingly, *Exebotrigona* may have profound implications for understanding broad-scale biogeographic and dispersal patterns among lineages of Meliponini. Thus, a phylogenetic analysis is needed that includes *Exebotrigona* as well as the other extinct genera of Meliponini. To date, the only attempt to investigate the phylogenetic placement of a stingless bee fossil is that of Engel (2000). Unfortunately, *Exebotrigona* is currently represented by a single worker for which it is not presently possible to obtain complete information. Given the abundance of amber in the Fushan Coalfield, the possibility of obtaining additional material in the future is quite good and researchers on this paleofauna should watch for further specimens of these minute insects.

ACKNOWLEDGEMENTS

We are deeply grateful for the kindness, generosity, and enthusiasm expressed by our friend and colleague, Jürgen Velten. This small contribution would not have been possible without his tireless passion for amber inclusions of all kinds. We are also indebted to two reviewers for their suggested improvements to the manuscript. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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APPENDIX

List of described fossil and subfossil stingless bees (Meliponini); all preserved in amber or copal [modified from Engel (2001), Michez *et al*. (2012), and Engel & Michener (2013)].

CRETACEOUS	
Maastrichtian	
Genus †*Cretotrigona* Engel, 2000	
†*C. prisca* (Michener & Grimaldi, 1988)	New Jersey, USA
PALEOGENE	
Eocene	
Genus †*Kelneriapis* Sakagami, 1978	
†*K. eocenica* (Kelner-Pillault, 1969)	Baltic region
Genus †*Liotrigonopsis* Engel, 2001	
†*L. rozeni* Engel, 2001	Baltic region
Genus †*Exebotrigona* Engel & Michener, n. gen.	
†*E. velteni* Engel & Michener, n. sp.	Liaoning, China
NEOGENE	
Miocene	
Genus *Nogueirapis* Moure, 1953	
†*N. silacea* (Wille, 1959)[1]	Chiapas, Mexico
Genus †*Proplebeia* Michener, 1982	
†*P. abdita* Greco & Engel in Greco *et al*., 2011	Dominican Republic
†*P. dominicana* (Wille & Chandler, 1964)	Dominican Republic
†*P. tantilla* Camargo *et al*., 2000	Dominican Republic
†*P. vetusta* Camargo *et al*., 2000	Dominican Republic
Genus †*Meliponorytes* Tosi, 1896	
†*M. sicula* Tosi, 1896	Sicily
†*M. succini* Tosi, 1896	Sicily
Pleistocene	
Genus *Hypotrigona* Cockerell, 1934	
H. gribodoi (Magretti, 1884) (Engel, 2001)	East African copal
Genus *Liotrigona* Moure, 1961	
†*L. vetula* Moure & Camargo, 1978	East African copal
L. madecassa (Saussure, 1890) (Rasmussen, pers. comm.)	Malagasy copal
Genus *Meliponula* Cockerell, 1934	
M. ferruginea (Lepeletier de Saint Fargeau, 1841)[2] (Zeuner & Manning, 1976)	East African copal
Genus *Tetragonula* Moure, 1961	
T. iridipennis (Smith, 1854)[3] (Cockerell, 1921)	Burmese copal

Appendix. Continued from preceding page.

Genus *Ptilotrigona* Moure, 1951	
P. lurida (Smith, 1854) (Engel, 2001)	Colombian copal
Genus *Trigonisca* Moure, 1950	
T. sp. (Engel, 2001)	Colombian copal

[1] Camargo & Pedro (2007) have placed this species in *Proplebeia*.
[2] Originally recorded as *Meliponula erythra* (Schletterer, 1891), a subjective junior synonym of *M. ferruginea* (Eardley, 2004).
[3] Originally described as *Meliponorytes devictus* Cockerell, 1921 (Sakagami, 1978; Moure & Camargo, 1978).

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The *Journal of Melittology* was established at the University of Kansas through the efforts of Michael S. Engel, Victor H. Gonzalez, Ismael A. Hinojosa-Díaz, and Charles D. Michener in 2013 and each article is published as its own number, with issues appearing online as soon as they are ready. Papers are composed using Microsoft Word® and Adobe InDesign® in Lawrence, Kansas, USA.

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ISSN 2325-4467