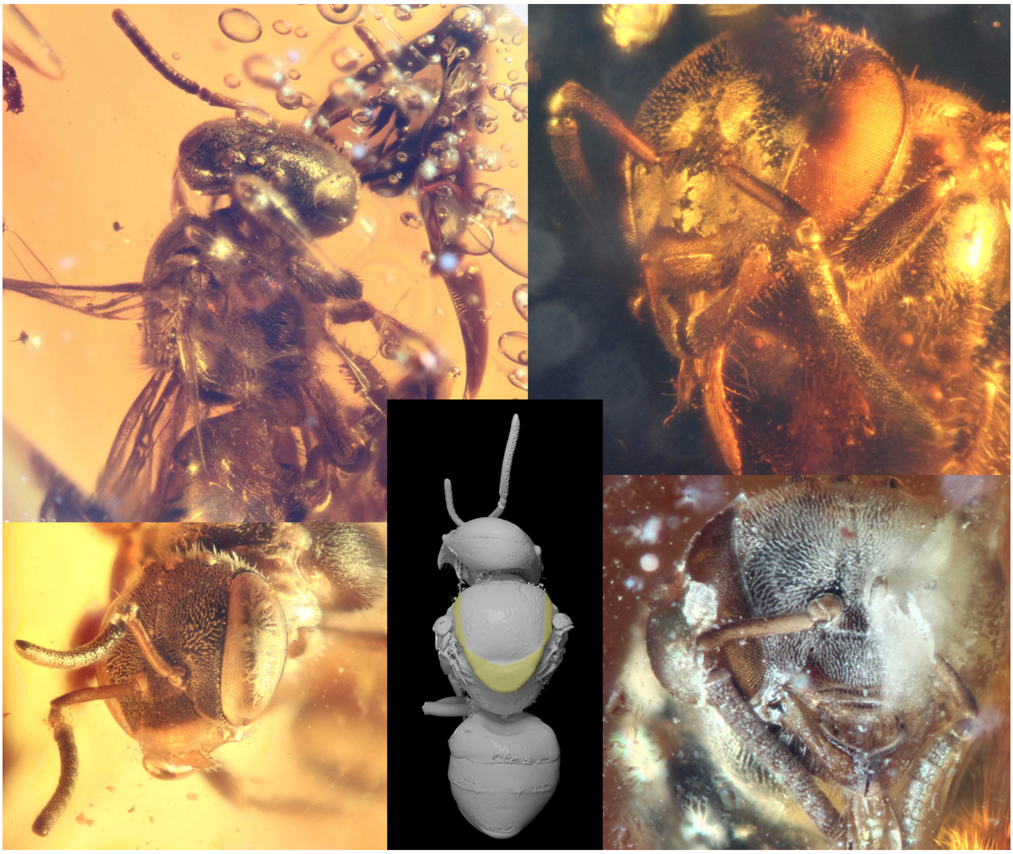
Stingless bees in Miocene amber of southeastern China (Hymenoptera: Apidae)

Michael S. Engel, Hollister W. Herhold,
Steven R. Davis, Bo Wang, & Jennifer C. Thomas



Journal of Melittology

No. 105 ISSN 2325-4467 26 August 2021

On the cover: A collage of photographs and a μCT scan of Miocene Zhanpu amber stingless bees.

Journal *of* Melittology
Bee Biology, Ecology, Evolution, & Systematics *The latest buzz in bee biology*
No. 105, pp. 1–83 26 August 2021

Stingless bees in Miocene amber of southeastern China (Hymenoptera: Apidae)

Michael S. Engel[1,2,3], Hollister W. Herhold[3],
Steven R. Davis[3], Bo Wang[4], & Jennifer C. Thomas[1]

Abstract. Among the many inclusions from the exceptionally rich fossiliferous amber of Zhangpu, China (Middle Miocene: Langhian), stingless bees (Apinae: Meliponini) are particularly common, analogous to the merely slightly older amber sites of Mexico and the Dominican Republic. While there is a large number of workers in Zhangpu amber, only two species are represented. The systematics and morphology of the tribe Meliponini is outlined, including a revision to terms of orientation and direction when discussing surfaces and features of appendages, all in order to better discuss the traits of the fossils as well as place them into a broader context in the global systematics of stingless bees. The two amber species are representative of two Old World genera of Meliponini: *Tetragonula* Moure and *Austroplebeia* Moure. While the former is widespread across southern Asia, Malesia, Papuasia, and Australia, the latter is today known only from New Guinea and Australia. Neither genus occurs in the environs of Zhangpu today. ***Tetragonula* (*Tetragonula*) *florilega*** Engel, new species, is a generally typical species of the subgenus although it intermingles traits otherwise found in two large species groups of non-Australian *Tetragonula s.str*. The species of *Austroplebeia* from Zhangpu is sufficiently distinct to place in a new subgenus, ***Anteplebeina*** Engel. ***Austroplebeia* (*Anteplebeina*) *fujianica*** Engel, new species, shares a long list of character states with *Austroplebeia s.str*., including the presence of yellow maculation on the face, mesoscutum, mesoscutellum, and metepisternum, found only in this clade among Asiatic Meliponini. Nonetheless, the species differs in the length of the malar space and various features of wing venation. Keys are provided to the genera in Zhangpu amber and the subgenera of both genera. The diversity of stingless bees in amber is discussed,

---

[1] Division of Entomology, Natural History Museum, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045-4415, USA (msengel@ku.edu, jct@ku.edu).
[2] Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045, USA.
[3] Division of Invertebrate Zoölogy, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA (mengel@amnh.org, hherhold@amnh.org, sdavis@amnh.org).
[4] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing, China (bowang@nigpas.ac.cn).
doi: http://dx.doi.org/10.17161/jom.i105.15734

ISSN 2325-4467

CONTENTS

as well as the presence of these two fossils in the Middle Miocene of mainland Asia in relation to prior divergence time estimates, phylogenetic relationships, as well as the paleogeography of the region and potential biogeographic hypotheses. The biological association of stingless bees with resins, particularly the collection of dipterocarp resins, is discussed as Zhangpu amber is a Class II resin likely produced by an extinct species of Dipterocarpaceae (Malvales). Also discussed are the ecological preferences of modern *Tetragonula* and *Austroplebeia* relative to the reconstructed paleoenvironment of the Zhangpu amber rainforest. Emendations to the classification of Meliponini are appended, with the following new taxa proposed: ***Atrichotrigona*** Engel, new subgenus of *Axestotrigona* Moure; ***Lispotrigona*** V.H. Gonzalez & Engel, new subgenus of *Nannotrigona* Cockerell; ***Asperplebeia*** Engel, new genus; ***Nanoplebeia*** Engel, new subgenus of *Plebeia* Schwarz; ***Aphaneuropsis*** Engel, ***Koilotrigona*** Engel, ***Necrotrigona*** Engel, ***Dichrotrigona*** Engel, ***Nostotrigona*** Engel, ***Ktinotrofia*** Engel, all new subgenera of *Trigona* Jurine; ***Chapadapis*** Engel, new subgenus of *Schwarziana* Moure. The following higher groups are also established: **Hypotrigonina** Engel, new sutribe; **Heterotrigonitae** Engel, new infratribe; **Trigoniscitae** Engel, new infratribe.

INTRODUCTION

By the very nature of their biology, stingless bees (Apinae: Meliponini) are often among the most frequently encountered Apoidea in amber (Michez *et al.*, 2012; Engel & Michener, 2013a; Barden & Engel, 2021). Stingless bees are highly eusocial, living in often large, perennial colonies and workers frequently collect plant resins and other exudates as part of nest construction and for antimicrobial properties (Wille & Michener, 1973; Wille, 1983; Roubik, 2006; Michener, 2007, 2013; Grüter, 2020). Thus, individuals are sometimes abundant at resin sources, lending themselves to capture and preservation in amber despite their adeptness at manipulating such material (Solórzano Kraemer *et al.*, 2018). In the prolific deposits of the Dominican Republic, stingless bees of one species, *Proplebeia dominicana* (Wille & Chandler), can number into the tens of thousands of workers, representing the greatest magnitude of fossil material for any lineage of bees (Camargo *et al.*, 2000). Indeed, at present the superabundance of known workers from *P. dominicana* exceeds that of all other individuals of fossil bees, regardless of family, combined. In the roughly coeval amber from southern Mexico the same can be found of *P. silacea* (Wille), albeit not with quite the same glut of known specimens, but still overly abundant. In Paleogene or Cretaceous ambers, however, stingless bees are downright rare, with isolated individuals in Baltic and New Jersey ambers (Kelner-Pillault, 1969, 1970; Michener & Grimaldi, 1988; Engel, 2000, 2001a; Engel & Michener, 2013a), although other corbiculate bee lineages, including the closely related Melikertini, can be quite common in Eocene deposits (Engel, 2001a; Engel *et al.*, 2013; Engel & Davis, 2021), including those represented as compression fossils in roughly contemporaneous oil shales (Wappler & Engel, 2003; Wappler *et al.*, 2015). Similarly, the related and also highly eusocial honey bees (Apini) can be abundant in certain Neogene deposits (*e.g.*, Zhang, 1989, 1990; Kotthoff *et al.*, 2011, 2013), although they have not yet been recovered from amber. Despite the large worker force of their colonies, in most deposits where honey bees are found they are relatively few in number (*e.g.*, Engel, 1998, 2006; Engel *et al.*, 2009, 2018). Although bumble bees (Bombini) are also eusocial, albeit of a less organized behavioral grade (Michener, 1974, 2007; Engel & Rasmussen, 2021), their crown-group is more diverse in temperate habitats and accordingly are unknown from amber, which forms in more tropical environments, and *Bombus* Latreille are in fact comparatively uncommon as compressions (Rasnitsyn

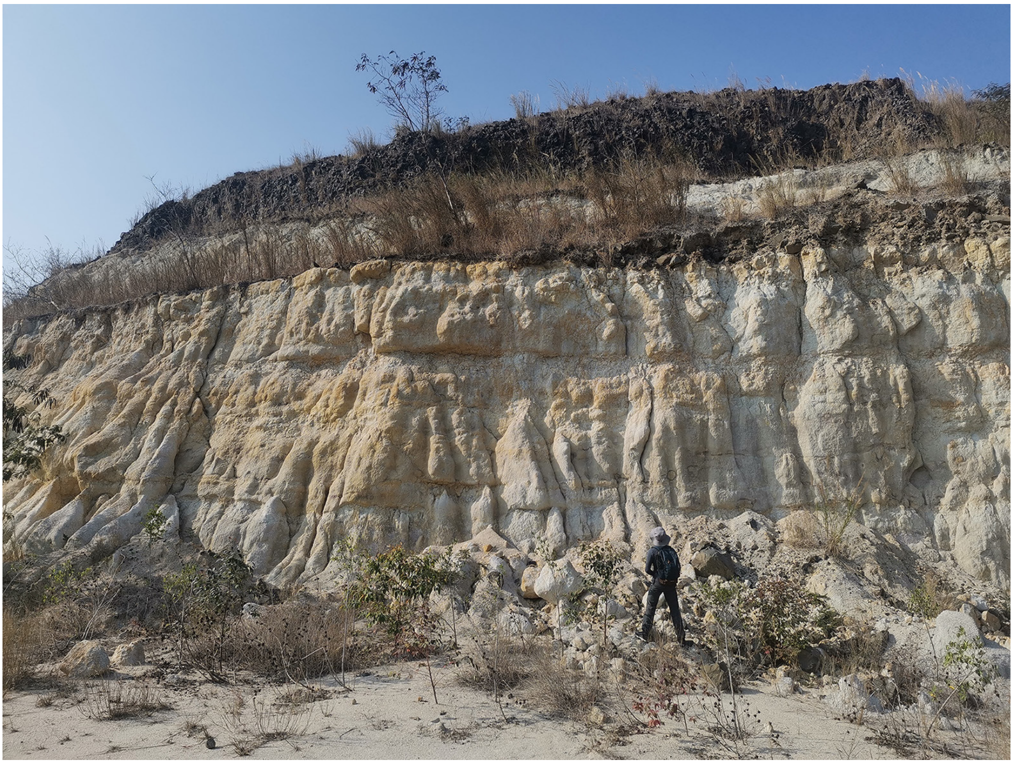


Figure 1. Photograph of the Zhangpu outcrop, Fujian Province, China. The white amber-bearing sedimentary layer is above, beneath the overlying basalt.

& Michener, 1991; Michez *et al*., 2012; Wappler *et al*., 2012; Prokop *et al*., 2017; Dehon *et al*., 2019). Thus, among the eusocial bees, stingless bees are the lineage with by far the greatest preponderance of material from which to work.

Hitherto there have been 11 species of Meliponini described from various amber sources (Table 1), most of which are found in the Nearctic and northern Neotropical regions. Comparatively few fossil stingless bees are known from the Palearctic, all of which are restricted to Europe. Herein we report the discovery of an abundance of Middle Miocene (14.7 Ma: Langhian) amber stingless bees from southeastern China, representing two species in two genera — *Tetragonula* Moure and *Austroplebeia* Moure. The recently documented Zhangpu amber deposit is a prolific source of Middle Miocene inclusions from eastern Asia, and representative of a diverse dipterocarp rainforest (Wang *et al*., 2021). Given that stingless bees are abundant in tropical rainforests, it is little wonder that they should be present in Zhangpu amber. Nonetheless, the biogeographic connections of at least one of these species is unexpected and astonishing.

MATERIAL AND METHODS

Geological Setting

Zhangpu amber is preserved in the Middle Miocene sandy mudstone of the Fotan Group in Zhangpu County, Fujian Province, southeastern China (Wang *et al*., 2021) (Fig. 1). The Fotan Group consists primarily of three basaltic layers and three sedi-

Table 1. Described amber stingless bees (Meliponini).

Taxon	**Age**	**Locality**	**References**
Austroplebeia fujianica Engel, n. sp.	Miocene (Langhian)	Zhangpu, China	Herein
Cretotrigona prisca (Michener & Grimaldi)	Cretaceous (Maastrichtian)	New Jersey, USA	Michener & Grimaldi, 1988; Engel, 2000
Exebotrigona velteni Engel & Michener	Eocene (Bartonian)*	Baltic region	Engel & Michener, 2013b
Kelneriapis eocenica (Kelner-Pillault)	Eocene (Bartonian)*	Baltic region	Kelner-Pillault, 1969, 1970; Sakagami, 1978; Engel, 2001a
Liotrigonopsis rozeni Engel	Eocene (Bartonian)*	Baltic region	Engel, 2001a
Meliponorytes sicula Tosi	Miocene (Langhian?)	Sicily	Tosi, 1896
Meliponorytes succini Tosi	Miocene (Langhian?)	Sicily	Tosi, 1896
Proplebeia abdita Greco & Engel	Miocene (Burdigalian)	Dominican Republic	Greco *et al.*, 2011
Proplebeia dominicana (Wille & Chandler)	Miocene (Burdigalian)	Dominican Republic	Wille & Chandler, 1964; Michener, 1982; Camargo *et al.*, 2000
Proplebeia silacea (Wille)	Miocene (Burdigalian)	Chiapas, Mexico	Wille, 1959
Proplebeia tantilla Camargo *et al.*	Miocene (Burdigalian)	Dominican Republic	Camargo *et al.*, 2000
Proplebeia vetusta Camargo *et al.*	Miocene (Burdigalian)	Dominican Republic	Camargo *et al.*, 2000
Tetragonula florilega Engel, n. sp.	Miocene (Langhian)	Zhangpu, China	Herein

* The age of the amber-bearing deposits of the blaue Erde have recently been redated (Kasiński *et al.*, 2020).

mentary layers, and occurs widely throughout eastern and western Fujian (Zheng *et al.*, 2019). The geological age of the amber-bearing layers is constrained by the overlying basalt with an age of 14.7 ± 0.4 Ma (Zheng *et al.*, 2019). The paleoclimate and local paleoenvironment are summarized by Wang *et al.* (2021).

Specimen Repositories and Descriptive Terminology

In total 89 specimens of Zhangpu amber Meliponini were examined. The material was compared with pertinent extant species in the collections of the Division of Invertebrate Zoölogy, American Museum of Natural History, New York (AMNH) and the Division of Entomology, University of Kansas Natural History Museum, Lawrence (SEMC). The material of Zhangpu amber bees is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (NIGP), SEMC, and AMNH. Novel nomenclatural acts proposed herein are the responsibility of M.S.E., and all new taxa are attributed to Engel for the purposes of authorship under the International Code of Zoölogical Nomenclature. Standard, translingual typographic symbols for sex and caste are employed in reporting specimens examined, specifically ♀, for sterile or non-reproductive females (= worker caste). Metrics for specimens were measured using an ocular micrometer on an Olympus SZX12 stereomicroscope. Given that not every measurement was possible from every specimen, values are taken from the entire series of individuals. Morphological terminology largely follows that of Engel (2001a), Michener (2007), and Rasmussen *et al.* (2017), with the overall format used for the descriptions modified from those of Moure (1961), Rasmussen *et al.* (2017), Engel *et al.* (2017), and Engel (2019). The only changes in terminology employed here are:

> **Fundus**: That portion of the metatibia proximal to the corbicula, differentiated by the convexity of the surface, or at least more flattened, relative to the variously concave surface of the corbicula, as well as changes in surface sculpturing (often more noticeably sculptured in comparison to the polished surface of the corbicula) and pilosity (more densely covered with surface setae) (Figs. 6, 8, 15). The length of the fundal area in relation to the length of the metatibia occupied by the corbicula is often a distinctive feature of certain stingless bee genera, subgenera, or groups of species. The profundal surface is the prolateral (*vide infra* for definition) surface occupied by the fundus. The term is taken from the Latin *fundus*, meaning, "foundation" or "base," and is adopted from the arachnological literature (although therein it is based on the French form, *fond*: Simon, 1879, 1880).
>
> **Gonotrichia**: minute setae, often keirotrichia- (*sensu* Michener, 1981, 1990) or micotrichia-like, forming fine fields on the genital sclerites, in this case particularly the worker gonostyli. The term is a combination of the Greek *trícha* (*τρίχα*, meaning, "hair"; plural *tríches*) and *gónos* (*γόνος*, meaning, "genitals", "seed", or "that which is begotten"), analogous to keirotrichia [*keírō* (*κείρω*), meaning, "cut short" or "shear"] and microtrichia [*mikrós* (*μῑκρός*), meaning, "small"]. Singular = gonotrichium.

Terms of surface orientation: There is at times confusion over the proper terms used to refer to different surfaces of appendages. Terms for the orientation of surfaces on the podites of the legs, for example, either refer to their observed orientation regardless of the serial homology to podites from other appendages and segments ("posterior margin" of metatibia, *e.g.*, Michener, 1990), or attempt to more precisely reflect homologous surfaces in relation to a laterally outstretched appendage (*e.g.*, "upper margin" of metatibia, *e.g.*, Michener, 2007) (Michener, 1990: 78). The latter is to be preferred as it avoids potential confusion when homologizing across segments (metameres) and podites. However, the current terminology further confuses as, for example, "upper" is used in so many different contexts on the same podite: upper margin referring to that margin that appears posteriorly when the leg is positioned at the side, yet upper in the same context on a different surface of the same podite may refer to a position that is proximal on the anterior / outer surface.

Following excellent examples from the arachnological literature (*e.g.*, Bird *et al.*, 2015), and in order to avoid confusion and aid the identification of primary homology as established by topographical identity (Remane, 1952; Patterson, 1982, 1988; Rutishauser & Moline, 2005) (a critical step in comparative observations used to establish patterns and from these hypotheses of process: Brady, 1985, 1994), herein a terminology for orientation is employed that is largely centered around an appendage extended straight laterally and orthogonal with the sagittal plane of the body [*vide etiam* Engel & Rasmussen (2021) and Engel (in press-a), for the application of a subset of these terms, although those presented here are hopefully a further refinement upon earlier attempts] (Figs. 2–5). The proposed terminology attempts to standardize terms for the metatibial surfaces of corbiculate Apinae, although some of these can be easily adopted for other podites and other bee lineages. The terms take into account not only the serial homology of surfaces but also merely descriptive modifiers that hopefully make it easier for melittologists to adopt such terms given that the metatibia (and other leg podites) are never oriented straight out from the body in life and almost never in preserved material unless specifically prepared in such a position. For example, a less-rigid, augmented system may be preferable and easier to manage than one that strictly refers to what is, by preserved position, an anterior-facing surface but technically a ventral surface, employing instead *proventral* as a compromise between the truly ventral nature of the surface (as a laterally extended appendage) but recognizing its anterior-facing orientation as observed. Note that there is not a universal one-to-one equivalence between frequently used descriptive terms and the surfaces discussed here. By example, what is often referred to as "outer" may reference utterly different surfaces. On the mesotibia of Euglossini one might note that the characteristic velvet patch of males is on the "outer" surface, and similarly consider on the metatibia of the same male to have the metatibial organ slit on the posterior edge of the "outer" surface. Yet, if these appendages are oriented properly out from the body, one finds that the mesotibial "outer" surface is the dorsal surface, while for the metatibia the "outer" surface is an anterior surface (*prolateral*) (Engel, in press-a). Thus, "outer" is a sufficient descriptor for an observed orientation, but fails to reflect the serial homology of the podite surfaces.

As a brief summary, the primary planes of orientation for the insect body are as follows:

Sagittal (longitudinal) plane: that plane that divides the insect body into equal right (dextral) and left (sinistral) halves; parasagittal sections are sagittal sections situated dextral or sinistral to the median line.

Transverse plane: that plane that divides the insect body into anterior (cephalic or cranial) and posterior (caudal) halves.

Frontal plane: that plane that divides the insect body into equal superior (dorsal) and inferior (ventral) halves; a superior parafrontal plane is a frontal section shifted superior to the mediofrontal line, while an inferior parafrontal plane would be the same but in the opposing (inferior) direction.

When the appendage is extended straight laterally relative to the sagittal plane, the length of the appendage is bisected by a transverse plane passing through the body, resulting in anterior and posterior halves to the appendage. In the context of the appendage alone, however, when viewed from above the longitudinal axis extending from proximal to apical makes an identical bisection with these same surfaces being lateral to such an axial (or longitudinal in the context of the appendage in isolation) plane. In the context of a corbiculate apine metatibia this means that what are lateral surfaces in the context of the axial plane of the appendage, are anterior and posterior surfaces in relation to the sagittal plane of the body. The terms prolateral and retrolateral are suitable for identifying these dual realities, with *prolateral* identifying that appendicular lateral surface that is truly a forward-facing surface (hence the prefix *pro*–), and with *retrolateral* representing the opposite. Naturally, the length of the appendage is also bisected by the frontal plane and therefore has dorsal and ventral surfaces, which when taken in the context of the appendage itself are still dorsal and ventral.

When the leg is at rest or the bee is standing upon a surface, the leg is oriented such that the prolateral surface faces abaxially, the retrolateral surface faces adaxially, the ventral surface faces anteriorly, and the dorsal surface faces posteriorly, the abaxial surface faces ventrally, and the adaxial surface faces dorsally (Figs. 4, 5). In this context, the hind leg, when fully extended orthogonal to the body's sagittal line, has the corbicular surface facing anterior and that surface with the keirotrichiate field facing to the posterior.

Terms adopted here are (terms are also summarized in figures 2–17):

Abaxial: a surface facing away ("outer") from the sagittal (median longitudinal) axis of the insect. In the context of a corbiculate apine metatibia, the abaxial surface is that distal from the body (Figs. 16, 17) and facing the opposing proximal surface of the metabasitarsus, and forms the proximal (historically referred to as the "upper") surface of the pollen press (Fig. 13).

Adaxial: a surface facing toward ("inner" or "mesial") the sagittal axis of the insect. For example, the surface of the auricle of the pollen press is situated on the adaxial surface of the metabasitarsus (Fig. 13).

Ectal: the external (outside, outer) surface of the integument.

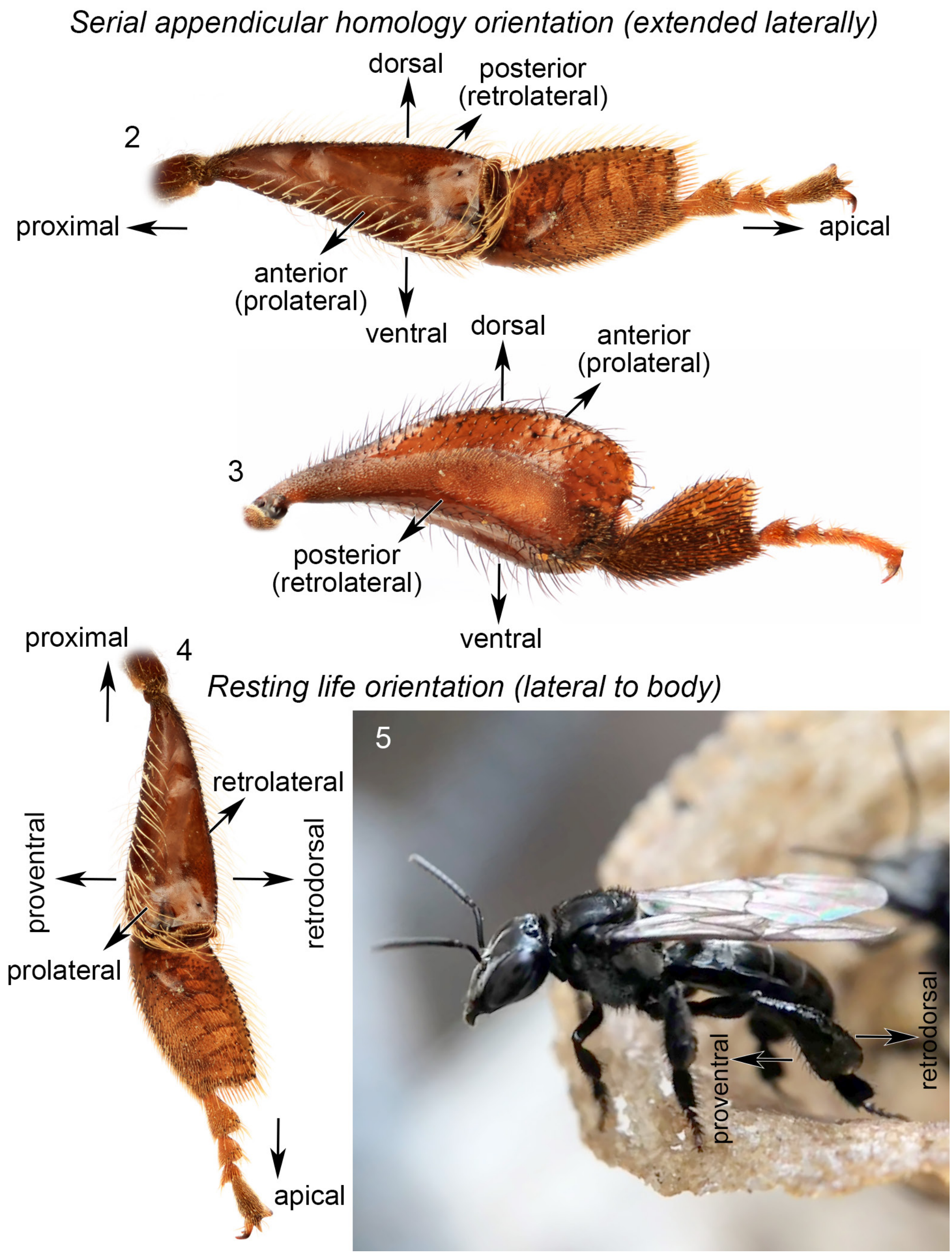
Ental: the internal (inside, inner) surface of the integument.

Mesal: a point on or in the sagittal plane of the body, appendage, or podite.

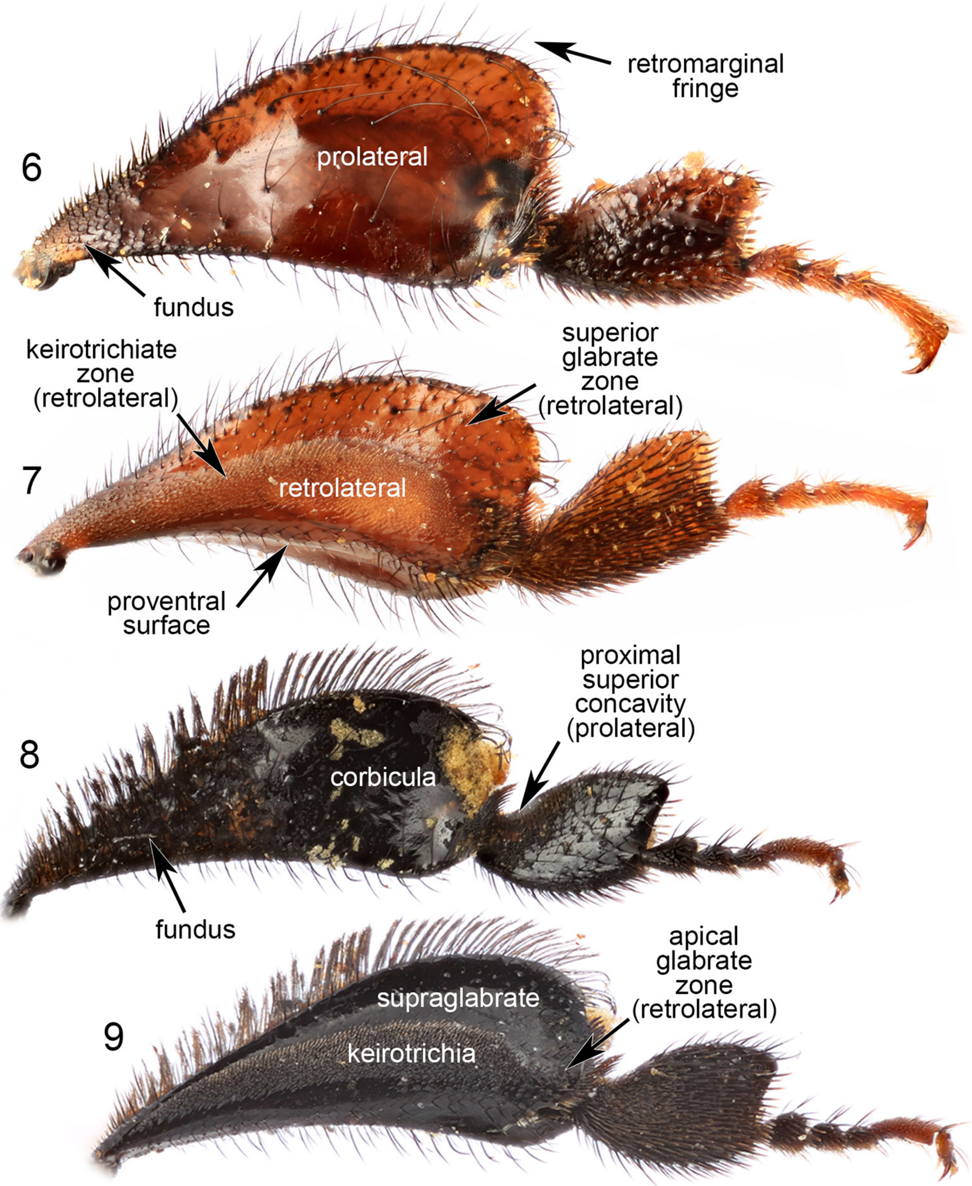
Prolateral: a lateral surface from an extended appendage that faces forward in a fully extended orientation (Figs. 2–4, 6, 8, 11, 15, 17). In corbiculate bees this surface is equivalent to the "outer" surface of Michener (1990) or the "anterior" surface of Michener (2007).

Proventral: a ventral surface from an extended appendage that faces forward in natural resting orientation (Figs. 4, 7, 11). In stingless bees, this is equivalent to the "anterior" margin of Michener (1990) or the "lower" margin of Michener (2007).

Retrodorsal: a dorsal surface from an extended appendage that typically faces backward in natural resting orientation (Figs. 4, 6, 12, 16, 17). For stingless bees,



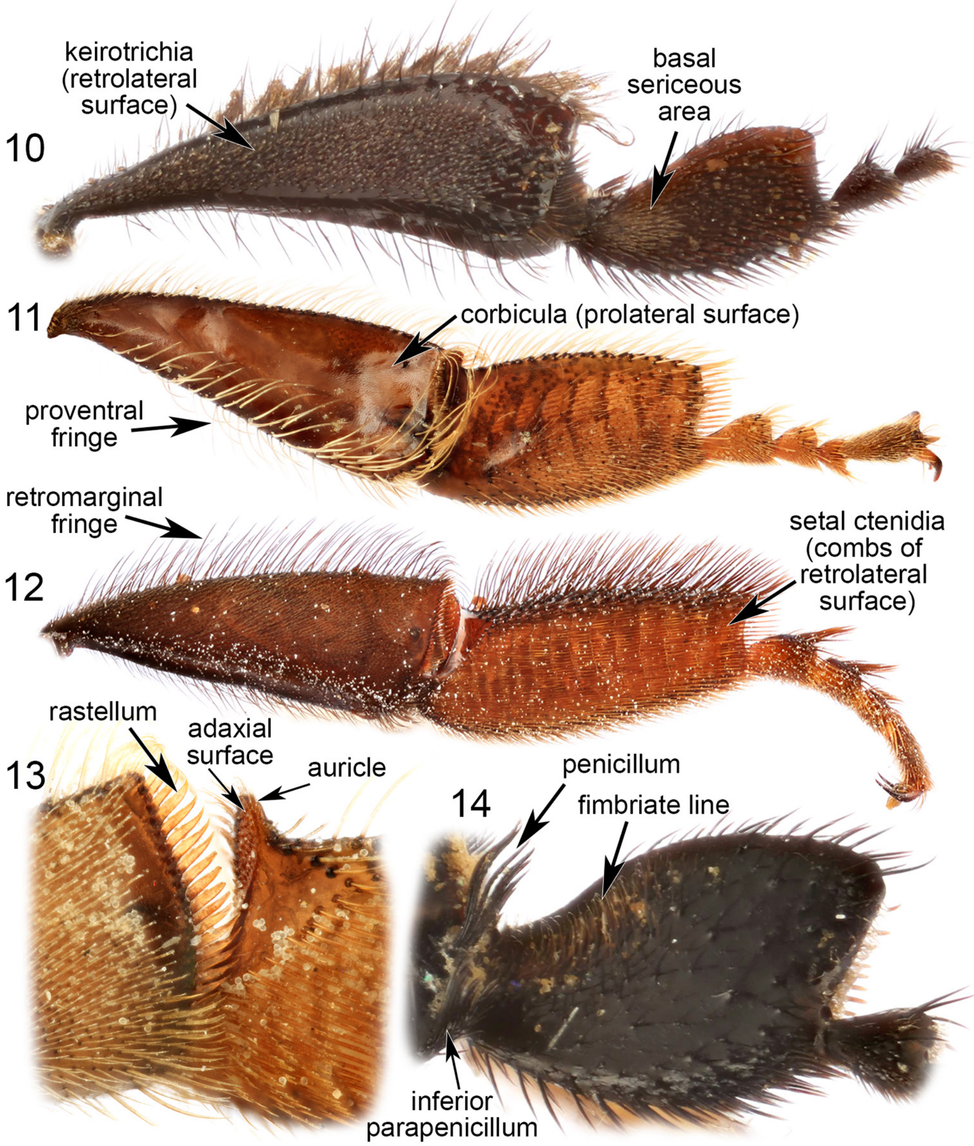
Figures 2–5. Directions and terms of orientation for corbiculate apine metatibiae. **2.** Frontal view of metatibia and metatarsus of worker of *Apis* (*Apis*) mellifera Linnaeus, oriented as it would be if extended straight laterally from body to identify serially homologous surfaces. **3.** Posterior view of metatibia and metatarsus of worker of *Cephalotrigona capitata* (Smith), oriented as leg in figure 2. **4.** Frontal view of figure 2 except oriented as leg would be positioned in life. **5.** Frame capture of worker of *Heterotrigona* (*Heterotrigona*) *itama* (Cockerell) from Brunei (M.S. Engel, 1 September 2018) showing orientation of hind leg in life and direction of particular surfaces.



Figures 6–9. Metatibiae and metatarsi of workers of representative stingless bees (Meliponini). **6.** Prolateral view of *Cephalotrigona capitata* (Smith). **7.** Retrolateral view of *C. capitata*. **8.** Prolateral view of *Geniotrigona thoracica* (Smith). **9.** Retrolateral view of *G. thoracica*.

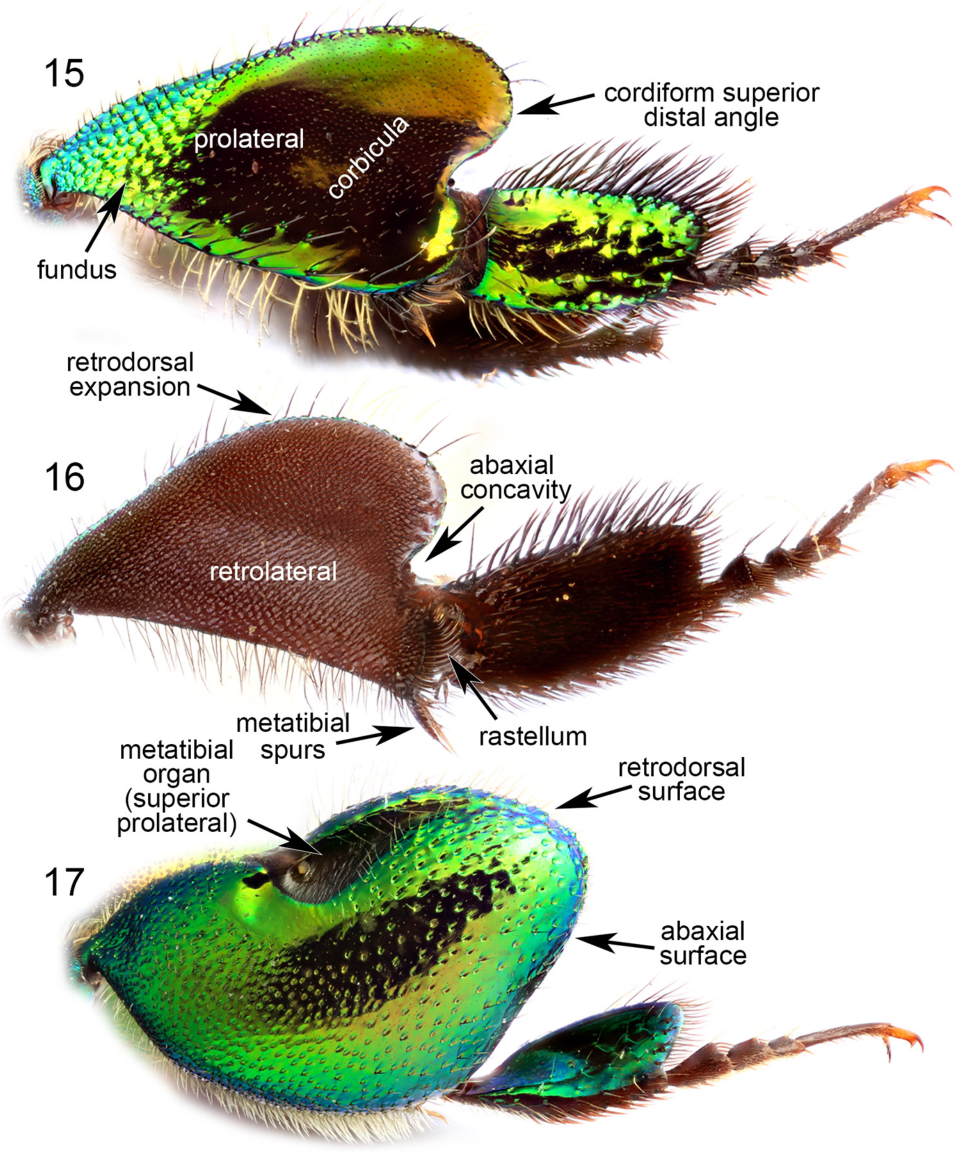
this is equivalent to the "posterior" margin of Michener (1990) or the "upper margin" of Michener (2007).

Retrolateral: a lateral surface from an extended appendage that faces backward in a fully extended orientation (Figs. 2–4, 7, 9, 10, 12, 16). In corbiculate bees this is equivalent to the "inner" surface of Michener (1990) or the "posterior" surface of Michener (2007).



Figures 10–14. Metatibiae and metatarsi of workers of a representative stingless bee (Meliponini) and two honey bees (Apini). **10.** Retrolateral view of *Heterotrigona* (*Sahulotrigona*) *paradisaea* Engel & Rasmussen. **11.** Prolateral view of *Apis* (*Apis*) *mellifera* Linnaeus. **12.** Retrolateral view of *A.* (*Megapis*) *dorsata* Fabricius. **13.** Detail of metatibial-metabasitarsal articulation and pollen press of *A.* (*A.*) *mellifera*, retrolateral view. **14.** Detail of metatibial apex and metabastarsus of *Geniotrigona thoracica* (Smith).

Retromarginal: a narrowed retrodorsal surface forming a distinct margin (rather than a broad surface) (Figs. 6–12, 16, 17). This is specifically equivalent to the narrowed retrodorsal margin bearing a fringe of setae on the metatibia and referred to as the "posterior" fringe by Michener (1990) or the "upper" margin fringe by Michener (2007).



Figures 15–17. Metatibiae and metatarsi of a female and male of the orchid bee *Euglossa* (*Euglossa*) *igniventris* Friese (Euglossini). **15.** Prolateral view of female. **16.** Retrolateral view of female. **17.** Prolateral view of male.

Directional terms: Structures or points on a given oriented surface (*vide supra*) can be refined by directional terms:

Apical (or distal, apico-): directed away from the point of origin of a surface, *i.e.*, away from the body in the case of an appendage or podite. Apicad / distad = apical to, of / distal to, of.

Basal (or baso-): directed toward the point of a surface nearest the body in the case of an appendage or podite. Basad = basal to, of.

Inferior (infra-): directed to a point situated lower down on a surface or toward the ventral surface.

Mesial (mesio-): descriptive of point or structure directed toward or near the sagittal plane of the body, appendage, or podite. Mesiad / mesad = mesial to, of / mesal to, of.

Proximal (proximo-, proxi-): directed toward the point of origin of surface, *i.e.*, toward the body in the case of an appendage or podite. Proximad = proximal to, of.

Superior (supra-): directed to a point situated further upward on a surface or toward the dorsal surface.

Amber Preparation and Imaging

Zhangpu amber is characterized by amyrone-based triterpenoids and cadalene-based sesquiterpenoids, and originated as exuded resin from Dipterocarpaceae (Eudicots: Malvales) (Shi *et al.*, 2014; Wang *et al.*, 2021). Zhangpu amber is a Class II resin (Anderson *et al.*, 1992), like the older (Early Eocene: Ypresian) amber from the Cambay Basin, which is also a Class II dipterocarp resin (Rust *et al.*, 2010). Like other Class II resins, the amber remains somewhat tacky and friable (particularly sensitive to humidity and temperature changes that can result in the formation of new internal fissures), with dust from the air quickly adhering to surfaces and necessitating additional polishing to maintain a clear view of inclusions. In fact, simply touching the surface can leave a fingerprint, also requiring cleaning. The amber pieces were trimmed with a water-fed, circular diamond saw, and polished with progressively finer grit papers on a horizontal, water-fed, motorized lapidary wheel in the Division of Entomology, University of Kansas Natural History Museum, with repeated polishing as necessary to account for the tacky surfaces.

The amber is usually a rather dark reddish brown or yellowish brown color, but when cut thin and polished it can be quite translucent yellow. Specimens can be difficult to examine if not polished close to the inclusion (not always possible depending on other inclusions or the stability of the amber piece), and with considerable reflected and transmitted light. The dark color of the amber results in a visual dulling of the integumental coloration of the bees, even under optimal lighting. Nonetheless, areas of yellow maculation can be discerned despite augmentation through fossilization. Standard light photographs were taken with a Canon EOS7 digital camera with various microscopic lens attachments and illuminated by a Xenon flash.

X-ray micro-computed tomography (micro-CT) scanning was performed at the American Museum of Natural History Microscopy and Imaging Facility. Scans were taken with a GE Phoenix v|tome|x s240 (Germany), equipped with either a 240 or 180 kV X-ray source. A diamond target was used for all scans. A specimen of *Tetragonula* was scanned at 60 kV and 230 μA with 500 msec exposures for a total of 1500 projections. Each projection image was the average of six exposures with one skipped exposure, for a total scan time of approximately 90 minutes. The reconstructed volume's voxel size was 2.8 μm. The specimen of *Austroplebia* was scanned at 90 kV and 222 μA, also with 500 msec exposures, with six averaged and one skipped. Horizontal tiling was used for 1800 projections, resulting in a total scan time of approximately 210 minutes and a reconstructed volume voxel size of 6.3 μm. Volume reconstruction from raw X-ray projections was achieved using GE phoenix datos|x v2.3.2 with manual geometry correction. Datasets were post-processed, segmented, and volume rendered with 3D Slicer 4.9 (nightly builds) (Fedorov *et al*., 2017). Images in figures were rendered with Blender 2.79 and the Cycles render engine (Blender Online Community, 2017). While scans were capable of rendering general shape, finer details were unresolved, such as many of the setae (some of the thicker bristles did resolve, *e.g*., on the retrolateral surface of the metabasitarsus), integumental sculpture, *&c*.

SYSTEMATIC PALEONTOLOGY

Subfamily Apinae Latreille
Clade Corbiculata Engel

Tribe Meliponini Lepeletier de Saint Fargeau

The stingless bees, tribe Meliponini, are one of two lineages of exclusively highly eusocial bees in the apine clade Corbiculata (Michener, 2007; Engel & Rasmussen, 2021; Engel *et al*., 2021; Melo, 2021). Like honey bees (Apini), meliponines live in typically large, perennial colonies, and are actively managed (meliponiculture) in certain regions of the tropics for the production of honey, pollination services, as well as other materials (*e.g*., propolis, resin). The 520 modern species are distributed pantropically and are most diverse in those regions where honey bees are not native (*i.e*., South and Central America), perhaps reflecting a historical competitive pressure between these two eusocial rivals (Engel, 2001a). Unlike honey bees, not all stingless bees collect pollen. Species of the Asian genera *Lisotrigona* Moure and *Pariotrigona* Moure are lachryphages (tear-drinking bees), collecting tears from a variety of vertebrates and using this as a source of nutrients (Bänziger *et al*., 2009, 2011; Bänziger & Bänziger, 2010; Bänziger, 2018). Although the minute species of *Trigonisca* (*Leurotrigona*) Moure are known as "lambe olhos" (eye lickers), they are apparently not lachryphagous as in the aforementioned genera. Species of *Lestrimelitta* Friese (Neotropical) and *Liotrigona* (*Cleptotrigona*) Moure (Afrotropical) are robber bees (cleptobiotic) and make mass raids on other meliponine colonies, during which they steal resources to bring back to their home nest (Portugal-Araújo, 1958; Wille, 1983; Sakagami *et al*., 1993; Grüter *et al*., 2016). Species of *Trichotrigona* Camargo & Moure are also robber bees, but these make solitary raids on their hosts (Engel & Rasmussen, 2021). Lastly, there is a small clade of vulture bees (necrophages) in the genus *Trigona* Jurine (*Necrotrigona* Engel, n. subgen.: Appendix), species of which harvest tissues from vertebrate carcasses and store these in pots within the nest (Camargo & Roubik, 1991; Noll *et al*., 1996; Noll, 1997; Mateus & Noll, 2004).

The tribe is most closely related to the extinct tribe Melikertini (Engel, 2001a, 2001b; Schultz *et al*., 2001; Cardinal & Packer, 2007), known only from Eocene amber deposits of Europe and Asia. Characteristics of melikertines have recently been summarized in detail (Engel & Davis, 2021), and that material is not repeated here. The closest relative of the Melikertini + Meliponini clade remains somewhat controversial. Many analyses based on diverse data support the highly eusocial Apini as sister, along with the concomitant reconstruction of a single origin of highly eusocial behavior among corbiculate bees (*e.g*., Roig-Alsina & Michener, 1993; Schultz *et al*., 1999, 2001; Engel, 2001b; Noll, 2002; Cardinal & Packer, 2007; Canevazzi & Noll, 2015; Porto *et al*., 2016, 2017, 2021; Porto & Almeida, 2021; Noll *et al*., in press). Nonetheless, some analyses suggest that meliponines are more closely related to the primitively eusocial bumble bees, with *Apis* Linnaeus clustering with the orchid bees or as sister to Meliponini +

Bombini (*e.g*., Kawakita *et al*., 2008; Ramírez *et al*., 2010; Martins *et al*., 2014; Romiguier *et al*., 2016; Kwong *et al*., 2017; Bossert *et al*., 2019).

Meliponines are distinguished by a large number of traits relative to other corbiculate bees, and particularly from their relatives in the Melikertini and Apini. As their cognomen implies, the sting apparatus of stingless bees is vestigial, although the sting stylet itself is still distinct with an acutely sharp apex and therefore sting-like in *Melipona* Illiger, *Liotrigona* (*Cleptotrigona*), *Meliplebeia* Moure, *Axestotrigona* Moure, *Meliponula* Cockerell, and somewhat in *Plebeiella* Moure. Beyond the structure of the sting, stingless bees lack extensive outer mandibular grooves (as in Melikertini, Apini, and those weakened grooves in Electrapini), have the anterior mandibular condyle contiguous with the clypeal border (as in Apini and Melikertini, covered by the clypeal border in Euglossini and Bombini), have the mentum and submentum separated (as in Apini and Bombini, rather than fused in Euglossini), and the compound eyes usually bare (hirsute in Apini). The mesoscutum lacks the supraälar carina that is otherwise present in all other living and fossil corbiculate bees. The wings of stingless bees are noteworthy for the reduction of the distal wing venation, rather than the complete venation of all other corbiculate bees. The distal portion of the wing lacks alar papillae (as is the case in Apini and Melikertini, while papillae are generally present in Euglossini, Bombini, Electrobombini, and Electrapini), and the jugal lobe of the hind is present proximally (as is the case in all corbiculate bees with the exception of Euglossini and Bombini). The protibial strigilis lacks an anterior velum, as in Melikertini, that is otherwise present in all other living and fossil corbiculate bees. The meliponine metatibia has a distinct penicillum at the distal inferior angle [except absent in the cleptobiotic *Lestrimelitta* and *Liotrigona* (*Cleptotrigona*), and rudimentary in *Trichotrigona*], a unique trait not otherwise known in any other living and fossil corbiculate bees, although there is a patch of setae in Melikertini that is situated in the position of the penicillum and that could be a homologous precursor (Engel & Davis, 2021). Metatibial spurs are completely absent in Meliponini, as well as in Apini, while a single spur, sometimes reduced, is present in Melikertini and Electrapini, and the normal complement and development of spurs are present in Euglossini, Bombini, and Electrobombini. The auricle that is present in all corbiculate bees (except parasitic forms), is characteristically absent in stingless bees. The pretarsal claws are simple (toothed to some degree in all other corbiculate bees), and the arolium is present (as in all living and fossil corbiculate bees with the exception of Euglossini and Bombini). In males, the hidden metasomal sterna VII and VIII are reduced (as in Apini, well-developed in Euglossini and Bombini), and the gonobase is absent or vestigial (as in Apini, present in Euglossini and Bombini). Although a single melikertine male is known (Engel *et al*., 2014), it has yet to be scanned to see if the terminalia could be visualized and compared with that of Meliponini and other corbiculate bees.

The Old World fauna of stingless bees, while diverse, is minor by comparison to the plethora of species found in the New World tropics (Michener, 2007; Rasmussen, 2008; Rasmussen *et al*., 2017). Nonetheless, there is considerable variety in the lineages and biology of the Eastern Hemisphere Meliponini. This fauna was largely assigned to the otherwise New World genus *Trigona* until Moure (1961) provided a far-reaching, and in some ways prescient, rearrangement of the fauna (in the same fashion as he had for the New World fauna earlier: Moure, 1951), ascribing the numerous species to a series of unique genera and subgenera. While some chose to retain most of Moure's groups within *Trigona* (*e.g*., Michener, 1990, 2007), gradually an augmented version of his system has become adopted (*e.g*., Michener, 2013; Rasmussen *et al*., 2017; Engel *et al.*, 2018; Engel, 2019; Grüter, 2020; Melo, 2021; herein) and is followed herein. The classification of the tribe can be outlined as follows (Table 2) (Appendix):

Subtribe **Hypotrigonina** Engel, new subtribe (type genus: *Hypotrigona* Cockerell): This clade comprises all extant Eastern Hemisphere stingless bees. The group is quite heterogenous and there are repeated convergences with genera of the Meliponina, such as the presence of the basal sericeous area on the proximal retrolateral surface of the metabastarsus. Nonetheless, the group includes those species with flattened worker gonostyli bearing gonotrichia (except also present in Trigoniscitae, but in those bees the marginal cell base is greatly broadened such that the basal angle is slightly acute to orthogonal), or species with a distinctive pollen pocket proximally on the prolateral surface of the metabasitarsus (those species with the pollen pocket have the worker gonostyli cylindrical and lack gonotrichia). Wille (1979) and Michener (2007) discussed some of these convergences in greater detail. The occurrence of gonotrichia on the worker gonostyli is largely split between the two internal clades of this subtribe, with none present among Heterotrigonitae and gonotrichia largely present in Hypotrigonitae aside from two exceptions (*vide infra*). The two major clades of the subtribe are:

Infratribe **Heterotrigonitae** Engel, new infratribe (type genus: *Heterotrigona* Schwarz): The genera of this clade all possess a distinctive apical glabrate (apicoglabrate) zone on the retrolateral surface of the metatibia and have a robust, broad, ovoid metasoma that tapers in width apically from the third segment. The worker gonostyli, where known, are cylindrical and lack gonotrichia. On the prolateral surface of the metabasitarsus there is a proximal superior concavity, inferiorly bordered by a ridge (sometimes the ridge is strong but can vary to exceptionally weak and largely grading onto the otherwise normal planar prolateral surface) that bears a distinctive fimbria of fine, simple, superiorly directed setae (the fimbriate line) that border the otherwise largely glabrous concave surface. Wille (1979) considered this to be a "pollen press" of sorts, but not to be confused with the more typical pollen press formed by the auricle which is present in other corbiculate bee lineages. The function of this structure is unknown but to avoid confusion with the actual pollen press of other bees, we here refer to it as a *pollen pocket*. A pollen pocket is found in all Heterotrigonitae, albeit more weakly so in some of the minute species of *Tetragonula s.str*. In fact, the pollen pocket is generally weaker in *Tetragonula s.l.* than in other Heterotrigonitae. A pollen pocket is also present in *Oxytrigona* Cockerell (Meliponina: Meliponitae). The clade includes seven genera: *Tetragonula* Moure (*Tetragonula s.str*. and *Tetragonilla* Moure), *Homotrigona* Moure (*Homotrigona s.str*., *Lophotrigona* Moure, *Odontotrigona* Moure, and *Tetrigona* Moure), *Geniotrigona* Moure, *Heterotrigona* Schwarz (*Heterotrigona s.str*., *Sundatrigona* Inoue & Sakagami, *Borneotrigona* Engel, *Platytrigona* Moure, *Sahulotrigona* Engel & Rasmussen), *Papuatrigona* Michener & Sakagami, *Lepidotrigona* Schwarz, and *Wallacetrigona* Engel & Rasmussen.

Table 2. Hierarchical classification of stingless bees (Meliponini). →

Tribe MELIPONINI Lepeletier de Saint Fargeau

- Subtribe **Meliponina** Lepeletier [New World]
  - Infratribe Trigoniscitae Engel, n. infratrib.
    - *Trigonisca* Genus Group
      - Genus *Trigonisca* Moure
        - Subgenus *Leurotrigona* Moure
        - Subgenus *Exochotrigona* Engel
        - Subgenus *Celetrigona* Moure
        - Subgenus *Trigonisca* Moure, *s.str.*
      - Genus †*Exebotrigona* Engel & Michener
  - Infratribe Meliponitae Lepeletier
    - Clan *Trigona*
      - *Paratrigona* Genus Group
        - Genus *Paratrigona* Schwarz
          - Subgenus *Aparatrigona* Moure
          - Subgenus *Paratrigona* Schwarz, *s.str.*
        - Genus *Paratrigonoides* Camargo & Roubik
        - Genus *Nogueirapis* Moure
        - Genus *Partamona* Schwarz
          - Subgenus *Partamona* Schwarz, *s.str.*
          - Subgenus *Parapartamona* Schwarz
      - *Trigona* Genus Group
        - Genus *Oxytrigona* Cockerell
        - Genus *Scaptotrigona* Moure
        - Genus *Geotrigona* Moure
        - Genus *Ptilotrigona* Moure
        - Genus *Tetragona* Lepeletier & Audinet-Serville
          - Subgenus *Camargoia* Moure
          - Subgenus *Tetragona s.str.*
        - Genus *Trigona* Jurine
          - Subgenus *Aphaneuropsis* Engel, n. subgen.
          - Subgenus *Koilotrigona* Engel, n. subgen.
          - Subgenus *Necrotrigona* Engel, n. subgen.
          - Subgenus *Nostotrigona* Engel, n. subgen.
          - Subgenus *Ktinotrofia* Engel, n. subgen.
          - Subgenus *Aphaneura* Gray
          - Subgenus *Trigona* Jurine, *s.str.*
          - Subgenus *Dichrotrigona* Engel, n. subgen.
        - Genus *Cephalotrigona* Schwarz
        - Genus *Meliwillea* Roubik, Segura, & Camargo
      - *Plebeia* Genus Group
        - Genus *Tetragonisca* Moure
        - Genus *Frieseomelitta* Ihering
        - Genus *Trichotrigona* Camargo & Moure
        - Genus *Duckeola* Moure
        - Genus *Plectoplebeia* Melo
        - Genus *Plebeia* Schwarz
          - Subgenus *Nanoplebeia* Engel, n. subgen.
          - Subgenus *Plebeia* Schwarz, *s.str.*
        - Genus *Lestrimelitta* Friese
        - Genus *Friesella* Moure
        - Genus *Asperplebeia* Engel, n. gen.
        - Genus *Nannotrigona* Cockerell
          - Subgenus *Lispotrigona* Gonzalez & Engel, n. subgen.
          - Subgenus *Nannotrigona* Cockerell, *s.str.*
        - Genus *Schwarziana* Moure
          - Subgenus *Mourella* Schwarz
          - Subgenus *Chapadapis* Engel, n. subgen.
          - Subgenus *Schwarziana* Moure, *s.str.*
        - Genus *Scaura* Schwarz
          - Subgenus *Scaura* Schwarz, *s.str.*
          - Subgenus *Schwarzula* Moure
        - Genus †*Proplebeia* Michener
    - Clan *Melipona*
      - Genus *Melipona* Illiger
        - Subgenus *Melipona* Illiger, *s.str.*
        - Subgenus *Meliponotes* Engel
        - Subgenus *Melikerria* Moure
        - Subgenus *Eomelipona* Moure
        - Subgenus *Mouremelia* Engel
        - Subgenus *Michmelia* Moure

- Subtribe **Hypotrigonina** Engel, n. subtrib. [Old World]
  - Infratribe Heterotrigonitae Engel, n. infratrib.
    - Clan *Heterotrigona*
      - *Heterotrigona* Genus Group
        - Genus *Geniotrigona* Moure
        - Genus *Heterotrigona* Schwarz
          - Subgenus *Borneotrigona* Engel
          - Subgenus *Sundatrigona* Inoue & Sakagami
          - Subgenus *Heterotrigona* Schwarz, *s.str.*
          - Subgenus *Platytrigona* Moure
          - Subgenus *Sahulotrigona* Engel & Rasmussen
        - Genus *Papuatrigona* Michener & Sakagami
        - Genus *Lepidotrigona* Schwarz
        - Genus *Wallacetrigona* Engel & Rasmussen
      - *Homotrigona* Genus Group
        - Genus *Homotrigona* Moure
          - Subgenus *Lophotrigona* Moure
          - Subgenus *Homotrigona* Moure, *s.str.*
          - Subgenus *Odontotrigona* Moure
          - Subgenus *Tetrigona* Moure
    - Clan *Tetragonula*
      - Genus *Tetragonula* Moure
        - Subgenus *Tetragonilla* Moure
        - Subgenus *Tetragonula* Moure, *s.str.*
  - Infratribe Hypotrigonitae Engel, n. infratrib.
    - *Hypotrigona* Genus Group
      - Genus *Hypotrigona* Cockerell
      - Genus *Liotrigona* Moure
        - Subgenus *Cleptotrigona* Moure
        - Subgenus *Liotrigona* Moure, *s.str.*
      - Genus *Pariotrigona* Moure
      - Genus *Lisotrigona* Moure
      - Genus *Austroplebeia* Moure
        - Subgenus †*Anteplebeina* Engel, n. subgen.
        - Subgenus *Austroplebeia* Moure, *s.str.*
      - Genus †*Kelneriapis* Sakagami
      - Genus †*Liotrigonopsis* Engel
    - *Meliponula* Genus Group
      - Genus *Meliplebeia* Moure
        - Subgenus *Apotrigona* Moure
        - Subgenus *Meliplebeia* Moure, *s.str.*
      - Genus *Axestotrigona* Moure
        - Subgenus *Atrichotrigona* Engel, n. subgen.
        - Subgenus *Axestotrigona* Moure, *s.str.*
      - Genus *Plebeiella* Moure
      - Genus *Dactylurina* Cockerell
      - Genus *Meliponula* Cockerell
      - Genus *Plebeina* Moure

- Subtribe *Incertae sedis*
  - Genus †*Cretotrigona* Engel [Meliponina?]
  - Genus †*Meliponorytes* Tosi [Heterotrigonina?]

Infratribe **Hypotrigonitae** Engel, new infratribe (type genus: autobasic with Hypotrigonina Engel, *vide supra*): The genera of this clade all lack a broad apical glabrate zone on the retrolateral surface of the metatibia, with the exception of *Dactylurina* Cockerell, which, while having such a glabrate zone, combines it with an elongate, subclavate, finger-like metasoma, not found in the Heterotrigonitae. The worker gonostyli, where known, are flattened and have gonotrichia, with the exception of the minute species of *Hypotrigona* Cockerell and *Pariotrigona*, which have the gonostyli greatly reduced and almost tuberculiform. The pollen pocket of the Heterotrigonitae is lacking, with the proximal superior surface where it would otherwise be found largely coplanar with the remainder of the metabasitarsal prolateral surface (sometimes there is a faint slope leading to the retrodorsal margin) and the setae are largely uniform across the surface (*i.e.*, not defining a line bordering a polished superior surface), although often subappressed and superiorly directed. This clade includes 11 extant genera: *Lisotrigona*, *Pariotrigona*, and *Austroplebeia* Moure in the Indomalayan and Papuan and Australian regions, respectively; and the African *Hypotrigona*, *Liotrigona* Moure (*Liotrigona s.str.* and *Cleptotrigona*), *Plebeina* Moure, *Meliponula*, *Dactylurina*, *Plebeiella*, *Axestotrigona* [*Atrichotrigona* Engel, new subgenus (Appendix), and *Axestotrigona s.str.*], and *Meliplebeia* (*Meliplebeia s.str.* and *Apotrigona* Moure) [Note: contra Michener (2007), one of us (M.S.E.) considers *Meliponula*, *Axestotrigona*, and *Plebeiella* to be distinct genera (Appendix), and that *Meliplebeia* here constitutes those species with yellow markings, a sloping basal area distinct from the vertical posterior surface, and the propodeal basal area covered with fine erect setae. The subgenera are then distinguished by the mesoscutum tessellate in *Meliplebeia s.str.* versus punctate in *Apotrigona*, the mandible with small teeth in *Meliplebeia s.str.* versus pronounced and strong in *Apotrigona*, the scape as long as the torulocellar distance in *Meliplebeia s.str.* versus shorter in *Apotrigona*, the basal vein (1M) slightly distad 1cu-a in *Meliplebeia s.str.* versus slightly basad in *Apotrigona*; the superior parapenicillum is well developed in *Meliplebeia s.str.* and poorly developed, scarcely definable as a parapenicillum, in *Apotrigona*; *Apotrigona* also has a faint opalescence observable under certain lightings that is seemingly not present in *Meliplebeia s.str.* The superior parapenicillum is only present in *Meliplebeia*, *Axestotrigona*, *Plebeiella*, and *Meliponula*.]. Although *Dactylurina* has been placed as sister to *Meliponula* (Rasmussen & Cameron, 2010), most morphological characters suggest it should be in a more basal position along with or just basal to *Plebeina* (*e.g.*, absence of superior parapenicillum), with *Meliponula* more closely related to *Plebeiella*, *Axestotrigona*, and *Meliplebeia*. A possible set of relationships that should be more fully explored would be: *Dactylurina* (*Plebeina* (*Meliponula* (*Plebeiella* (*Axestotrigona* + *Meliplebeia*)))). Under such an arrangement, the superior parapenicillum and the more developed sting would unite everything from *Meliponula* onward (and those groups could potentially all be classified as subgenera of *Meliponula* once again, analogous to but not equivalent to the system of Wille, 1979, and Michener, 2007). The fossil genera *Kelneriapis* Sakagami and *Liotrigonopsis* Engel, both in Eocene Baltic amber, belong to this clade.

Subtribe Meliponina Lepeletier de Saint Fargeau (type genus: *Melipona* Illiger): The subtribe is characterized by the absence of features otherwise distinctive for the Hypotrigonina. The worker gonostyli of the subtribe lack gonotrichia in all genera except those of the basal Trigoniscitae (likely a plesiomorphic feature for that subtribe, shared symplesiomorphically with the Hypotrigonitae, and then independently lost in Meliponitae, Heterotrigonitae, *Hypotrigona*, and *Pariotrigona*; such loss is clearly not linked to minute body sizes as the minute species of Trigoniscitae, *Liotrigona s.l.*, *Lisotrigona*, and *Austroplebeia* all retain such gonotrichia). The subtribe is exclusively distributed in the Western Hemisphere, from Mexico to northern Argentina, although *Plebeia* (*Plebeia*) *frontalis* (Friese) has been introduced into coastal central California (M. Hauser, pers. comm.; M.S.E., per. obs.).

Infratribe **Trigoniscitae** Engel, new infratribe (type genus: *Trigonisca* Moure): This group was characterized recently (as the "*Trigonisca* Genus Group") by Engel *et al.* (2019). The included species are united by the distinctively broadened base to the marginal cell in which the basal angle is slightly acute to orthogonal (68°–90°), and with the marginal cell, at the apex of the pterostigma, broader than the area encompassed by the submarginal cells. The forewing is less, usually much less, than 4 mm in length. The worker gonostyli have a field of gonotrichia (otherwise known only in most African and two Indomalayan-Australasian genera). Additionally, the retromarginal edge of the metatibia is typically nodulose to tuberculate, sometimes weakly so, with the exception of the fossil genus *Exebotrigona* Engel & Michener. The clade includes the extant genus *Trigonisca* Moure (*Trigonisca s.str.*, *Leurotrigona* Moure, *Exochotrigona* Engel, and *Celetrigona* Moure). The fossil genus *Exebotrigona*, in Baltic amber, belongs to this clade as evidenced by the form of the marginal cell and small body size. Modern species of the infratribe occur from southern Mexico to southern Peru, Bolivia, and the southern reaches of the Central-West and Southeast Regions of Brazil.

Infratribe Meliponitae Lepeletier de Saint Fargeau (= Trigonini Moure, Lestrimelittini Moure): This group differs from Trigoniscitae by the distinctly acute base to the marginal cell, with it's breadth at the apex of the pterostigma little if any broader than the area encompassed by the submarginal cells. The forewing is usually over 4 mm in length. The worker gonostyli lack gonotrichia. The retromarginal edge of the metatibia is not nodulose or tuberculate. The clade includes all remaining extant genera of Meliponini [Table 2: subgeneric system of *Melipona* from Engel (in press-b)]. The Miocene genus *Proplebeia* Michener, in Dominican and Mexican amber, belongs to the *Plebeia*-group of this infratribe.

The fossil genera *Meliponorytes* Tosi and *Cretotrigona* Engel are currently considered *incertae sedis*, pending further study. *Meliponorytes* is a poorly understood genus of putatively two species in Sicilian amber, but has not been studied since the Bolognese archeologist Alessandro Tosi (1865–1949) described and figured the group in 1896. The material was in the Collezione di Mineralogia (Museo di Mineralogia), Universitá di Bologna but the current state of preservation relative to oxidation (Sicilian amber can turn quite black), crazing, and deterioration is unknown. The species are minute and have various features typical of minute Meliponini (*e.g.*, Michener, 2002), but other peculiar traits illustrated by Tosi (1896) require confirmation, although *Meliponorytes* appears to be similar to some African forms and is likely of the Hypotrigonina: Hypotrigonitae. The genus *Cretotrigona*, a stingless bee from the latest Cretaceous of eastern North America, is currently the oldest occurrence of eusocial bees and the earliest definitive crown-group bee (Michener & Grimaldi, 1988; Engel, 2000). Its placement among Meliponini is uncertain and so the genus is considered as unplaced among the subtribes. Other fossil meliponines have been recovered from Eocene amber of the Baltic region, and the Miocene of China, Ethiopia (M.S.E., unpubl. data), Mexico, and the Dominican Republic (Table 1).

As alluded to in the Introduction, stingless bees are not uncommon in the fossil record, and although the number of fossil species is not great, the abundance of individuals can be prodigious for certain taxa (Camargo *et al.*, 2000; Engel & Michener, 2013a). The same is true for meliponines in the Miocene deposits of Zhangpu. The stingless bees in Zhangpu amber represent both the Heterotrigonitae (*Tetragonula*) and Hypotrigonitae (*Austroplebeia*).

Key to Genera of Meliponini in Zhangpu Amber
(worker caste)

1. Retrolateral surface of metabasitarsus with basal sericeous area (Fig. 41); retrolateral surface of metatibia with keirotrichiate zone separated from apical margin by distinct apical glabrate zone and from retrodorsal margin by well-developed superior glabrate zone, at its widest about 0.5× width of keirotrichiate zone (Fig. 41); clivulus demarcating keirotrichate zone a distinct ridge; malar space linear; fringe of bristles on retromarginal edge of metatibia plumose (Fig. 42); yellow maculation lacking from mesoscutum and mesoscutellum .... *Tetragonula* Moure

—. Retrolateral surface of metabasitarsus without basal sericeous area (Figs. 59, 60); retrolateral surface of metatibia with keirotrichiate zone extending to apical margin and separated from retrodorsal margin by narrow superior glabrate zone, much narrower than 0.5× width of keirotrichiate zone (Figs. 59, 60); clivulus virtually absent, indistinct, keirotrichate zone gradually and shallowly sloping into superior glabrate zone (Fig. 58); malar space distinct, not linear (Fig. 54); fringe of bristles on retromarginal edge of metatibia simple (Fig. 60); yellow maculation present on mesoscutum and mesoscutellum (sometimes difficult to observe in fossils depending on preservation) (Figs. 52, 53, 55) .... *Austroplebeia* Moure

Genus *Tetragonula* Moure

The genus *Tetragonula* is the most diverse and widespread of the lineages of Asian Meliponini (Figs. 18–22), extending from northwestern India to Sri Lank in the west, across Southeast Asia to Yunnan in the north, southward throughout mainland Southeast Asia, across Malesia (north to Camiguin) and Papuasia to eastern Santa Isabel in the Solomon Islands (although it likely also extends to San Cristobal), and across northern and eastern Australia (Fig. 23). The genus is challenging for the presence of many cryptic species (*e.g.*, Sakagami, 1978; Franck *et al.*, 2004; Engel *et al.*, 2017; M.S.E.,

Figures 18–22. Photographs of workers of modern *Tetragonula* Moure. **18.** Dorsal habitus of *Tetragonula* (*Tetragonula*) *malaipanae* Engel, Michener, & Boontop from Thailand. **19.** Lateral habitus of *T.* (*T.*) *malaipanae*. **20.** Facial view of *T.* (*T.*) *malaipanae*. **21.** Facial view of *T.* (*Tetragonilla*) *collina* (Smith) from Thailand. **22.** Lateral habitus of *T.* (*T.*) *collina*.

pers. obs.), distinguished by seemingly trivial morphological differences or morphometrics but distinct in terms of their nesting biology and perhaps also ecology. Thus, while there are already a large number of species, this diversity may grow as further data are gathered.

Two subgenera are recognized among the modern fauna (Figs. 18–22): *Tetragonilla*, with four species, and the remainder in *Tetragonula s.str*. (Rasmussen *et al*., 2017; Engel *et al*., 2018). Although some authors have considered these two groups to be distinct genera (*e.g*., Moure, 1961; Rasmussen, 2008), the distinctions between them are fairly minor and it seems more beneficial to treat them as reciprocally monophyletic subgenera of a single, more broadly circumscribed genus. Indeed, when united together, *Tetragonula* in this sense is easily diagnosed and separated from other Asian genera (Rasmussen *et al*., 2017; Engel *et al*., 2018).

Interestingly, a single species of *Tetragonula* is relatively common in Zhangpu amber, analogous to the situation of *Proplebeia* in Dominican and Mexican ambers. The species is assigned to the nominate subgenus.

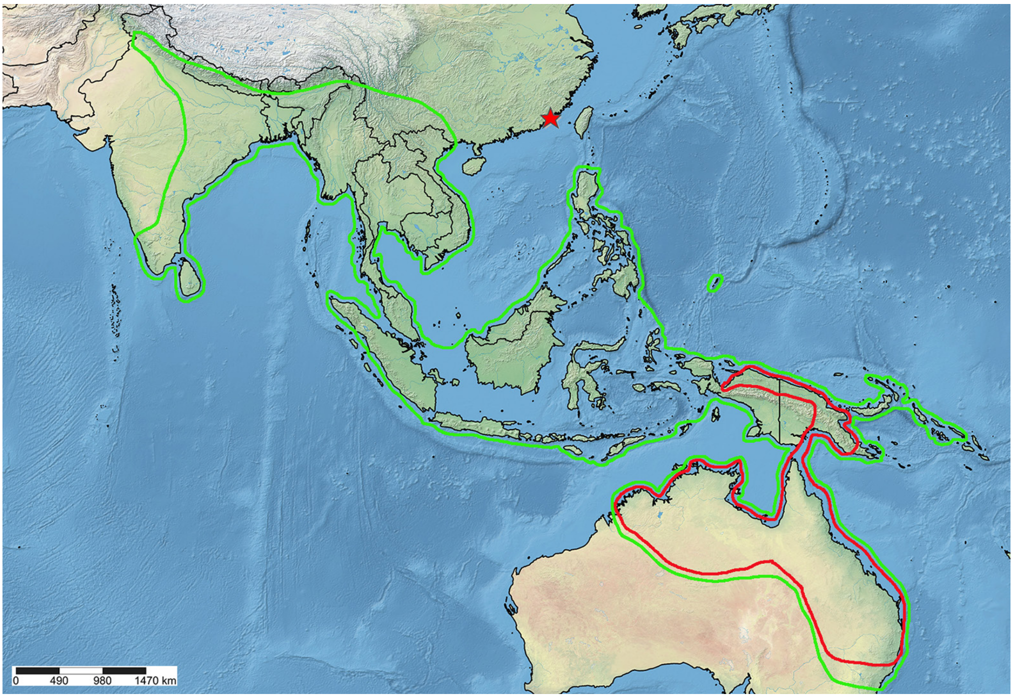


Figure 23. Map depicting modern day distributions of *Tetragonula* Moure (green line) and *Austroplebeia* Moure (red line) in relation to the deposits at Zhangpu (red star). Map produced using Shorthouse (2010).

Key to Subgenera of *Tetragonula s.l.*
(worker caste; modified from Engel *et al*., 2018)

1. Scape shorter than torulocellar distance (Figs. 20, 28, 32); about five distal hamuli (Fig. 39); retromarginal contour of metatibia slightly convex, with superior distal angle subangulate (Figs. 19, 33, 34, 40, 41); rastellum and penicillum usually composed of soft setae; forewing membrane rather uniformly colored, typically clear to lightly infuscate (Figs. 19, 37); pleural setae pale (Fig. 19); forewing marginal cell nearly closed, sometimes with apex of Rs bent and nebulous (*i.e.*, appendiculate), with or without 2r-rs stub arising at bend .... *Tetragonula* Moure, *s.str.*

—. Scape at least as long as torulocellar distance (Fig. 21); six distal hamuli; retromarginal contour of metatibia distinctly and broadly convex (Fig. 22), with superior distal angle rounded, almost without angulation; rastellum and penicillum composed of stiff setae; forewing membrane markedly bicolored, proximally darkly fuscate (Fig. 22); pleural setae fuscous to black (Fig. 22); forewing marginal cell more broadly opened apically, apex of Rs never bent (*i.e.*, never appendiculate) .... *Tetragonilla* Moure

Subgenus *Tetragonula* Moure

Tetragonula Moure, 1961: 206. Type species: *Trigona iridipennis* Smith, 1854, by original designation.

Flavotetragonula Shanas in Shanas & Faseeh, 2019: 34. Type species: *Tetragonula* (*Flavotetragonula*) *calophyllae* Shanas & Faseeh, 2019, by original designation. Synonymy *vide* Engel (2019).

The subgenus *Tetragonula* comprises the bulk of diversity within the genus as well as all Asian-Malesian-Papuasian Meliponini, with at least 31 species. *Tetragonula* is quite distinctive and was recognized as a group, albeit more informally as the "iridipennis-group" or "*Tetragonula*-group" (variably including *Tetragonilla*), even when it was lumped under *Trigona* or *Heterotrigona* (*e.g.*, Sakagami, 1978; Michener, 1990, 2007; Dollin *et al.*, 1997). The subgenus is easily recognized by the combination of the basal sericeous area of the proximal superior retrolateral surface of the metabasitarsus and the thickened and rounded mesoscutellum overhanging the metanotum and partially the propodeum, along with the slightly convex retromarginal metatibial contour bearing a subangulate superior distal angle, a narrowly open marginal cell apex, a uniformly colored forewing membrane, a scape that is shorter than the torulocellar distance, and a rastellum composed of soft setae, among other traits.

The proposal of a new subgenus for *T.* (*T.*) *gressitti* (Sakagami) and species putatively similar to it (Shanas & Faseeh, 2019) renders *Tetragonula s.str.* paraphyletic (Rasmussen & Cameron, 2010) and should be avoided, particularly as the proposed differences are exceptionally minor and somewhat subjective distinctions in wing venation or wing microtrichia. For example, the putative patch, narrower than 1Rs, beneath the juncture of 1Rs and the pterostigmal base is exceptionally variable, not only across Indomalayan *Tetragonula*, but even in some species between individuals within a nest. Furthermore, the present fossil species intermingles some of the traits between their subgenus and *Tetragonula s.str.*, demonstrating the failure of these characters to distinguish natural groups in *Tetragonula s.str.* Shanas & Faseeh (2019) also failed to recognize that the stub sometimes present at the apical bend of Rs is Rs_2 (beyond Rs_1 or 2r-rs), needlessly proposing a term (unculus) for this abscissa.

Key to Species Groups of *Tetragonula s.str.*
(worker caste)

Note that these groups are seemingly not natural, with the possible exception of the *carbonaria*-group (Rasmussen & Cameron, 2010). Accordingly, these groups are merely a convenience for aiding identification through the exclusion of blocks of diversity in this complicated and large genus, and should not be considered as representing natural groups from which evolutionary hypotheses can be based. Once the genus is comprehensively revised and a more extensive robust phylogeny including all of the known species is produced, then natural species groups should be circumscribed to aid the identification of these bees. For the time being, two groups of Sakagami (1978) — the *gressitti*-group and *geissleri*-group — are considered synonymous with the *laeviceps*-group. The key is adapted from Sakagami (1978) and Dollin *et al.* (1997).

1. Mesepisternum posteriorly sparsely setose, contrasting with rather densely setose anterior portion and metepisternum (Fig. 36); malar space linear or nearly so (Figs. 20, 32) 2

—. Mesepisternum and metepisternum densely and evenly covered with fine short setae; malar space developed, not linear [mesoscutal setal banding present, albeit sometimes poorly defined] .... *carbonaria*-group

Figures 24–26. Photographs of workers of *Tetragonula* (*Tetragonula*) *florilega*, new species, in mid-Miocene amber from Zhangpu, China. **24.** Right frontal oblique habitus of SEMC F002514. **25.** Right lateral habitus of NIGP 176108. **26.** Dorsal habitus of NIGP 176122.

2(1). Small bees, forewing including tegula 3.0–4.0 mm; mesoscutum with distinct setal bands separated by broad glabrous interspaces .... *iridipennis*-group

—. Larger bees, forewing including tegula 3.9–4.8 mm; mesoscutum rather evenly setose (*e.g.*, Fig. 38) .... *laeviceps*-group

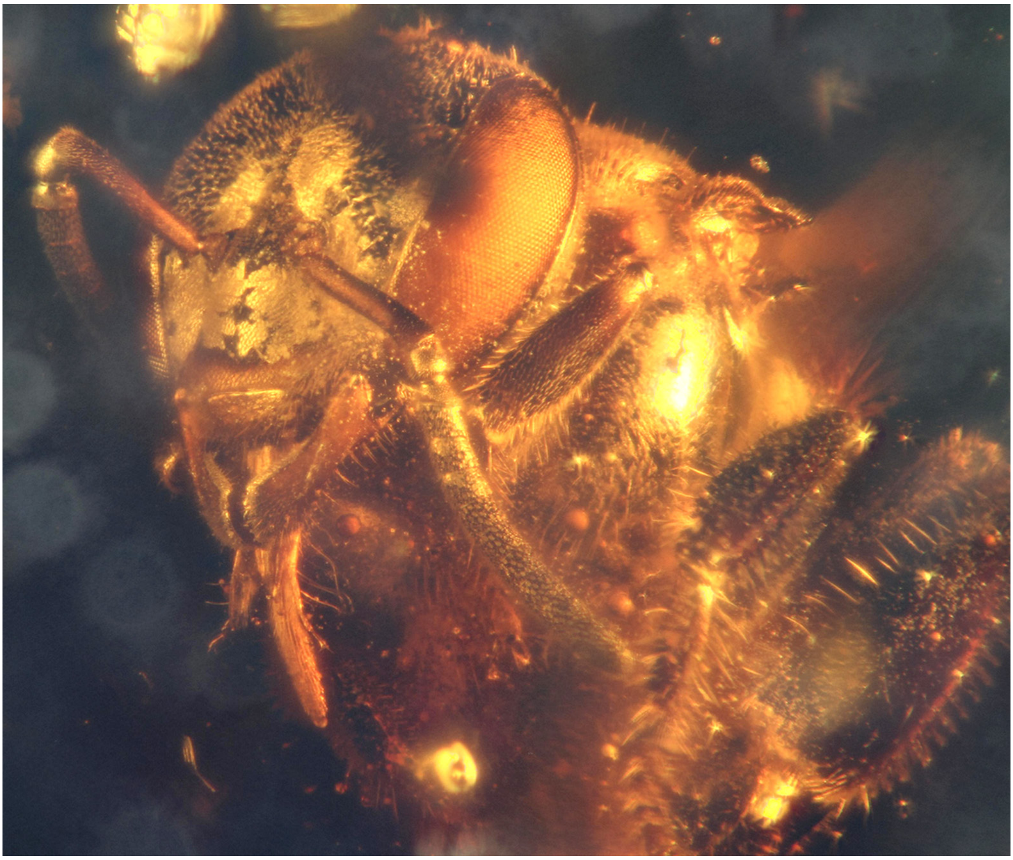


Figure 27. Left frontolateral oblique view of worker (SEMC F002514) of *Tetragonula* (*Tetragonula*) *florilega*, new species. Note elongate ventral setae of labial palpomeres I and II.

Tetragonula* (*Tetragonula*) *florilega Engel, new species

ZooBank: urn:lsid:zoobank.org:act:E37B966D-89B6-4F39-8C2E-CF9EDDAEFB27

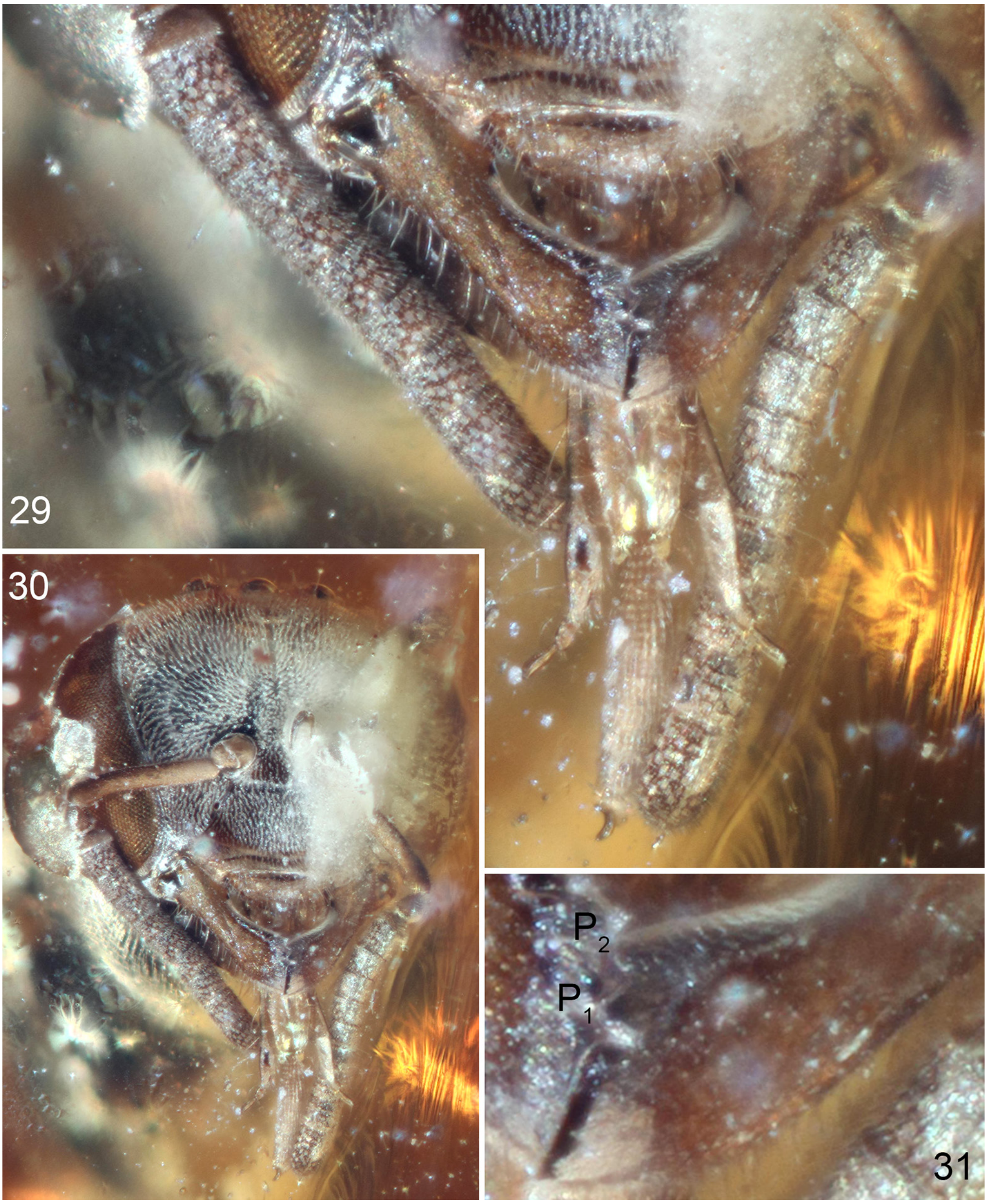
(Figs. 24–43)

Diagnosis: *Tetragonula florilega* intermingles traits of the last two informal species groups in the above key: the forewing length, including the tegula, is approximately 3.3 mm in most specimens, fitting the *iridipennis*-group, yet the mesoscutum is quite clearly evenly and finely setose (Fig. 38), without any longitudinal glabrous bands as is otherwise present the *laeviceps*-group. In addition, the clypeus is apically marked with tawny to yellow coloration (Figs. 27–30), and the mesoscutellum is sometimes tawny brown. As in most *Tetragonula*, the setae of the mesepisternum are distinctly sparser posteriorly (Fig. 36), contrasting with the more numerous setae of the anterior portion as well as the metepisternum.

Description: ♀: Total body length approximately 3.0–3.3 mm, forewing length (including tegula) 3.2–3.5 mm. Head wider than long, width 1.1–1.5 mm, length 1.12–1.15 mm; compound eye length 0.92–0.95 mm; upper interorbital distance 0.82–0.86, lower interorbital distance 0.58–0.63. Scape length 0.44–0.46 mm, shorter than torulocellar

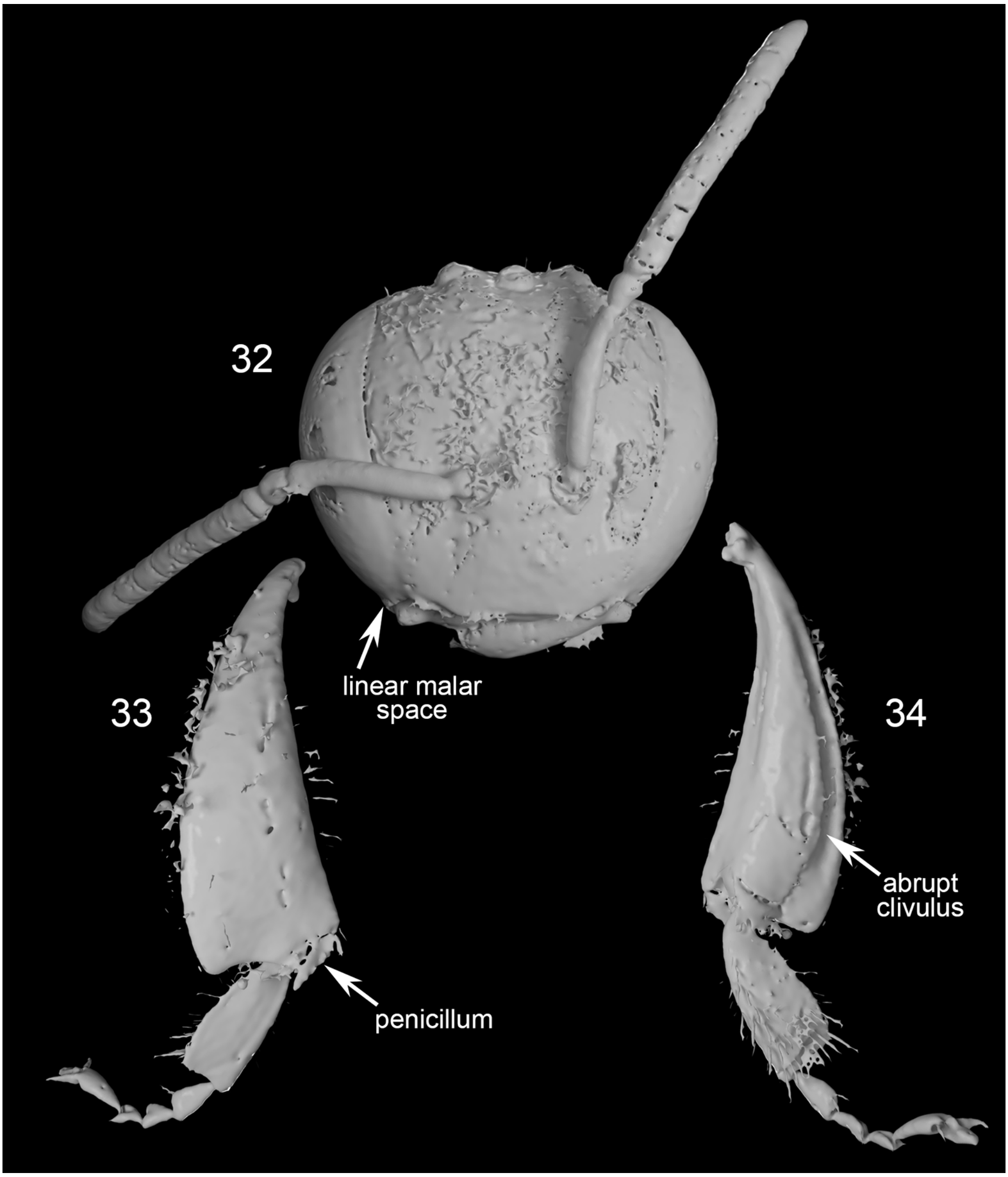
Figure 28. Oblique facial view of worker (NIGP 176110) of *Tetragonula* (*Tetragonula*) *florilega*, new species. Note yellowish apical two-fifths of clypeus.

distance, torulocellar distance 0.63 mm. Clypeus broader than long, approximately 2× as wide as long, length 0.14–0.15 mm, width 0.28–0.30 mm. Malar space linear (Figs. 24, 27–30, 32). Mandible with two, small preapical teeth (Fig. 31), with narrow incision separating first preapical tooth (P_1) from apical edentate margin; incision separating P_1 and P_2 slightly less than orthogonal, with acutely rounded angular geometric vertex. Labrum transverse, surface gently convex, apical margin faintly and broadly convex. Labial palpomeres I and II with elongate straight to slightly wavy ventral setae (Figs. 27, 29, 30). Mesoscutellum comparatively thick and broadly rounded in profile, overhanging metanotum and base of propodeum; basal area of propodeum subequal or slightly shorter than mesoscutellum, steeply sloping to rounded angle with vertical posterior surface. Forewing extending beyond apex of metasoma, marginal cell narrowly open apically, with faint nebulous stub (appendiculate), stub not bent and without stub of 2r-rs at origin; 1M slightly offset proximad 1cu-a; M straight, 2M terminating bluntly at nebulous 1m-cu (Fig. 37); hind wing with 5 distal hamuli (Fig.



Figures 29–31. Facial view and mouthpart structures of worker (SEMC F002515) of *Tetragonula* (*Tetragonula*) *florilega*, new species. **29.** Detail of labrum, mandibles, apical portions of labial palpomeres, portions of antennae, and glossa. **30.** Facial view. **31.** Detail of dentition of left mandible (P_1 and P_2 = first and second preapical teeth).

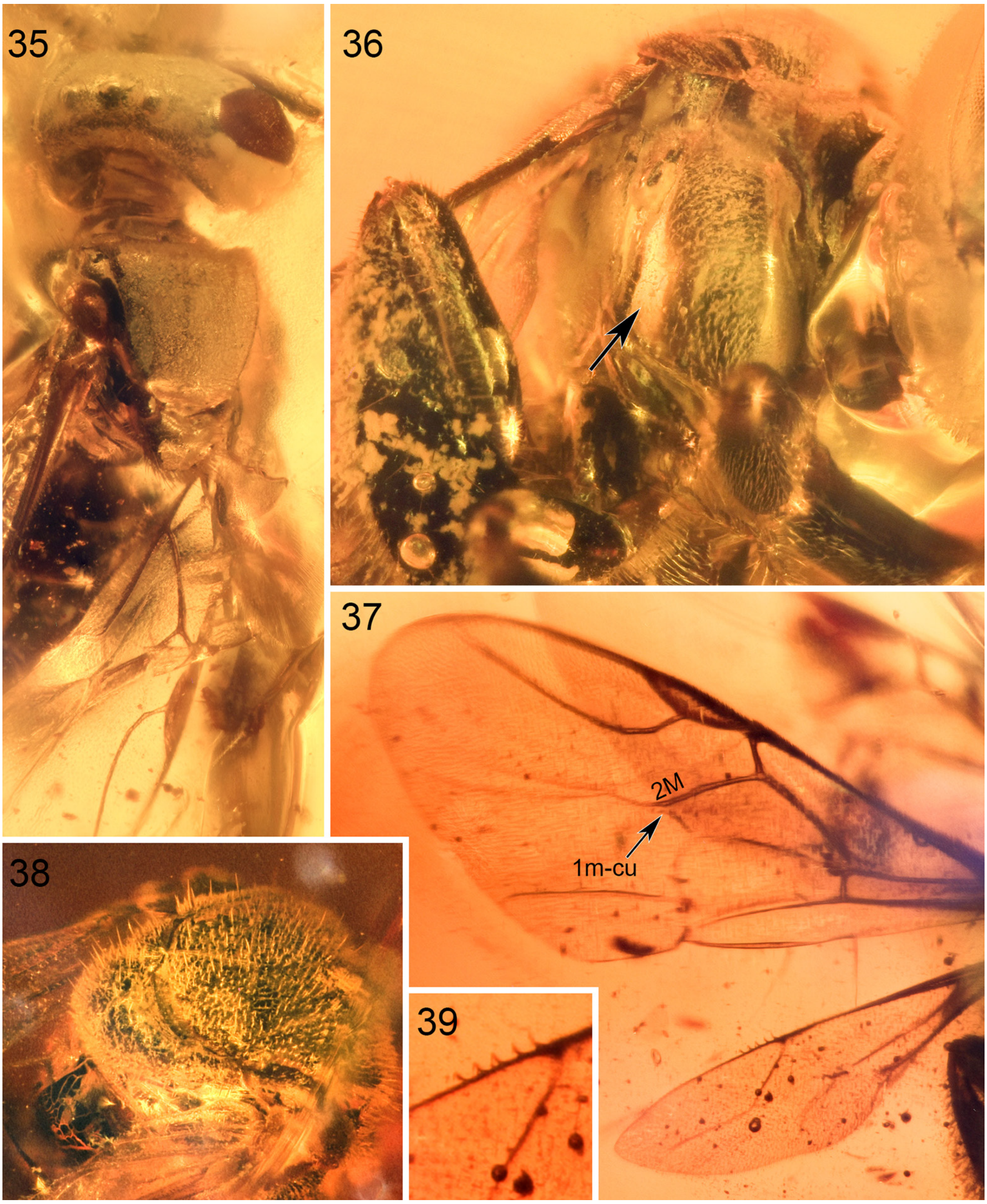
39), 1M distinctly bent proximally. Metatibia triangular, approximately 3× as long as greatest width; retromarginal contour slightly convex, with subangulate superior distal angle; corbicula shallowly concave, occupying distal third of prolateral surface (Fig. 40); keirotrichiate zone of retrolateral surface separated from supraglabrate zone by steep clivulus. Metabasitarsus with proventral margin straight, retrodorsal margin



Figures 32–34. Worker (NIGP 176093) of *Tetragonula* (*Tetragonula*) *florilega*, new species, µCT scans. **32.** Facial view. **33.** Prolateral view of metatibia and metatarsus. **34.** Retrolateral view of metatibia and metatarsus.

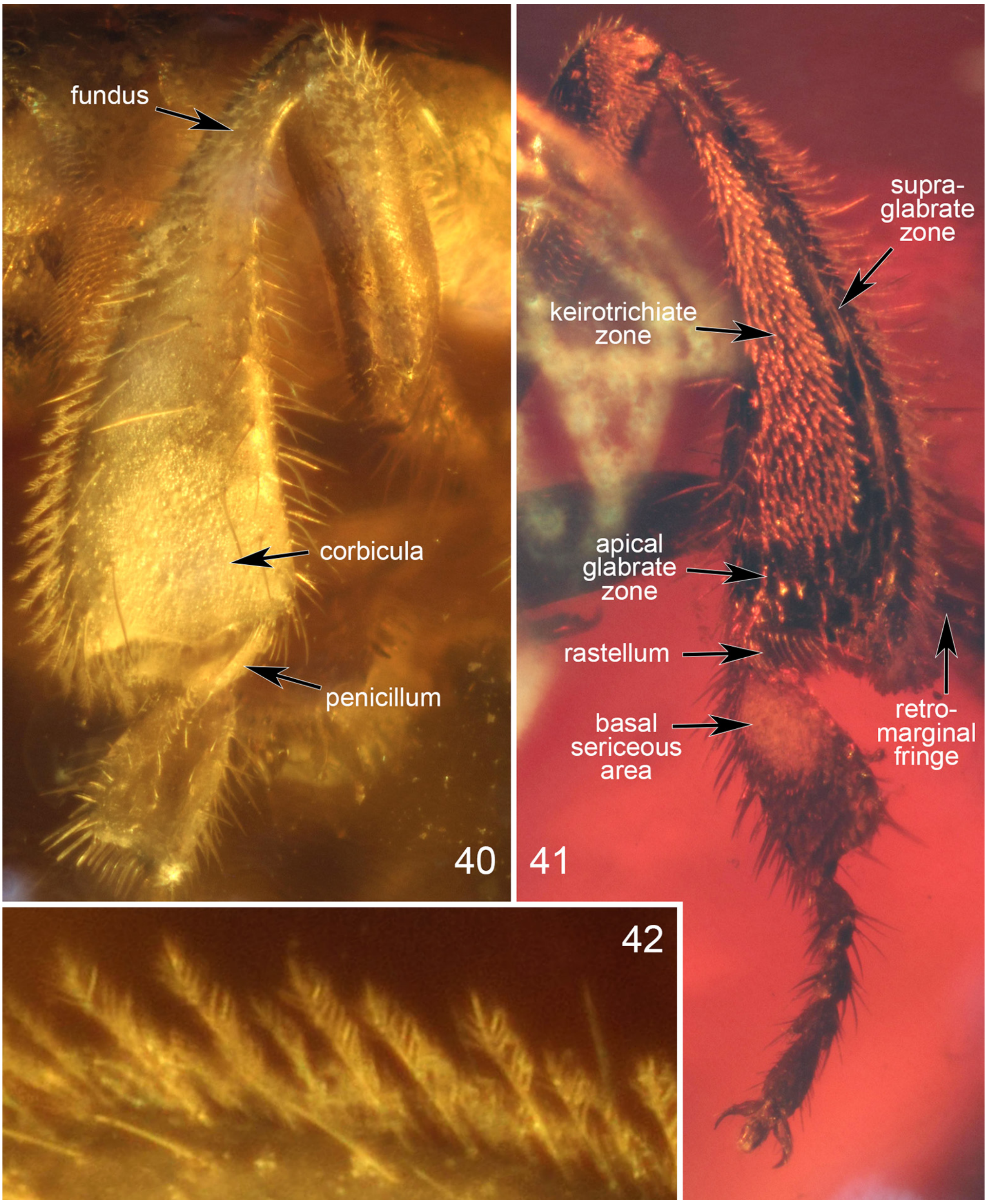
gently convex; superior distal angle not projecting (Figs. 33, 34, 40, 41); retrolateral surface with prominent basal sericeous area (Fig. 41). Metasoma short, subequal to head width, widest second and third segments, remaining terga progressively narrower.

Integument generally black to dark brown (silvery reflective surfaces on some specimens result from microscopic separation of integument from amber matrix; separation produces microscopic reflective air spaces that appear silvery, particularly under strong reflective lighting); mouthparts pale brown; mandible largely tawny to yellow, with black apical margin (Figs. 29–31); labrum brown to tawny; clypeus



Figures 35–39. Workers of *Tetragonula* (*Tetragonula*) *florilega*, new species. **35.** Dorsal view of head and oblique dorsal view of mesosoma (NIGP 176093). **36.** Mesosoma in profile, with arrow indicating largely bare posterior surface of mesepisternum relative to the more abundant, appressed, white, plumose setae of the anterior portion (AMNH Zh-001). **37.** Wing venation (SEMC F002514). **38.** Oblique dorsal view of mesosoma, noting uniform setation (NIGP 176124). **39.** Expanded detail of leading edge of hind wing showing distal hamuli (SEMC F002514).

largely black except apically tawny to yellow (in finest preserved specimens clypeus is apically yellow, progressing to a more brownish appearance in less well preserved individuals) (Figs. 24, 27–29); scape light brown to tawny, slightly darker dorsally (Figs. 25, 27, 28, 30), flagellum dark brown; remainder of head black. Mesosoma black, pro-



Figures 40–42. Leg details of workers of *Tetragonula* (*Tetragonula*) *florilega*, new species. **40.** Prolateral view of metatibia and metabasitarsus (NIGP 176111). **41.** Retrolateral view of metatibia and metatarsus (NIGP 176118). **42.** Detail of plumose retromarginal setal fringe along metatibia (NIGP 176111).

notum brown, pronotal lobe often light brown (Fig. 28); tegula light brown, sometimes appearing slightly semi-translucent; mesoscutellum black (Figs. 35, 38) to partly tawny brown with black or dark brown on axillae and anterior of mesoscutellum in some individuals (Fig. 26). Wing membranes hyaline clear (Figs. 24, 26, 37); tubular veins dark brown to brown, pterostigma lighter centrally, nebulous veins brown to light brown.

Figures 43–44. Lateral habitus μCT scans of workers of Zhangpu stingless bees. **43.** *Tetragonula* (*Tetragonula*) *florilega*, new species (NIGP 176093). **44.** *Austroplebeia* (*Anteplebeina*) *fujianica*, new subgenus and species (holotype, NIGP 176057). Note differences in malar spaces, metatibiae, and mesoscutella + propodea.

Legs largely black to dark brown, slightly lighter on pro- and mesotarsi. Metasoma dark brown to black.

Integument mostly smooth and shining, with scattered, faint, shallow, minute punctures; clypeus with minute punctures separated by 1–2× a puncture width, face with faint minute punctures sparser, separated by 2.5–5× a puncture width, punctures of gena as on face, postgena apparently impunctate and faintly imbricate. Mesosoma largely smooth and shining; mesoscutum and mesoscutellum with sparse, faint, shallow, minute punctures; tegula finely and faintly imbricate; mesepisternum apparently impunctate; basal area of propodeum smooth, polished. Metasomal terga smooth, impunctate; sterna faintly imbricate.

Pubescence largely decumbent and pale. Labrum with sparse, minute, simple setae except apically setae longer; face with abundant, fine, decumbent, minute, simple setae, not obscuring integument (Figs. 24, 28, 30), such setae on lower two thirds to one half of face minutely plumose, particularly around antennal toruli; setae of vertex and ocellocular area longer and erect; setae of gena like those of face; postgena with scattered, erect, simple setae. Mesoscutum with scattered, fine, erect, short, simple, such setae abundant but not obscuring integument, uniformly distributed (*i.e.*, not organized into linear bands with longitudinal glabrous interspaces) (Figs. 35, 38); mesoscutellum with setation as on mesoscutellum except some setae slightly longer (Fig. 38), particularly posteriorly; mesepisternum with decumbent, fine, minutely plumose setae anteriorly, posteriorly largely glabrous (Fig. 36), with some fine, simple setae largely ventrally; metepisternum and lateral surface of propodeum with setae like anterior half of mesepisternum, albeit those of propodeum not as numerous as those of metepisternum. Wing membrane with scattered microtrichia, area beneath costal notch with microtrichia; microtrichia along forewing apical margin absent. Metatibia with scattered, long, erect, simple setae on proventral surface, retromarginal fringe almost entirely composed of long (although not as long as setae of proventral surface), plmuose setae (Figs. 40–42); setae on fundus largely short, subappressed to suberect, fine, largely simple setae (Fig. 40); remainder of prolateral surface including corbicula sparse, elongate, erect to suberect, simple setae; penicillum composed of fine waxy setae (Fig. 40), rastellum composed of semi-soft setae (Fig. 41); retrolateral surface of metatibia with keirotrichiate zone ooccupying majority of surface, broader than supraglabrate zone, apical with about as long as apicoglabrate zone (Fig. 41); prolateral surface of metabasitarsus with pollen pocket, ridge for fine fimbriate line exceedingly weak, prolateral surface otherwise with scattered, sparse, short, erect, simple setae; proventral surface with scattered elongate, suberect setae; retrodorsal margin with a few short setae; retrolateral surface of metabasitarsus with elongate, apically directed, simple bristles forming rough setal ctenidia (Fig. 41), apically last row forming apical bristle comb projecting beyond metabasitarsal apex. Metasomal terga largely glabrous, with exceptionally sparse minute, appressed, fine, simple setae largely present laterally, and with similar minute, appressed, apically directed, fine, simple setae scattered apically and subapically, discs with exceedingly sparse, short, erect, simple setae; terga V and VI with erect discal setae seemingly slightly less sparse than preceding terga and with suberect, apically directed, short setae apically; metasomal sterna with long, erect, simple setae.

♀: *Latet.*

♂: *Latet.*

HOLOTYPE: ♀, NIGP 176093; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

PARATYPES (47♀♀): 1♀ (with pollen in corbicula), NIGP 176094; 1♀, NIGP 176095; 1♀, NIGP 176096; 1♀, NIGP 176097; 1♀, NIGP 176098; 1♀, NIGP 176099; 1♀, NIGP 176100; 1♀, NIGP 176101; 1♀, NIGP 176102; 1♀, NIGP 176103; 1♀, NIGP 176104; 1♀, NIGP 176105; 1♀, NIGP 176106; 1♀, NIGP 176107; 1♀, NIGP 176108; 1♀, NIGP 176109; 1♀, NIGP 176110; 1♀, NIGP 176111; 1♀, NIGP 176112; 1♀, NIGP 176113; 1♀, NIGP 176114; 1♀, NIGP 176115; 1♀, NIGP 176116; 1♀, NIGP 176117; 1♀, NIGP 176118; 1♀, NIGP 176119; 1♀, NIGP 176120; 1♀, NIGP 176121; 1♀, NIGP 176122; 1♀, NIGP 176123; 1♀, NIGP 176124; 1♀, NIGP 176125; 1♀, NIGP 176126; 1♀, NIGP 176127; 5♀♀, NIGP 176128; 3♀♀ (tightly clustered together), NIGP 176129, same locality and repository as holotype; 1♀, SEMC F002514; 1♀, SEMC F002515; 2♀♀, SEMC F002516, in Division of Entomology, University of Kansas Natural History Museum; 1♀, AMNH Zh-001, in Division of Invertebrate Zoölogy, American Museum of Natural History.

ATTRIBUTED NON-TYPE MATERIAL (37♀♀): 1♀, NIGP 176060; 1♀, NIGP 176061; 1♀, NIGP 176062; 1♀, NIGP 176063; 1♀, NIGP 176064; 1♀, NIGP 176065; 1♀, NIGP 176066;

1♀, NIGP 176067; 1♀, NIGP 176068; 1♀ (partial), NIGP 176069; 1♀ (partial), NIGP 176070; 1♀, NIGP 176071; 1♀, NIGP 176072; 3♀♀, NIGP 176073; 1♀, NIGP 176074; 1♀, NIGP 176075; 1♀, NIGP 176076; 3♀♀, NIGP 176077; 1♀, NIGP 176078; 1♀, NIGP 176079; 1♀, NIGP 176080; 1♀, NIGP 176081; 1♀, NIGP 176082; 1♀, NIGP 176083; 1♀, NIGP 176084; 1♀ (head only), NIGP 176085; 1♀, NIGP 176086; 1♀, NIGP 176087; 1♀, NIGP 176088; 1♀, NIGP 176089; 1♀, NIGP 176090; 1♀, NIGP 176091; 1♀, NIGP 176092; same locality and repository as holotype.

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

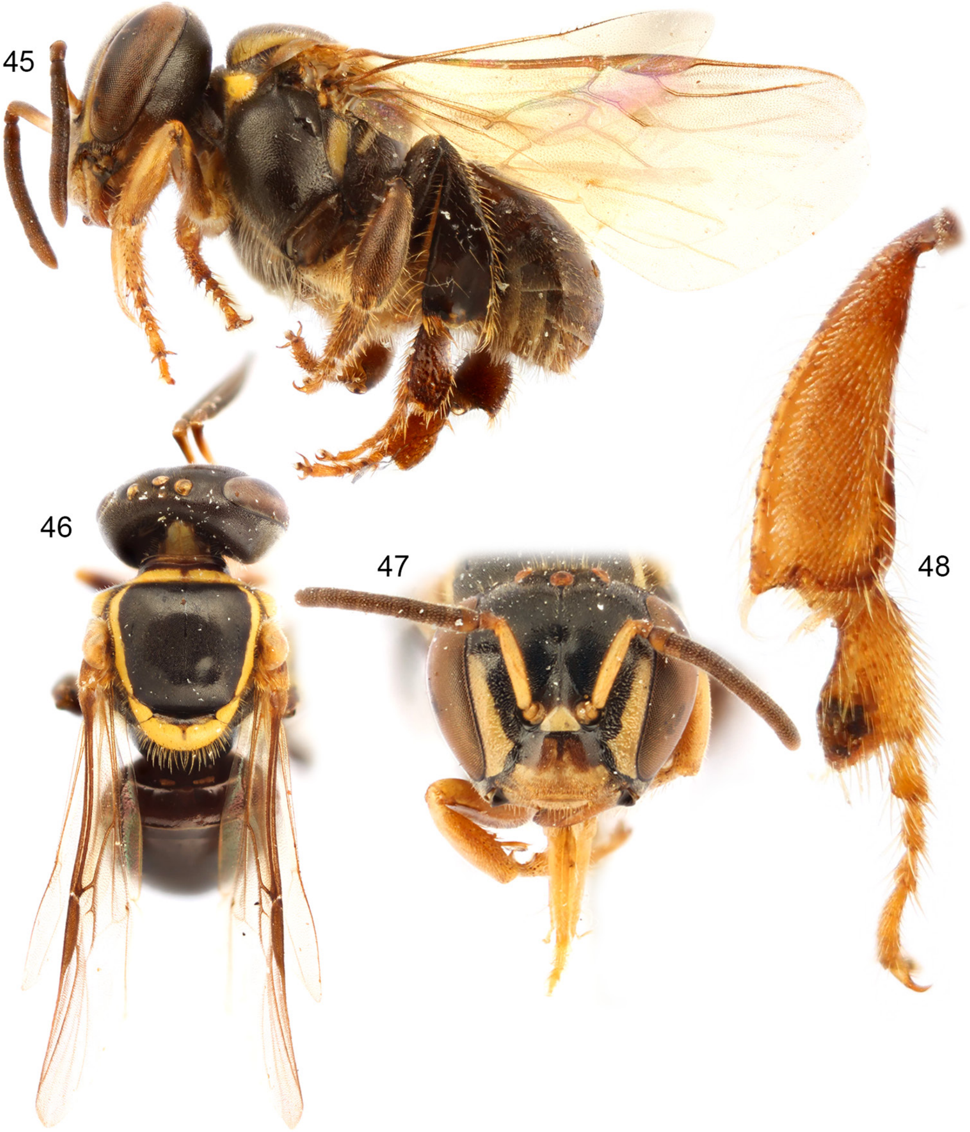
Horizon: Middle Miocene: Langhian, 14.7 Ma; sedimentary layer II, Fotan Group.

Etymology: The specific epithet is taken from the Latin *florilegus*, meaning, "flower-gathering."

Comments: It was initially believed that those individuals with a more tawny brown mesoscutellum represented a separate distinct species of *Tetragonula*. However, no further differences could be identified among the series of specimens available and so it was considered merely a variation. As more material becomes available in the future, correlations between differences in the degree of tawny brown to yellow on the clypeus (those with yellow have a larger part of the clypeal apex colored versus those with more tawny or brown colors, although the latter almost universally have the integument seemingly more augmented by preservation) and that of tawny color on the mesoscutellum to see if these are associated with morphometric distinctions, suggesting two cryptic species in the Zhangpu biota.

Genus *Austroplebeia* Moure

The genus *Austroplebeia* encompasses five species of rather distinctive Australian and Papuan stingless bees (Moure, 1961; Michener, 1990, 2007; Dollin *et al.*, 2015; Halcroft *et al.*, 2016) (Figs. 45–47). Within Australia, *Austroplebeia* occurs across the north and then along eastern Australia south to northern New South Wales. In addition, a single species is present in New Guinea, found throughout the Papuan (Bird's Tail) and Huon Peninsulas in the east and then westward north of the Central Highlands to at least the eastern boundaries of West Papua (Fig. 23). In New Guinea the genus is represented solely by *Austroplebeia cincta* (Mocsáry), and this species should be sought in the Doberai (Bird's Head) Peninsula, south of the Central Highlands, and perhaps also on the Tanimbar, Aru, and Kai Islands as these are biogeographically allied to Australia and east of Wallace's Line. Although Tanimbar and Kai are west of the Lydekker Line and so may not harbor a New Guinean species like *A. cincta*, there are Papuan and Australian endemic species in those faunas, such as the kangaroo *Thylogale brunii* (Schreber) (Macropodidae) in the Kai and Aru Islands. The Aru Islands are situated on the Arafura Shelf and during episodes of glaciation have been contiguous with New Guinea and northern Australia (Yokoyama *et al.*, 2001), and harbor largely evergreen forests that are part of the Vogelkop-Aru Lowland Rainforest Ecosubregion (Wikramanayake *et al.*, 2002). Thus, populations of *A. cincta* would have had easy access to at least these small islands during periods of the recent past. Kai and Tanimbar are part of the Banda Sea Islands Moist Deciduous Forests Ecoregion (Monk *et al.*, 1997), all which would seemingly represent suitable habitat for *A. cincta* as long as some long-distance dispersal event allowed for the arrival of the bees. These islands have been poorly surveyed for Anthophila and this must be addressed to better understand the regional biogeography and evolution of Papuasian bees.



Figures 45–48. Photographs of workers of *Austroplebeia* (*Austroplebeia*) *cincta* (Mocsáry) from New Guinea. **45.** Lateral habitus. **46.** Dorsal habitus. **47.** Facial view. **48.** Retrolateral surface of metatibia and metabasitarsus.

The genus can be quickly distinguished from other Indomalayan-Australasian lineages of Meliponini by the presence of distinct yellow maculation on the head and mesosoma (Figs. 45–47). In addition, the genus has the keirotrichiate zone of the retrolateral metatibial surface broad, with only a narrow, slightly depressed, superior glabrate zone, and the keirotrichia extend to the apical margin rather than separated by a broad apical glabrate zone (Fig. 48). The fringe setae along the retromargin of the metatibia are simple, and the corbicula is comparatively shallow on the prolateral surface apically. The mesoscutellum is rounded but not thickened in profile, and somewhat projects over the metanotum medially. The basal area of the propodeum is about as long as or slightly longer than the mesoscutellum and slopes gently to a rounded angle with the vertical posterior surface.

Quite remarkably, a single distinctive species of *Austroplebeia* was recovered from Zhangpu, although in far lesser abundance than *T. florilega*, described above. The fossil agrees with the circumscription of *Austroplebeia* in virtually all details, with the exception of some differences in the head and wing venation. Based on these differences the species is placed into a new subgenus, but there are far more shared characters than differences. In order to emphasize these shared similarities and the interesting biogeographic connection, we have preferred such a classificatory arrangement to a more extreme and finely split system in which the fossil is placed in its own genus that, while exceptionally similar and related to *Austroplebeia*, would still obscure its linkage to those species of Australia and New Guinea. Regardless, the presence of a species from the *Austroplebeia* clade in southeastern China during the Middle Miocene greatly expands the historical geographic occurrence of the genus outside of the Sahul (= Meganesia or Austrolinea) and into mainland Asia.

In the keys to genera of Indomalayan and Papuasian Meliponini (Rasmussen *et al.*, 2017; Engel *et al.*, 2018), the fossil runs naturally to *Austroplebeia*. The following couplet allows for distinguishing the two subgenera now included therein and can be used in conjunction with the earlier keys.

Key to Subgenera of *Austroplebeia*
(worker caste)

1\. Malar space short, one-half or less of flagellar diameter; basal vein (1M) distad 1cu-a; 6 distal hamuli .... *Austroplebeia* Moure, *s.str*.

—. Malar space of moderate length, as long as flagellar diameter (Fig. 54); basal vein (1M) confluent with 1cu-a (Fig. 62); 5 distal hamuli .... *Anteplebeina* Engel, n. subgen.

Anteplebeina Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:C096F1FD-68A8-45F6-8518-41BD855A88A4

Type species: *Austroplebeia* (*Anteplebeina*) *fujianica* Engel, new species.

Diagnosis: The new subgenus can be most easily distinguished from *Austroplebeia s.str*. in the more developed malar space (Fig. 54), with a length approximately that of the flagellar diameter (or approximately 0.75–0.80× the basal mandibular width) (versus 0.4–0.5× the flagellar diameter or 0.2–0.3× the basal mandibular width in *Austroplebeia s.str*.). Additionally, 1M is confluent with 1cu-a rather than the slightly distad position in *Austroplebeia s.str*., and M is straight but extends slightly beyond 1m-cu as a tubular vein and therefore the proximal half of 3M is tubular, versus M straight and terminating at or slightly before 1m-cu as a tubular vein (*i.e.*, 2M tubular but 3M wholly nebulous) (Fig. 62). Lastly, while 2Rs and 1rs-m are not evident in *Austroplebeia s.str*., these veins are weakly nebulous in *Anteplebeina*.

Description: Workers small, total length ca. 4.4 mm, forewing length ca. 3.6 mm; integument faintly tessellate, some places with widely-scattered minute punctures on head and mesosoma, with distinct pale yellow maculation on face (Fig. 54), particularly below tangent of antennal toruli, mesoscutum, mesoscutellum, and metepisternum (Figs. 50, 52, 53, 55, 61). Setae on body mostly fine, short, and simple; mesoscutum with abundant erect, fine, short, simple setae; disc of mesoscutellum with similar setae

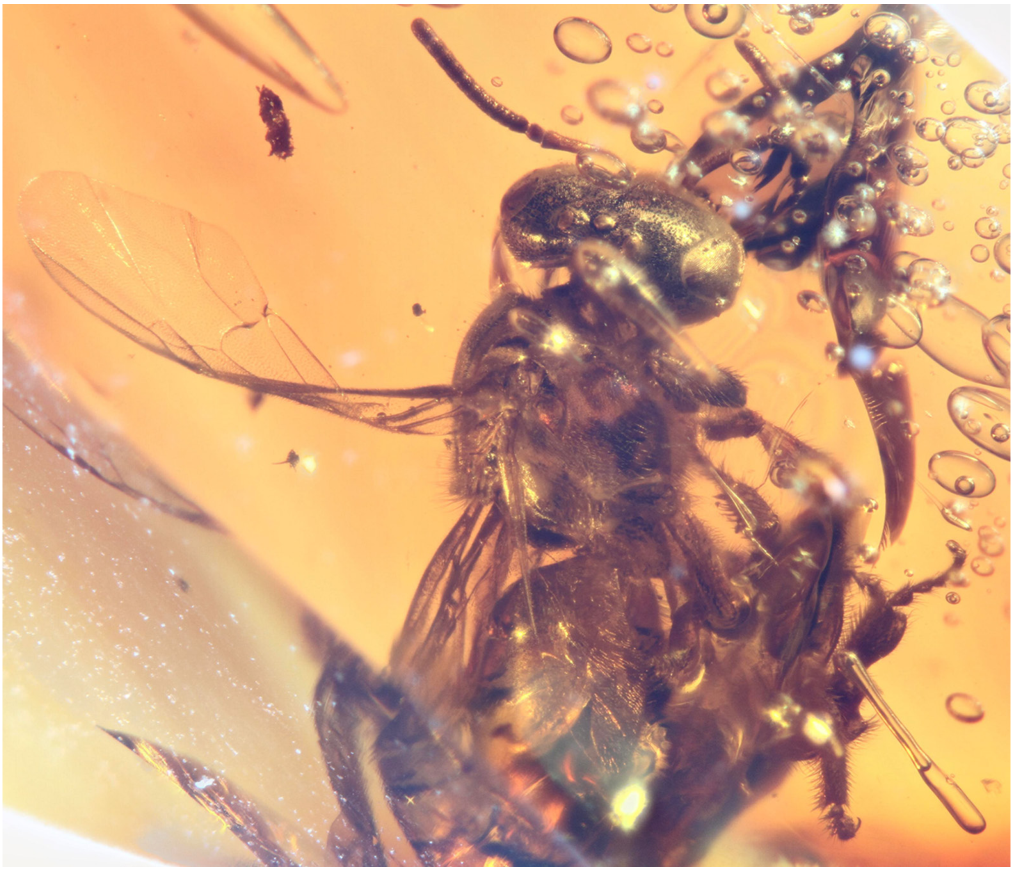
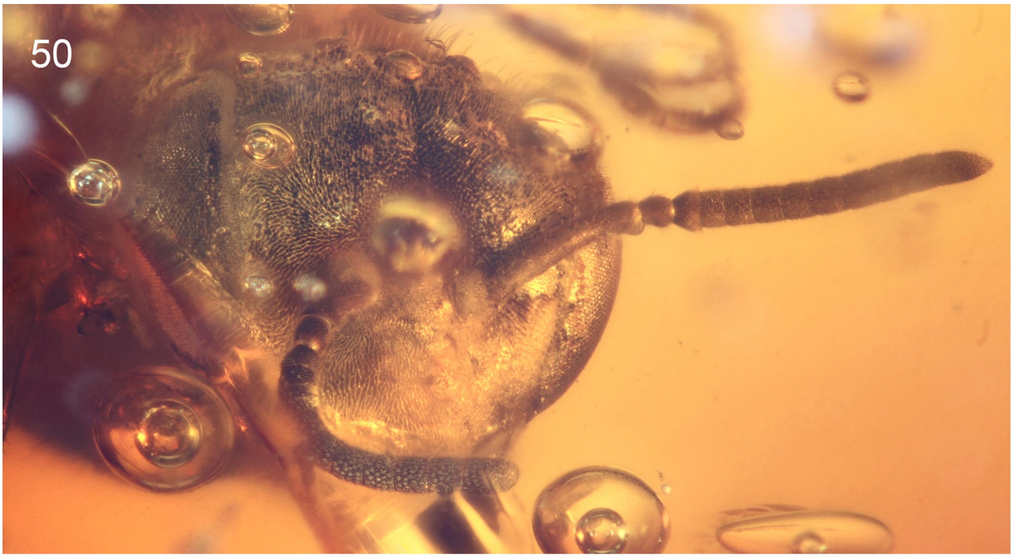
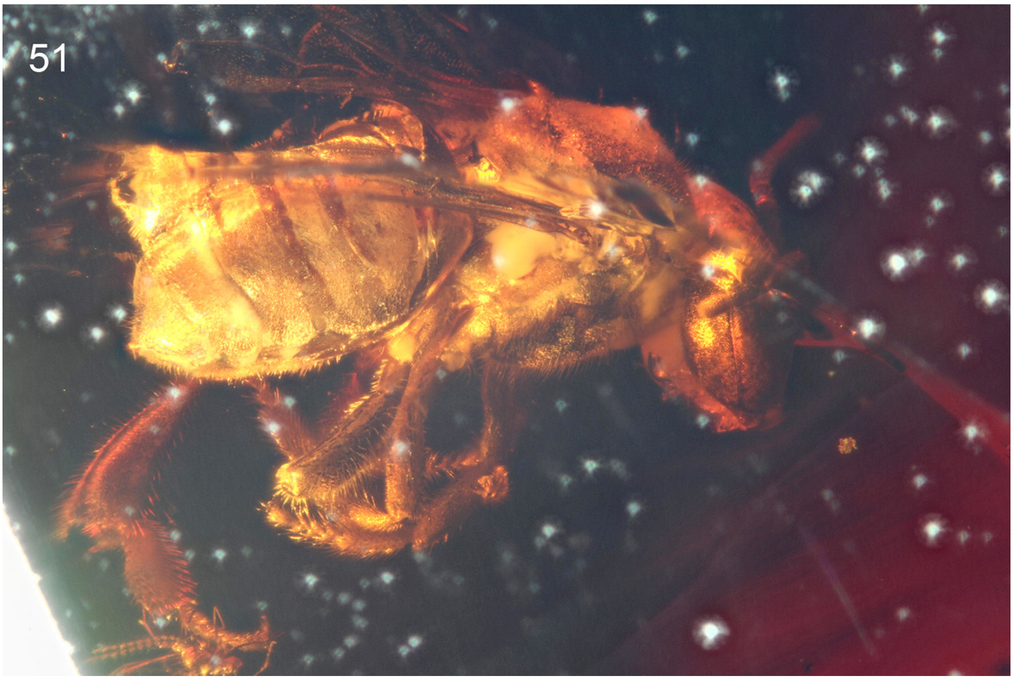


Figure 49. Right lateral habitus of holotype worker (NIGP 176057) of *Austroplebeia* (*Anteplebeina*) *fujianica*, new species, in mid-Miocene amber from Zhangpu, China.

to those of mesoscutum except nearly twice as long, particularly along posterior margin; setation pale to white.

Head as broad as mesosoma, broader than long, with face broader than compound eye length; vertex gently rounded, not produced or ridged; preoccipital area rounded; ocelloccipital distance slightly more than one ocellar diameter; interocellar distance about 3× median ocellar diameter, greater than ocellocular distance (interocellar distance 1.3× ocellocular distance); ocellocular distance about 2.25× ocellar diameter; scape shorter than antennal-ocellar distance, not reaching median ocellus; ocelli near top of vertex; flagellomeres about as long as or slightly longer than wide; flagellomere I trapezoidal, shorter than flagellomere II; flagellomere II about as long as flagellomere III (Fig. 54); intertorular distance slightly shorter than torulocular distance; upper torular tangent slightly below facial midlength (Fig. 54); gena rounded, slightly narrower than compound eye in profile; supraäntennal area with triangular medial elevation; frontal carina absent; malar area produced, moderate length, as long as flagellar diameter (Fig. 54); labrum transverse, simple, apical margin rounded; mandible bidentate, teeth well defined, acute, and incised, interdental spaces distinct but not broadly incised, instead narrowly V-shaped, first preapical tooth (P_1) distinctly forward of P_2; labial palpomeres I and II with a few, scattered, long (slightly to much longer than width of palpomeres), straight to slightly wavy setae.

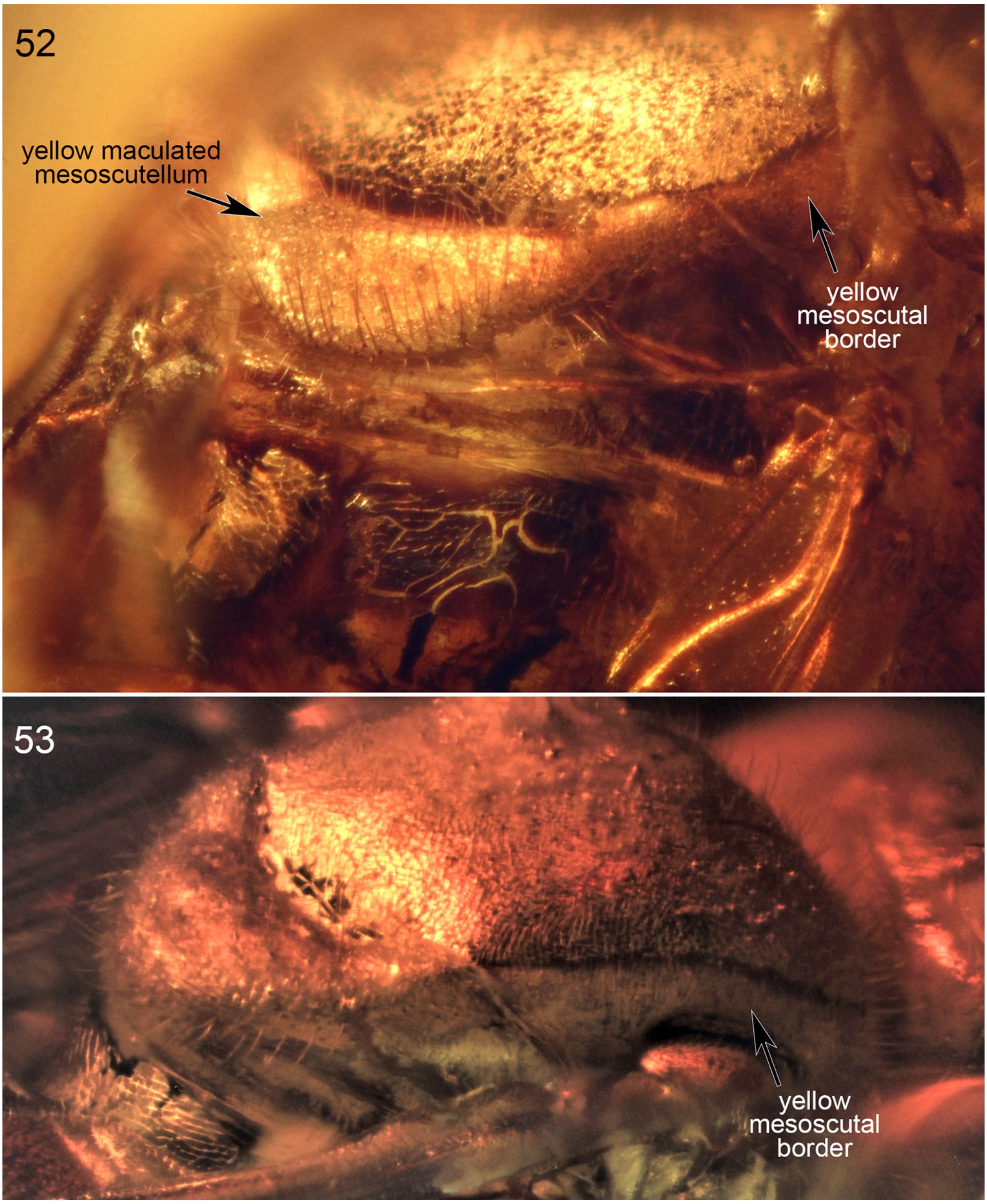




Figures 50–51. Workers of *Austroplebeia* (*Anteplebeina*) *fujianica*, new species. **50.** Facial view of holotype (NIGP 176057). **51.** Right lateral habitus of SEMC F002513.

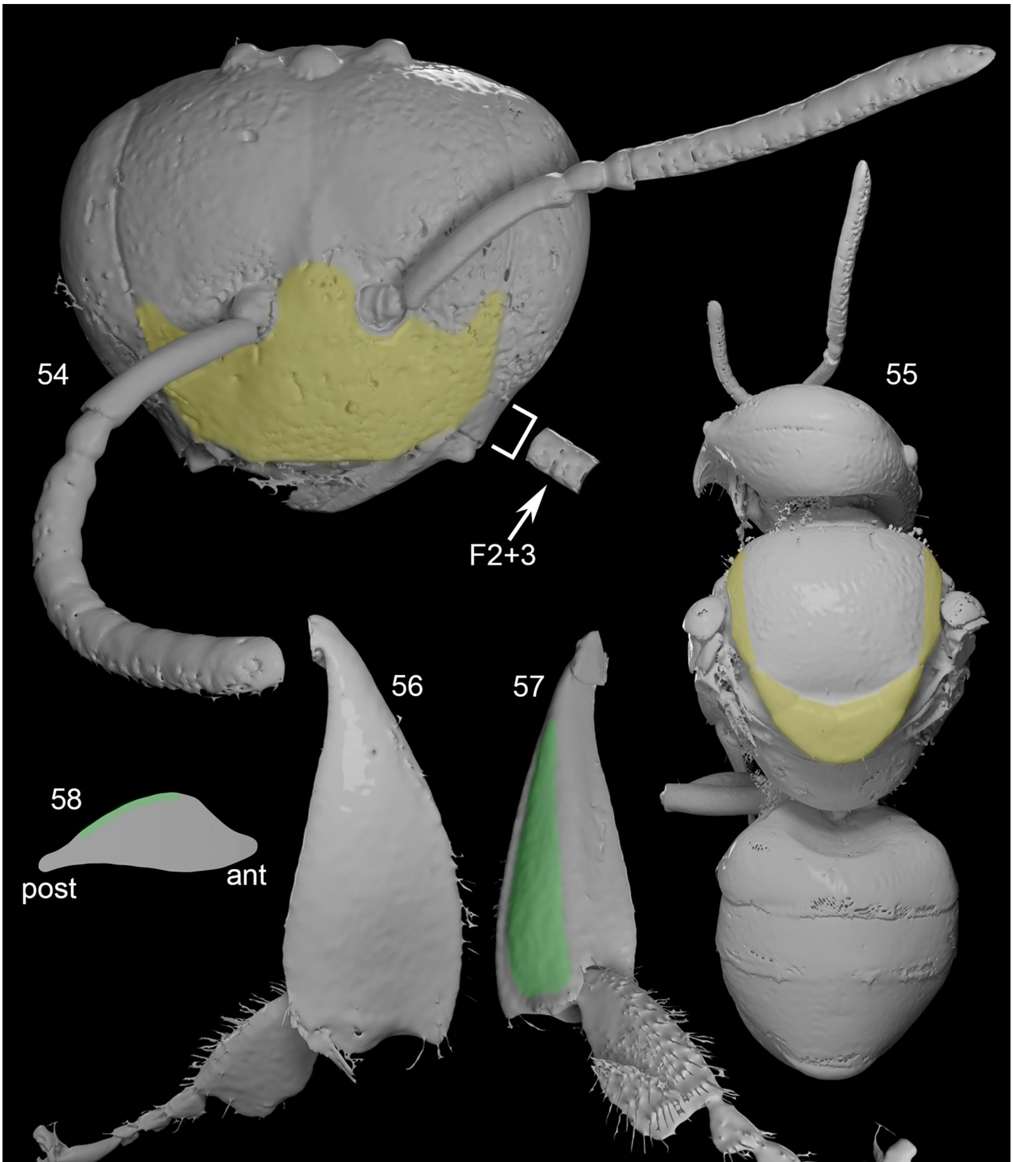
Mesoscutum with median sulcus faintly impressed, extending to slightly beyond mesoscutal midlength; notauli scarcely evident, not impressed; mesoscutellum short, acutely rounded in lateral aspect (Figs. 44, 51–53), slightly overhanging metanotum in dorsal view, shining transverse depression on mesoscuto-mesoscutellar sulcus simple; propodeum gently sloping; basal area slightly longer than mesoscutellum, glabrous, shining, faintly reticulate (Figs. 52, 53); propodeal spiracle elongate.

Forewing extending beyond apex of metasoma, with 2Rs, 1rs-m, 1m-cu, apical half 3M, 4M, apical half 1Cu, 2Cu, 3Cu, and 2cu-a indicated by brownish or pale nebu-



Figures 52–53. Mesosomal details of workers of *Austroplebeia* (*Anteplebeina*) *fujianica*, new species (note also finely polished reticulate propodeal sculpturing in both specimens). **52.** Posterior-dorsal-oblique view of NIGP 176057 (holotype). **53.** Posterior-dorsal-oblique view of SEMC F002513.

lous traces and fenestrae demarcated by faint white spectral lines on wing membrane; membrane with light brown microtrichia; prestigma short, scarcely longer than anterior width of 1Rs; pterostigma slender; marginal cell slightly more than 4× as long as maximum breadth, separated from wing apex by slightly more than its maximum width, apex narrowly open, opening about one-quarter maximum marginal cell width, 4Rs with nebulous, angled apex (*i.e.*, appendiculate), without nebulous stub of 2r-rs



Figures 54–58. Worker (holotype, NIGP 176057) of *Austroplebeia* (*Anteplebeina*) *fujianica*, new species, μCT scans (yellow highlights indicate areas of yellow maculation; green indicates area of keirotrichiate zone). **54.** Facial view (note malar space in relation to diameter of flagellomeres II + III). **55.** Dorsal habitus. **56.** Prolateral view of metatibia and metatarsus. **57.** Retrolateral view of metatibia and metatarsus. **58.** Cross-section of metatibia showing gently sloping clivulus.

(Fig. 62); 1M confluent with 1cu-a (Fig. 62); submarginal angle nearly orthogonal; M straight, not angled at 1m-cu (*i.e.*, angle between 2M and 3M linear or at most faintly less than 180°); 3M tubular in basal half, then nebulous; 2Rs straight; 1rs-m straight; r-rs slightly longer than 3Rs; 1m-cu short, only weakly bent apically near M. Hind wing with 5 distal hamuli; radial and cubital cells closed by nebulous veins.

Metatibia approximately triangular (Figs. 56, 57, 59), approximately 2.4× as long as greatest width; retromargin gently curved with subangulate distal superior angle (Figs. 56, 57), retromarginal setae and superior prolateral surface simple (Figs. 59, 60); prolateral surface shallowly concave apically, with corbicula occupying slightly less than apical half; retrolateral surface with broad weakly elevated keirotrichiate zone and narrow superior subglabrous zone (Figs. 57, 59, 60), with shallowly sloping clivulus (Fig. 58); keirotrichiate zone 2.5–3× as broad as superior glabrate zone (Figs. 59, 60), keirotrichiate zone extending to apical margin (Fig. 59), with keirotrichiate zone narrowing and superior glabrate zone broadening in apicalmost portion of metatibia; penicillum and rastellar comb present, each composed of fine stiff setae. Metabasitarsus with proventral margin straight, retrodorsal margin gently sloping posteriorly to about midlength, then paralleling proventral margin to apex (Fig. 60), proventral margin comparatively straight, distal superior angle not projecting; retrolateral surface without basal sericeous area (Figs. 59, 60).

Metasoma broad, almost as wide as mesosoma, with first metasomal tergum smooth and shining, laterally finely and faintly tessellate, remaining terga finely and faintly tessellate, all terga impunctate, terga with sparse, short to minute, erect, simple setae intermingled with exceedingly sparse appressed to subappressed, minute, simple setae; tergum VI with sparse erect setae distinctly longer, up to twice length of erect setae on preceding terga; sterna finely imbricate, with numerous elongate, fine, erect, simple setae and intermingled with more scattered, short, erect, simple setae.

ETYMOLOGY: The new subgeneric name is a combination of the Latin words *ante* ("before"), *plēbēia* ("plebeian", "commoner", "plebe"), and the feminine diminutive suffix *–īna* ("wife of," feminine suffix with diminutive implication). The gender of the name is considered feminine.

COMMENTS: It is interesting to note that *Anteplebeina* has 5 distal hamuli, the putatively plesiomorphic condition for the clade containing *Austroplebeia s.l.* and related genera (*i.e.*, *Hypotrigona*, *Liotrigona*, *Lisotrigona*, *Pariotrigona*), and relative to the condition of 6 distal hamuli in *Austroplebeia s.str.* Based on current understanding, *Lisotrigona* is the extant sister group to *Austroplebeia s.l.* (Rasmussen & Cameron, 2010), although *Pariotrigona* was not included in the analysis and certainly belongs to the broader clade containing these genera. If *Pariotrigona* is more closely related to *Austroplebeia* than *Lisotrigona*, then the elongate malar space of the former and *Anteplebeina* could be a shared plesiomorphy of the combined clade, with a reversal to shorter malar spaces in *Austroplebeia s.str.* Alternatively, both *Hypotrigona* and *Pariotrigona* have largely tuberculiform worker gonostyli that, because of their reduction, lack gonotrichia and this could be a shared reduction or plesiomorphic for the clade, in which case *Lisotrigona* would be more closely related to *Austroplebeia s.l.*, and the malar spaces would be independently derived. Regardless, the biogeographic implications (*vide* Discussion, *infra*) would not change except in relation to the stem lineage of *Pariotrigona*.

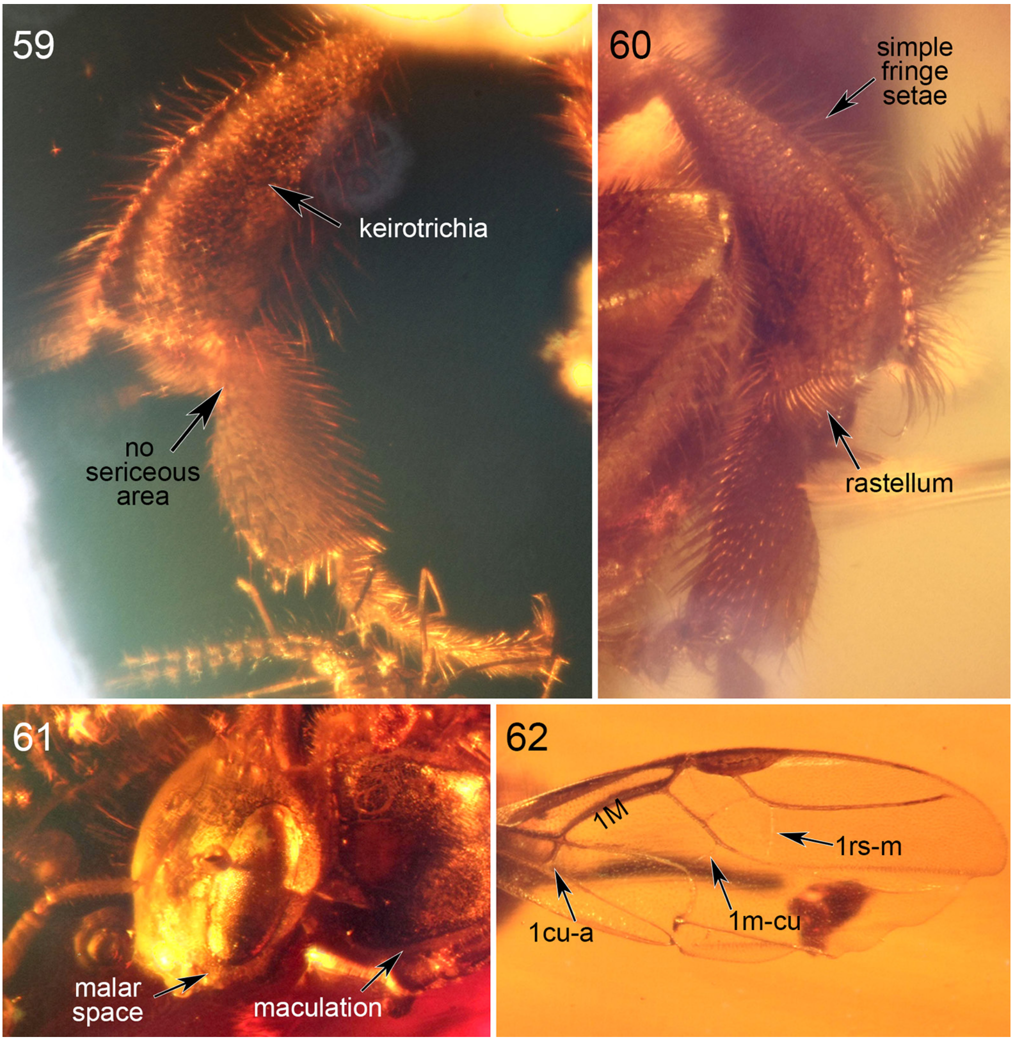
Austroplebeia* (*Anteplebeina*) *fujianica Engel, new species

ZooBank: urn:lsid:zoobank.org:act:1477B0D0-B05E-4B26-924D-27FCC2E7FAB7

(Figs. 44, 49–62)

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

DESCRIPTION: ♀: As described for the subgenus with the following minor additions: Total body length 4.4 mm, forewing length (including tegula) 3.6 mm. Head wider



Figures 59–62. Details of workers of *Austroplebeia* (*Anteplebeina*) *fujianica*, new species. **59.** Retrolateral view of metatibia and metatarsus of SEMC F002513. **60.** Retrolateral view of metatibia and metatarsus of NIGP 176057. **61.** Left view of head and mesoscutal dorsum of NIGP 176057. **62.** Forewing of NIGP 176057.

than long, width 1.61 mm, length 1.33 mm; upper interorbital distance 1.13 mm, lower interorbital distance 1.03 mm. Scape length 0.51 mm, torulocellar distance 0.67 mm.

Integument generally black to dark brown (coloration sometimes diagenetically altered in places where the integument is less finely preserved); mandible largely yellowish to yellowish brown, with black apical margin; clypeus yellow; supraclypeal area yellow; face below tangent of antennal toruli yellow, with slight extensions of yellow reaching upward along ocular border but not exceeding level of antennal toruli; antenna dark brown, although scape ventrally slightly lighter (perhaps brown to yellowish brown in life); mouthparts brown to yellowish brown; remainder of head black. Mesosoma black except with yellow maculation on pronotal lobe, lateral borders of mesoscutum, axillae, mesoscutellum, and metepisternum; upper portion of mespisternum (including hypoepimeral area) brown to yellowish brown (although darker in some paratypes and so likely either variation or fading due to diagenesis). Wing membranes hyaline clear; tubular veins dark brown to brown, with nebulous veins brown to faint brown. Legs largely dark brown (best observed on some of the paratypes). Metasoma brown to dark brown.

Integument mostly finely and sometimes faintly tessellate, with widely scattered, faint, shallow, minute punctures on upper face, remainder of head apparently impunctate. Mesosoma finely tessellate, more prominently so on mesoscutum; basal area of propodeum finely reticulate. Metasoma finely tessellate, except first metasomal tergum more polished and faintly tessellate and therefore appearing shinier, particularly anteriorly; apical marginal zones of terga not tessellate and sculpturally distinct from discs of terga, instead faintly imbricate; sterna faintly imbricate.

Pubescence largely decumbent and pale. Setae of face largely minute, decumbent, and simple, numerous but not obscuring integument; setae longer and erect on vertex and in ocellocular area; setae of gena like those of face; postgena with scattered, erect, simple setae, particularly along hypostomal area. Mesoscutum with scattered, fine, decumbent, minute, simple setae intermixed with sparse erect, short, simple setae, such erect setae more numerous along anterior border; mesoscutellum with erect setae longer and more numerous, particularly along posterior margin; mesepisternum with scattered, fine, decumbent, minute, simple setae like those on mesoscutum, such setae longer and more erect on lower half of mesepisternum; leg setation as described for subgenus. Metasomal terga with scattered, fine, decumbent, minute, simple setae, such setae particularly sparse on tergum I and intermixed with slightly longer subappressed setae on apical terga; apical tergum with long, erect to suberect, simple setae apically; metasomal sterna with long, erect, simple setae.

♀: *Latet*.

♂: *Latet*.

HOLOTYPE: ♀, NIGP 176057; amber, ~14.7 Ma (Langhian, Miocene, Zhangpu County, China; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

PARATYPES: 1♀, NIGP 176058; 1♀, NIGP 176059, same deposit and repository as holotype; 1♀, SEMC F002513, in Division of Entomology, University of Kansas Natural History Museum.

TYPE LOCALITY: Zhangpu County, Zhangzhou Prefecture, Fujian Province, China.

HORIZON: Middle Miocene: Langhian, 14.7 Ma; sedimentary layer II, Fotan Group.

ETYMOLOGY: The specific epithet is taken from Fujian Province in southeastern China, the region encompassing the Zhangpu locality.

DISCUSSION

In many respects, it is not surprising that a large number of stingless bees should be found in Neogene amber from China. Stingless bees live in perennial colonies with frequently large numbers of workers, with colonies of *Tetragonula* averaging about 750–7000 workers (with the largest colonies topping out around 11,000 workers), and *Austroplebeia* averaging 2000 workers (Grüter, 2020). Given that workers often collect resins, including those from modern dipterocarps like *Shorea* Roxb. ex C.F. Gaertn. and *Parashorea* Kurz. (Malvales: Dipterocarpaceae) (Leonhardt & Blüthgen, 2009; Leonhardt *et al.*, 2011a), it is likely that the fossil species would have had ample opportunity to become ensnared and eventually entombed in the exuded resin of the amber-producing Dipterocarpaceae of the mid-Miocene Zhangpu environs (Shi *et al.*, 2014; Wang *et al.*, 2021). In fact, in those habitats where dipterocarps occur, stingless bees tend to prefer collecting resins from these species (Grüter, 2020). The resins not only serve in nest production, but are actively used in nest defense (Schwarz, 1948; Lehmberg *et al.*, 2008) and dipterocarp resins inhibit pollen-associated fungi (Messer, 1985). Naturally, today most *Austroplebeia* (*i.e.*, those in Australia) do not encounter Dipterocarpaceae and therefore prefer other resin sources, just as do those *Tetragonula* of the *carbonaria*-group in Australia (Leonhardt *et al.*, 2011b) [note that the resin preferences of *A. cincta* have not been studied in New Guinea where *Austroplebeia* overlaps with four genera and at least seven species of Dipterocarpaceae (Foxworthy, 1946)]. Nonetheless, the bees collect resins from a variety of plant families. Although speculative, the significantly lower occurrence of *Austroplebeia* in Zhangpu amber could reflect an ancestral preference among ancient Asian species of the genus for alternative resins, preferentially visiting other plant families while still occasionally sampling dipterocarps (many stingless bees visit multiple resin-producing plants but nonetheless exhibit some preferences: Grüter, 2020). The same preponderance of workers in Neogene resin is observed for workers of *Proplebeia* in the slightly older (Early Miocene: Burdigalian) ambers of the Dominican Republic and Mexico, where they were assuredly using resin from *Hymenaea* L. (Fabaceae), like modern stingless bees (*e.g.*, Schwarz, 1948; Johnson, 1983). Preliminary observations suggest that at least one species of minute stingless bee is also comparatively numerous in Miocene amber from Ethiopia (M.S.E., pers. obs.).

A stark contrast to this pattern of abundance in Neogene amber, however, is that of meliponines in Paleogene ambers, specifically the Eocene (Bartonian) amber of the Baltic region where only three individuals are presently known (Engel, 2001a; Engel & Michener, 2013a) despite amber from the blaue Erde being one of the world's most prolific sources of fossil inclusions as well as one of the historically most exploited fossiliferous amber deposits. Meliponini are an ancient lineage, extending to the latest Cretaceous, and there is no reason to believe that colonies during the Eocene or earlier epochs were smaller or behaved differently from those in the Neogene, thereby accounting for lesser abundance in Paleogene resins. While Meliponini likely underwent a body-size constrained bottleneck early in their history, accounting for the reduction of wing venation and perhaps also the sting, they and their progenitors were universally highly eusocial and used resins for nest construction. Furthermore, as tropical bees, the globally warmer conditions of the Eocene and earlier epochs should have favored meliponine activity and diversification, and, indeed, if divergence estimates are accurate, then certainly significant cladogenesis across Meliponini was taking place during the early Paleogene. And yet it is not until well after the dramatic global cooling and drying following the Eocene-Oligocene transition that we observe a marked rise in resin-entombed stingless bees. It therefore remains a mystery as to why Paleogene resins should have virtually no stingless bees compared to the profusion of individuals in Neogene amber.

The present fossils accord nicely with estimations of divergence proposed by Rasmussen & Cameron (2010), whereby the clades for *Tetragonula* and *Austroplebeia* both extend into the Miocene. According to the estimate of Rasmussen & Cameron (2010), the common ancestor of *Austroplebeia* diverged from that of *Lisotrigona* about 35 Ma (around the Eocene-Oligocene transition and its associated climatic shift). Stem groups to *Austroplebeia* were, therefore, apparently present in mainland Asia during the Oligocene. Aside from the presence of the *Austroplebeia* clade in Asia during the Miocene, this is further supported by the fact that *Austroplebeia*'s closest relatives from whom it diverged are *Lisotrigona* and *Pariotrigona*, the former distributed in southern India and Sri Lank eastward to Yunnan and south through Southeast Asia and into Sumatra and northern Borneo, and the latter occurring from Thailand south to Sumatra and northern Borneo. Stem-*Austroplebeia* may have also extended into Sundaland. By at least the mid-Miocene, species identifiable as *Austroplebeia* had appeared in this region, with opportunities to expand through Sunda toward the Australian continent, which was approaching and colliding with Asia at the time (Hall, 2011, 2013). As islands were uplifted and eroded during the Miocene and Pliocene, many opportunities existed to disperse across the nascent elements of Sulawesi and the Sula Spur into New Guinea and from there into northern Australia (Fig. 63). The *Lisotrigona* + *Pariotrigona* + *Austroplebeia* clade had its origin in Asia, with *Austroplebeia* once occupying Asia before the common ancestor of *Austroplebeia s.str*. distributed via ancient Sunda and Wallacea into the Sahul. Similar dispersal pathways have proven instrumental in the biogeography and patterns of speciation for many groups (*e.g.*, Cruaud *et al*., 2011; Sklenarova *et al*., 2013; de Boer *et al*., 2015). All species and populations of *Austroplebeia s.l.* not occurring in Sahul eventually became extinct subsequent to the Miocene. The monophyletic *Austroplebeia s.str*. were eventually isolated east of the Lydekker Line in New Guinea and Australia, from which an ancestral population subsequently speciated into the diversity observed today, likely in the later Pliocene and/or during the Pleistocene. The island comprising part of New Guinea's landmass was first uplifted in the east around 30 Ma, moved westward about 20 Ma with the Central Range orogeny beginning in the latest mid-Miocene, and was eventually expanded around 5 Ma during renewed uplift of the peninsular region (Quarles van Ufford & Cloos, 2005). Opportunities to disperse southward from New Guinea were increasingly possible during the Pliocene and particularly during the complete land connections to Australia that became stable during the Pleistocene.

Tetragonula s.str. putatively diverged from *Tetragonilla* sometime around 22 Ma, and the *Tetragonula* group from others in the Heterotrigonitae as early as 48 Ma (Rasmussen & Cameron, 2010) (Fig. 64). From these estimates, *Tetragonula s.str*. would have had the same dispersal opportunities as outlined above for ancestral *Austroplebeia*, with putatively more basal divergences among those Asian and Indomalayan species, with Papuasian and Australian taxa putatively being more derived. Either that or there has been considerable independent and repeated westward and eastward long-distance dispersal events, which seems unlikely for these bees (*e.g.*, Smith *et al*., 2017). Why *Tetragonula* would have persisted in Asia and Malesia (*sensu* Brummitt, 2001) while *Austroplebeia* perished is a mystery as there does not seem to be anything intrinsic to either group that would account for one's continuous occupation through geological time or the other's localized extinction across Asia and Malesia.

Today *Austroplebeia* occurs in coastal and mountainous areas up 1300 m elevation, and with rainfalls of 1000–5000 mm/annum, with the exception of *A. essingtoni* (Cockerell), which occurs in more arid regions of the Northern Territory and Western Australia, with 300–1500 mm/annum (Dollin *et al*., 2015). Most species of *Tetragonula* also occur in similarly wet tropical habitats, with both genera reaching their southernmost occurrences in New South Wales at about 32.4° S for *Austroplebeia* and 36.4° S for *Tetragonula* (Dollin *et al*., 2015). Analogous climatic conditions were present in the mid-Miocene rainforest of Zhangpu, with rainfalls of 1929 ± 643 mm/annum and mean annual temperatures of 22.5° ± 2.4° C, with a cold month temperature of 17.2° ± 3.6° C (Wang *et al*., 2021). Thus, the paleoclimate of Zhangpu was ideal for a 12-month growing season, allowing the bees to be active and able to gather resources year round.

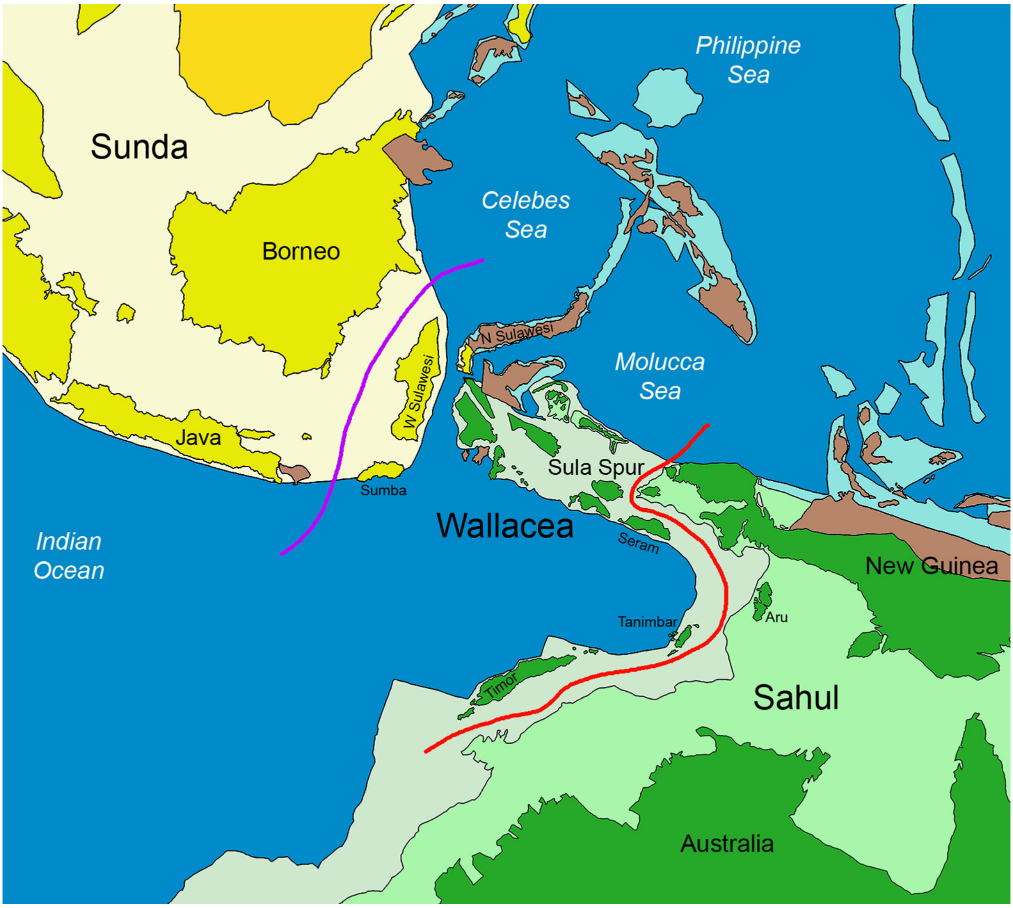


Figure 63. Middle Miocene (15 Ma, Langhian) paleogeography of Asia and Australia (redrawn from Hall, 2011). Purple line shows the present-day Wallace Line, while the red line demarcates the Lydekker Line.

Naturally, the fossil record of Meliponini is too meagre to provide broader insights into the evolution of the lineage and specifically allowing one to differentiate between competing hypotheses of historical biogeographic patterns. Further exploration from Zhangpu will hopefully provide additional material upon which to more fully understand the paleobiology of the species presented here, as well as additional species of bees, and not merely just Meliponini. More importantly, to better refine our paleontological view of stingless bee diversity, distribution, and ecology during the Neogene, material is needed from a far greater variety of amber deposits. Regional candidates include the Early Miocene amber of New Zealand (Schmidt *et al*., 2018: although meliponines are not present in Zealandia today), and potentially Late Miocene or even Pliocene amber of Borneo, although the latter is almost entirely lacking in inclusions (Kocsis *et al*., 2020). Australia is also rich in fossiliferous ambers and the potential for bees in these deposits, Eocene through Miocene, should be extensively surveyed (Hand *et al*., 2010; Stilwell *et al*., 2020). More globally, the Miocene ambers of Amazonian Peru or Venezuela are ripe for exploration and paleontological study (Antoine *et al*., 2006; Perrichot *et al*., 2014; Pérez *et al*., 2016), in conjunction with more detailed investigation of Mexican Miocene amber and Eocene amber from Arkansas

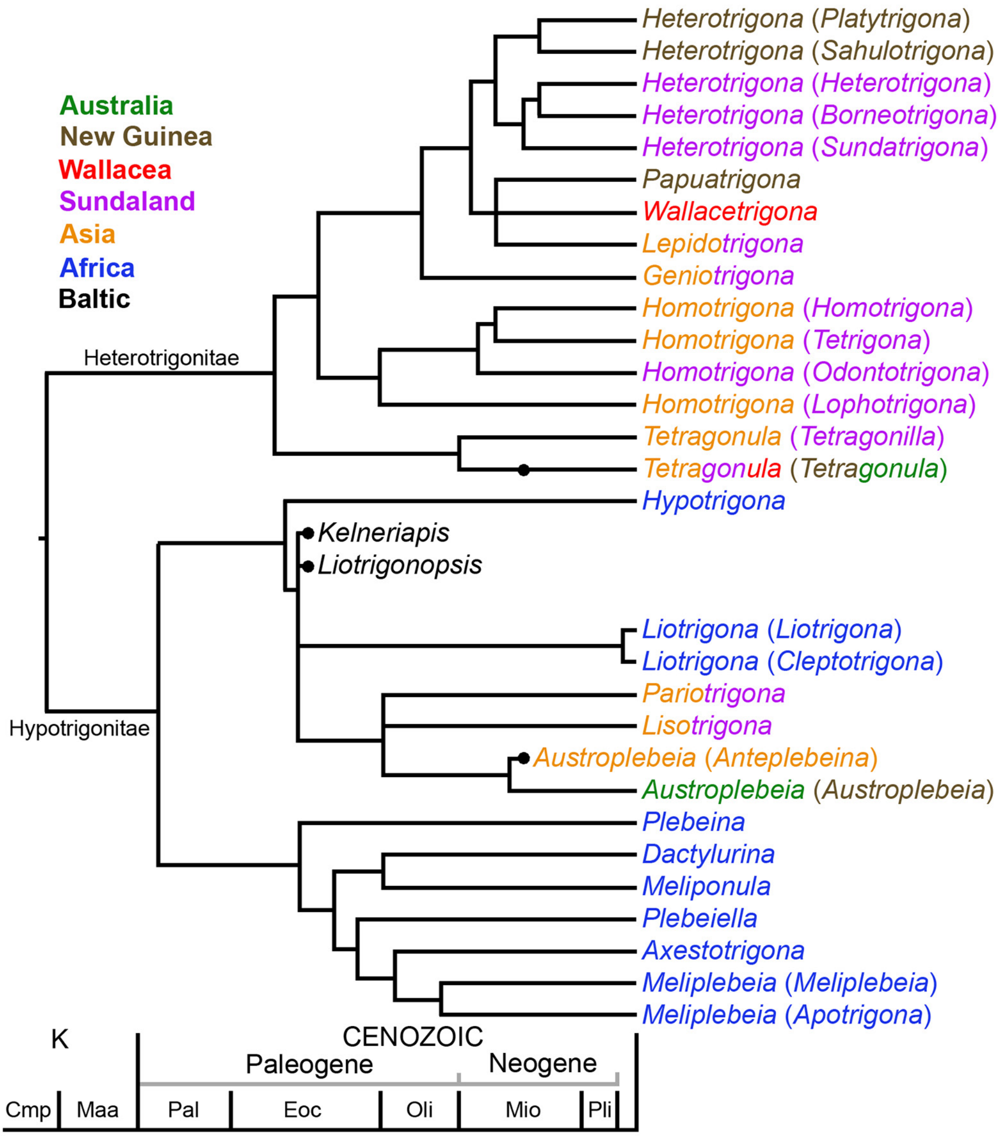


Figure 64. Hypothesis of phylogenetic relationships within subtribe Hypotrigonina, with gross approximations of distributions mapped. Relationships and divergence times largely based on Rasmussen & Cameron (2010), with estimated placements for *Kelneriapis* Sakagami, *Liotrigonopsis* Engel, *Anteplebeina*, new subgenus, *Pariotrigona* Moure, *Papuatrigona* Michener & Sakagami, *Platytrigona* Moure, and *Sahulotrigona* Engel & Rasmussen.

and Sakhalin. In this context, it is interesting to note that Arkansas amber has been chemically identified as most similar to the resin of Shorea (Saunders *et al.*, 1974). Even copal deposits from the region (*e.g.*, Sulawesi) may provide clues into more recent biogeographic patterns, localized extinctions of populations, recent expansions of species, or even previously unrecognized and comparatively modern losses of biodiversity (Solórzano-Kraemer *et al.*, 2020).

ACKNOWLEDGEMENTS

We are grateful to two anonymous reviewers for their insightful comments that helped to improve the final version, and to Kellie K. Magill Engel, Victor H. Gonzalez, Zachary H. Falin, and the late Charles D. Michener for their constant help during all or portions of this work. This research was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000) and National Natural Science Foundation of China (41688103). This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

REFERENCES

Anderson, K.B., R.E. Winans, & R.E. Botto. 1992. The nature and fate of natural resins in the geosphere–II. Identification, classification and nomenclature of resinites. *Organic Geochemistry* 18(6): 829–841.

Antoine, P.-O., D. De Franceschi, J.J. Flynn, A. Nel, P. Baby, M. Benammi, Y. Calderón, N. Espurt, A. Goswami, & R. Salas-Gismondi. 2006. Amber from western Amazonia reveals Neotropical diversity during the middle Miocene. *Proceedings of the National Academy of Sciences, U.S.A.* 103(37): 13595–13600.

Ayala, R. 1999. Revision de las abejas sin aguijon de Mexico (Hymenoptera: Apidae: Meliponini). *Folia Entomológica Mexicana* 106: 1–123.

Bänziger, H. 2018. Congregations of tear drinking bees at human eyes: Foraging strategies for an invaluable resource by *Lisotrigona* in Thailand (Apidae, Meliponini). *Natural History Bulletin of the Siam Society* 62(2): 161–193.

Bänziger, H., & S. Bänziger. 2010. Mammals, birds and reptiles as host of *Lisotrigona* bees, the tear drinkers with the broadest host range (Hymenoptera, Apidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* [*Bulletin de la Société Entomologique Suisse*] 83(3–4): 271–282.

Bänziger, H., S. Boongird, P. Sukumalanand, & S. Bänziger. 2009. Bees (Hymenoptera: Apidae) that drink human tears. *Journal of the Kansas Entomological Society* 82(2): 135–150.

Bänziger, H., S. Pumikong, & K.-O. Srimuang. 2011. The remarkable nest entrance of tear drinking *Pariotrigona klossi* and other stingless bees nesting in limestone cavities (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 84(1): 22–35.

Barden, P., & M.S. Engel. 2021. Fossil social insects. In: Starr, C.K. (Ed.), *Encyclopedia of Social Insects*: 384–403. Springer; Cham, Switzerland; xxvi+1049 pp.

Bird, T.L., R.A. Wharton, & L. Prendini. 2015. Cheliceral morphology in Solifugae (Arachnida): Primary homology, terminology, and character survey. *Bulletin of the American Museum of Natural History* 394: 1–355.

Blender Online Community. 2017. Blender – a 3D modeling and rendering package. Blender Foundation, Blender Institute; Amsterdam, The Netherlands. Online resource [http://www.blender.org; last accessed 22 July 2021].

Bossert, S., E.A. Murray, E.A.B. Almeida, S.G. Brady, B.B. Blaimer, & B.N. Danforth. 2019. Combining transcriptomes and ultraconserved elements to illuminate the phylogeny of Apidae. *Molecular Phylogenetics and Evolution* 130: 121–131.

Brady, R.H. 1985. On the independence of systematics. *Cladistics* 1(2): 113–126.

Brady, R.H. 1994. Pattern description, process explanation, and the history of morphological sciences. In: Grande, L., & O. Rieppel (Eds.), *Interpreting the Hierarchy of Nature: From Systematic Patterns to Evolutionary Process Theories*: 7–31. Academic Press; San Diego, CA; viii+[i]+298 pp.

Brummitt, R.K. 2001. *World Geographical Scheme for Recording Plant Distributions* [2nd Edition]. Hunt Institute for Botanical Documentation; Pittsburgh, PA; xv+137 pp.

Camargo, J.M.F., & D.W. Roubik. 1991. Systematics and bionomics of the apoid obligate necrophages: The *Trigona hypogea* group (Hymenoptera: Apidae; Meliponinae). *Biological Journal of the Linnean Society* 44(1): 13–39.

Camargo, J.M.F., D.A. Grimaldi, & S.R.M. Pedro. 2000. The extinct fauna of stingless bees (Hymenoptera: Apidae: Meliponini) in Dominican amber: Two new species and redescription of the male of *Proplebeia dominicana* (Wille and Chandler). *American Museum Novitates* 3293: 1–24.

Canevazzi, N.C., de Souza, & F.B. Noll. 2015. Cladistic analysis of self-grooming indicates a single origin of eusociality in corbiculate bees (Hymenoptera: Apidae). *Cladistics* 31(2): 126–141.

Cardinal, S., & L. Packer. 2007. Phylogenetic analysis of the corbiculate Apinae based on morphology of the sting apparatus (Hymenoptera: Apidae). *Cladistics* 23(2): 99–118.

Cowan, C.F. 1971. On Guérin's *Iconographie*: Particularly the insects. *Journal of the Society for the Bibliography of Natural History* 6(1): 18–29.

Cruaud, A., R. Jabbour-Zahab, G. Genson, A. Couloux, Y.-Q. Peng, Y.D. Rong, R. Ubaidillah, R.A.S. Pereira, F. Kjellberg, S. van Noort, C. Kerdelhué, & J.-Y. Rasplus. 2011. Out of Australia and back again: The world-wide historical biogeography of non-pollinating fig wasps (Hymenoptera: Sycophaginae). *Journal of Biogeography* 38(2): 209–225.

de Boer, H.J., K. Steffen, & W.E. Cooper. 2015. Sunda to Sahul dispersals in *Trichosanthes* (Cucurbitaceae): A dated phylogeny reveals five independent dispersal events to Australasia. *Journal of Biogeography* 42(3): 519–531.

Dehon, M., M.S. Engel, M. Gérard, A.M. Aytekin, G. Ghisbain, P.H. Williams, P. Rasmont, & D. Michez. 2019. Morphometric analysis of fossil bumble bees (Hymenoptera, Apidae, Bombini) reveals their taxonomic affinities. *ZooKeys* 891: 71–118.

Dollin, A.E., L.J. Dollin, & S.F. Sakagami. 1997. Australian stingless bees of the genus *Trigona* (Hymenoptera: Apidae). *Invertebrate Taxonomy* 11(6): 861–896.

Dollin, A.E., L.J. Dollin, & C. Rasmussen. 2015. Australian and New Guinean stingless bees of the genus *Austroplebeia* Moure (Hymenoptera: Apidae) – a revision. *Zootaxa* 4047(1): 1–73.

Eardley, C.D. 2004. Taxonomic revision of the African stingless bees (Apoidea: Apidae: Apinae: Meliponini). *African Plant Protection* 10(2): 63–96.

Engel, M.S. 1998. Fossil honey bees and evolution in the genus *Apis* (Hymenoptera: Apidae). *Apidologie* 29(3): 265–281.

Engel, M.S. 2000. A new interpretation of the oldest fossil bee (Hymenoptera: Apidae). *American Museum Novitates* 3296: 1–11.

Engel, M.S. 2001a. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History* 259: 1–192.

Engel, M.S. 2001b. Monophyly and extensive extinction of advanced eusocial bees: Insights from an unexpected Eocene diversity. *Proceedings of the National Academy of Sciences, U.S.A.* 98(4): 1661–1664.

Engel, M.S. 2006. A giant honey bee from the middle Miocene of Japan (Hymenoptera: Apidae). *American Museum Novitates* 3504: 1–12.

Engel, M.S. 2011. Systematic melittology: Where to from here? *Systematic Entomology* 36(1): 2–15.

Engel, M.S. 2019. Notes on Papuasian and Malesian stingless bees, with the descriptions of new taxa (Hymenoptera: Apidae). *Journal of Melittology* 88: 1–25.

Engel, M.S. In press-a. A key to the subgenera of the orchid bee genus *Euglossa* (Hymenoptera: Apidae). *Entomologist's Monthly Magazine*

Engel, M.S. In press-b. A key to the subgenera of the stingless bee genus *Melipona* (Hymenoptera: Apidae). *Entomologist's Monthly Magazine*

Engel, M.S. In press-c. A second species of the stingless bee genus *Plectoplebeia* (Hymenoptera: Apidae). *Entomologist's Monthly Magazine*

Engel, M.S. In press-d. A key to the species of *Nanoplebeia*, with descriptions of four new species (Hymenoptera: Apidae). *Journal of Melittology* 106: 1–14.

Engel, M.S., & S.R. Davis. 2021. New genera of melikertine bees with facial modifications in Baltic amber (Hymenoptera: Apidae). *Journal of Melittology* 103: 1–52.

Engel, M.S., & C.D. Michener. 2013a. Geological history of the stingless bees. In: Vit, P. & D.W. Roubik (Eds.), *Stingless Bees Process Honey and Pollen in Cerumen Pots*: 1–7. Facultad de Farmacia y Bioanálisis, Universidad de Los Andes; Mérida, Venezuela; 156 pp.

Engel, M.S., & C.D. Michener. 2013b. A minute stingless bee in Eocene Fushan [sic] amber from northeastern China (Hymenoptera: Apidae). *Journal of Melittology* 14: 1–10. [*Nota bene*: the provenance of this amber piece was falsified by the collector and the bee is in a piece of Baltic amber]

Engel, M.S., & C. Rasmussen. 2017. A new subgenus of *Heterotrigona* from New Guinea (Hymenoptera: Apidae). *Journal of Melittology* 73: 1–16.

Engel, M.S., & C. Rasmussen. 2021. Corbiculate bees. In: Starr, C.K. (Ed.), *Encyclopedia of Social Insects*: 302–310. Springer; Cham, Switzerland; xxvi+1049 pp.

Engel, M.S., I.A. Hinojosa-Díaz, & A.P. Rasnitsyn. 2009. A honey bee from the Miocene of Nevada and the biogeography of *Apis* (Hymenoptera: Apidae: Apini). *Proceedings of the California Academy of Sciences, 4th Series* 60(3): 23–38.

Engel, M.S., J. Ortega-Blanco, P.C. Nascimbene, & H. Singh. 2013. The bees of Early Eocene Cambay amber (Hymenoptera: Apidae). *Journal of Melittology* 25: 1–12.

Engel, M.S., L.C.V. Breitkreuz, & M. Ohl. 2014. The first male of the extinct bee tribe Melikertini (Hymenoptera: Apidae). *Journal of Melittology* 30: 1–18.

Engel, M.S., C.D. Michener, & Y. Boontop. 2017. Notes on Southeast Asian stingless bees of the genus *Tetragonula* (Hymenoptera: Apidae), with the description of a new species from Thailand. *American Museum Novitates* 3886: 1–17.

Engel, M.S., B. Wang, A.S. Alqarni, L.-B. Jia, T. Su, Z.-K. Zhou, & T. Wappler. 2018. A primitive honey bee from the middle Miocene deposits of southeastern Yunnan, China (Hymenoptera, Apidae). *ZooKeys* 775: 117–129.

Engel, M.S., S. Kahono, & D. Peggie. 2018. A key to the genera and subgenera of stingless bees in Indonesia (Hymenoptera: Apidae). *Treubia* 45: 65–84.

Engel, M.S., C. Rasmussen, & V.H. Gonzalez. 2021. Bees: Phylogeny and classification. In: Starr, C.K. (Ed.), *Encyclopedia of Social Insects*: 93–109. Springer; Cham, Switzerland; xxvi+1049 pp.

Fabricius, J.C. 1804. *Systema Piezatorum secundum ordines, genera, species, adiectis synonymis, locis, observationibus, descriptionibus*. Reichard; Brunsvigae [Braunschweig], Sacrum Imperium Romanum [Heiliges Römisches Reich, Herzogtum Braunschweig und Lüneburg]; 439+30 pp.

Fedorov, A., R. Beichel, J. Kalpathy-Cramer, J. Finet, J.-C. Fillion-Robin, S. Pujol, C. Bauer, D. Jennings, F. Fennessy, M. Sonka, J. Buatti, S. Aylward, J.V. Miller, S. Pieper, & R. Kikinis. 2012. 3D slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging* 30(9): 1323–1341.

Foxworthy, F.W. 1946. Distribution of the Dipterocarpaceae. *Journal of the Arnold Arboretum* 27(4): 347–354.

Franck, P., E. Cameron, G. Good, J.-Y. Rasplus, & B.P. Oldroyd. 2004. Nest architecture and genetic differentiation in a species complex of Australian stingless bees. *Molecular Ecology* 13(8): 2317–2331.

Friese, H. 1900. Neue Arten der Bienengattungen *Melipona* Ill., und *Trigona* Jur. *Természetrajzi Füzetek* 23(3–4): 381–394.

Friese, H. 1901. Neue Arten der Bienengattung *Trigona* Jur. (Hym.). *Zeitschrift für systematische Hymenopterologie und Dipterologie* 1(5): 265–271.

Greco, M.K., P.M. Welz, M. Siegrist, S.J. Ferguson, P. Gallmann, D.W. Roubik, & M.S. Engel. 2011. Description of an ancient social bee trapped in amber using diagnostic radioentomology. *Insectes Sociaux* 58(4): 487–494.

Gribodo, G. 1893. Note imenotterologiche. Nota. II. Nuovi generi e nuove specie di Imenotteri Antofili ed osservazioni sopra alcune specie giá conosciute. *Bollettino della Società Entomologica Italiana* 25(3): 248–287.

Grüter, C. 2020. *Stingless Bees: Their Behaviour, Ecology and Evolution*. Springer; Cham, Switzerland; xiv+385 pp.

Grüter, C., L.G. von Zuben, F.H.I.D. Segers, & J.P. Cunningham. 2016. Warfare in stingless bees. *Insectes Sociaux* 63(2): 223–236.

Guérin-Méneville, F.E. 1829–1838 [1844]. *Iconographie du Règne Animal de G. Cuvier, ou représentation d'après nature de l'une des espèces les plus remarquables, et souvent non encore figurées, de* *chaque genre d'animaux. Avec un texte descriptif mis au courant de la science. Ouvrage pouvant servir d'atlas à tous les traités de Zoologie. Insectes*. J.B. Baillière; Paris, Royaume de France; [iv]+576 pp., +110 pls. [*Nota bene*: while the text is from August or September 1844, plates date from March 1829 through December 1837: Cowan (1971); *T. fulviventris*, cited in herein, does not appear in the plates and it's only account is found in the 1844 text].

Halcroft, M.T., A. Dollin, T.M. Francoy, J.E. King, M. Riegler, A.M. Haigh, & R.N. Spooner-Hart. 2016. Delimiting the species within the genus *Austroplebeia*, an Australian stingless bee, using multiple methodologies. *Apidologie* 47(1): 76–89.

Hall, R. 2011. Australia-SE Asia collision: Plate tectonics and crustal flow. *Geological Society, Special Publications* 355: 75–109.

Hall, R. 2013. The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology* 72(S2): 1–17.

Hand, S., M. Archer, D. Bickel, P. Creaser, M. Dettmann, H. Godthelp, A. Jones, B. Norris, & D. Wicks. 2010. Australian Cape York amber. In: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*: 69–79. Siri Scientific Press; Manchester, UK; 304 pp.

Johnson, L.K. 1983. *Trigona fulviventris* (abeja atarrá, abeja jicote, culo de vaca, *Trigona*, stingless bee). In: Janzen, D.H. (Ed.), *Costa Rican Natural History*: 770–773. University of Chicago Press; Chicago, IL; xi+816 pp.

Kasiński, J.R., R. Kramarska, B. Słodkowska, V. Sivkov, & M. Piwocki. 2020. Paleocene and Eocene deposits on the eastern margin of the Gulf of Gdańsk (Yantarny P-1 borehole, Kaliningrad region, Russia). *Geological Quarterly* 64(1): 29–53.

Kawakita, A., J.S. Ascher, T. Sota, M. Kato, & D.W. Roubik. 2008. Phylogenetic analysis of the corbiculate bee tribes based on 12 nuclear protein-coding genes (Hymenoptera: Apoidea: Apidae). *Apidologie* 39(1): 163–175.

Kelner-Pillault, S. 1969. Abeilles fossiles ancetres des apides sociaux. *Proceedings VI Congress of the International Union for the Study of Social Insects, Bern* 1969: 85–93.

Kelner-Pillault, S. 1970. Une mélipone (s.l.) de l'ambre balte (Hym. Apidae). *Annales de la Société de la Entomologique de France* 6(2): 437–441.

Kocsis, L., A. Usman, A.-L. Jourdan, S.H. Hassan, N. Jumat, D. Daud, A. Briguglio, F. Slik, L. Rinyu, & I. Futó. 2020. The Bruneian record of "Borneo amber": A regional review of fossil tree resins in the Indo-Australian archipelago. *Earth-Science Reviews* 201: 103005 [1–21].

Kotthoff, U., T. Wappler, & M.S. Engel. 2011. Miocene honey bees from the Randeck Maar, southwestern Germany (Hymenoptera, Apidae). *ZooKeys* 96: 11–37.

Kotthoff, U., T. Wappler, & M.S. Engel. 2013. Greater past disparity and diversity hints at ancient migrations of European honey bee lineages into Africa and Asia. *Journal of Biogeography* 40(10): 1832–1838.

Kwong, W.K., L.A. Medina, H. Koch, K.-W. Sing, E.J.Y. Soh, J.S. Ascher, R. Jaffé, & N.A. Moran. 2017. Dynamic microbiome evolution in social bees. *Science Advances* 3(3): e1600513 [1–17].

Lehmberg, L., K. Dworschak, & N. Blüthgen. 2008. Defensive behavior and chemical deterrence against ants in the stingless bee genus *Trigona* (Apidae, Meliponini). *Journal of Apicultural Research* 47(1): 17–21. [*Nota bene*: The species tested in this study are no longer classified in *Trigona* Jurine, and are instead today recognized as *Lepidotrigona terminata* (Smith), *Tetragonula collina* (Smith), *T. fuscobalteata* (Cameron), *T. laeviceps* (Smith), and *T. melanocephala* (Gribodo)].

Leonhardt, S.D., & N. Blüthgen. 2009. A sticky affair: Resin collection by Bornean stingless bees. *Biotropica* 41(6): 730–736.

Leonhardt, S.D., T. Schmitt, & N. Blüthgen. 2011a. Tree resin composition, collection behavior and selective filters shape chemical profiles of tropical bees (Apidae: Meliponini). *PLoS ONE* 6(8): e23445 [1–10].

Leonhardt, S.D., H.M. Wallace, & T. Schmitt. 2011b. The cuticular profiles of Australian stingless bees are shaped by resin of the eucalypt tree *Corymbia torelliana*. *Austral Ecology* 36(5): 537–543.

Martins, A.C., G.A.R. Melo, & S.S. Renner. 2014. The corbiculate bees arose from New World oil-collecting bees: Implications for the origin of pollen baskets. *Molecular Phylogenetics and Evolution* 80: 88–94.

Mateus, S., & F.B. Noll. 2004. Predatory behavior in a necrophagous bee *Trigona hypogea* (Hymenoptera; Apidae, Meliponini). *Naturwissenschaften* 91(2): 94–96.

Melo, G.A.R. 2015. New species of the stingless bee genus *Schwarziana* (Hymenoptera: Apidae). *Revista Brasileira de Entomologia* 59(4): 290–293.

Melo, G.A.R. 2016. *Plectoplebeia*, a new Neotropical genus of stingless bees (Hymenoptera: Apidae). *Zoologia* 33 (1): e20150153 [1–8].

Melo, G.A.R. 2021. Stingless bees (Meliponini). In: Starr, C.K. (Ed.), *Encyclopedia of Social Insects*: 883–900. Springer; Cham, Switzerland; xxvi+1049 pp.

Messer, A.C. 1985. Fresh dipterocarp resins gathered by megachilid bees inhibit growth of pollen-associated fungi. *Biotropica* 17(2): 175–176.

Michener, C.D. 1974. *The Social Behavior of the Bees: A Comparative Study*. Harvard University Press; Cambridge, MA; xii+404 pp.

Michener, C.D. 1981. Classification of the bee family Melittidae, with a review of species of Meganomiinae. *Contributions of the American Entomological Institute* 18(3): 1–135.

Michener, C.D. 1982. A new interpretation of fossil social bees from the Dominican Republic. *Sociobiology* 7(1): 37–45.

Michener, C.D. 1990. Classification of the Apidae (Hymenoptera). *University of Kansas Science Bulletin* 54(4): 75–164.

Michener, C.D. 2002. Comments on minute Meliponini and the male of the genus *Pariotrigona* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 74(4): 231–236.

Michener, C.D. 2007. *The Bees of the World* [2nd Edition]. Johns Hopkins University Press; Baltimore, MD; xvi+[i]+953 pp., +20 pls.

Michener, C.D. 2013. The Meliponini. In: Vit, P., S.R.M. Pedro, & D.W. Roubik (Eds.), *Pot-Honey: A Legacy of Stingless Bees*: 3–17. Springer; Berlin, Germany; xxviii+654 pp.

Michener, C.D., & D.A. Grimaldi. 1988. A *Trigona* from Late Cretaceous amber of New Jersey (Hymenoptera: Apidae: Meliponinae). *American Museum Novitates* 2917: 1–10.

Michez, D., M. Vanderplanck, & M.S. Engel. 2012. Fossil bees and their plant associates. In: Patiny, S. (Ed.), *Evolution of Plant-Pollinator Relationships*: 103–164. Cambridge University Press; Cambridge, UK; xv+477+[6] pp.

Monk, K.A., Y. de Fretes, & G. Reksodihargo-Lilley. 1997. *The Ecology of Nusa Tenggara and Maluku – Ecology of Indonesia, Volume V*. Periplus Editions, HK Ltd.; Hong Kong, British Hong Kong; xvii+966+[32] pp.

Moure, J.S. 1951. Notas sôbre Meliponinae (Hymenopt.-Apoidea). *Dusenia* 2(1): 25–70.

Moure, J.S. 1961. A preliminary supra-specific classification of the Old World meliponine bees (Hymenoptera, Apoidea). *Studia Entomologica* 4(1–4): 181–242.

Noll, F.B. 1997. Foraging behavior on carcasses in the necrophagic bee *Trigona hypogea* (Hymenoptera: Apidae). *Journal of Insect Behavior* 10(3): 463–467.

Noll, F.B. 2002. Behavioral phylogeny of corbiculate Apidae (Hymenoptera; Apinae), with special reference to social behavior. *Cladistics* 18(2): 137–153.

Noll, F.B., R. Zucchi, J.A. Jorge, & S. Mateus. 1996. Food collection and maturation in the necrophagous stingless bee, *Trigona hypogea* (Hymenoptera: Meliponinae). *Journal of the Kansas Entomological Society* 69(supplement 4): 287–293.

Noll, F.B., C.E.L. Justino, E.A.B. Almeida, S. Mateus, & J. Billen. In press. Would wax glands help us to understand the relationships among corbiculate bees? *Insectes Sociaux*

Patterson, C. 1982. Morphological characters and homology. In: Joysey, K.A., & A.E. Friday (Eds.), *Problems of Phylogenetic Reconstruction*: 21–74. Academic Press; London, UK; 442 pp.

Patterson, C. 1988. Homology in classical and molecular biology. *Molecular Biology and Evolution* 5(6): 603–625.

Pérez, L.M., J.P. Pérez Panera, O.A. Aguilera, D.I. Ronchi, R. Sánchez, M.O. Manceñido, & M.R. Sánchez-Villagra. 2016. Palaeontology, sedimentology, and biostratigraphy of a fossiliferous outcrop of the Early Miocene Querales Formation, Falcón Basin, Venezuela. *Swiss Journal of Palaeontology* 135 (2): 187–203.

Perrichot, V., P.-O. Antoine, R. Salas-Gismondi, J.J. Flynn, & M.S. Engel. 2014. The genus *Mac-*

roteleia Westwood in Middle Miocene amber from Peru (Hymenoptera, Platygastridae *s.l.*, Scelioninae). *ZooKeys* 426: 119–127.

Porto, D.S., & E.A.B. Almeida. 2021. Corbiculate bees (Hymenoptera: Apidae): Exploring the limits of morphological data to solve a hard phylogenetic problem. *Insect Systematics and Diversity* 5(3): 2 [1–40].

Porto, D.S., L. Vilhelmsen, & E.A.B. Almeida. 2016. Comparative morphology of the mandibles and head structures of corbiculate bees (Hymenoptera: Apidae: Apini). *Systematic Entomology* 41(2): 339–368.

Porto, D.S., E.A.B. Almeida, & L. Vilhelmsen. 2017. Comparative morphology of internal structures of the mesosoma of bees with an emphasis on the corbiculate clade (Apidae: Apini). *Zoological Journal of the Linnean Society* 179(2): 303–337.

Porto, D.S., E.A.B. Almeida, & M.W. Pennell. 2021. Investigating morphological complexes using informational dissonance and Bayes factors: A case study in corbiculate bees. *Systematic Biology* 70(2): 295–306.

Portugal-Araújo, V., de. 1958. A contribution to the bionomics of *Lestrimelitta cubiceps* (Hymenoptera, Apidae). *Journal of the Kansas Entomological Society* 31(3): 203–211.

Prokop, J., M. Dehon, D. Michez, & M.S. Engel. 2017. An Early Miocene bumble bee from northern Bohemia (Hymenoptera, Apidae). *ZooKeys* 710: 43–63.

Ramírez, S.R., J.C. Nieh, T.B. Quental, D.W. Roubik, V.L. Imperatriz-Fonseca, & N.E. Pierce. 2010. A molecular phylogeny of the stingless bee genus *Melipona* (Hymenoptera: Apidae). *Molecular Phylogenetics and Evolution* 56(2): 519–525.

Rasmussen, C. 2008. Catalog of the Indo-Malayan/Australasian stingless bees (Hymenoptera: Apidae: Meliponini). *Zootaxa* 1935: 1–80.

Rasmussen, C., & S.A. Cameron. 2010. Global stingless bee phylogeny supports ancient divergence, vicariance, and long distance dispersal. *Biological Journal of the Linnean Society* 99(1): 206–232.

Rasmussen, C., & V.H. Gonzalez. 2017. The neotropical stingless bee genus *Nannotrigona* Cockerell (Hymenoptera: Apidae: Meliponini): An illustrated key, notes on the types, and designation of lectotypes. *Zootaxa* 4299(2): 191–220.

Rasmussen, C., J.C. Thomas, & M.S. Engel. 2017. A new genus of Eastern Hemisphere stingless bees (Hymenoptera: Apidae), with a key to the supraspecific groups of Indomalayan and Australasian Meliponini. *American Museum Novitates* 3888: 1–33.

Rasnitsyn, A.P., & C.D. Michener. 1991. Miocene fossil bumblebee from the Soviet Far East with comments on the chronology and distribution of fossil bees (Hymenoptera: Apidae). *Annals of Entomological Society of America* 84(6): 583–589.

Remane, A. 1952. *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Geest und Portig; Leipzig, German Democratic Republic; vi+400 pp.

Roig-Alsina, A., & C.D. Michener. 1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). *University of Kansas Science Bulletin* 55(4): 123–162.

Romiguier, J., S.A. Cameron, S.H. Woodard, B.J. Fischman, L. Keller, & C.J. Praz. 2016. Phylogenomics controlling for base compositional bias reveals a single origin of eusociality in corbiculate bees. *Molecular Biology and Evolution* 33(3): 670–678.

Roubik, D.W. 2006. Stingless bee nesting biology. *Apidologie* 37(2): 124–143.

Rust, J., H. Singh, R.S. Rana, T. McCann, L. Singh, K. Anderson, N. Sarkar, P.C. Nascimbene, F. Stebner, J.C. Thomas, M. Solórzano-Kraemer, C.J. Williams, M.S. Engel, A. Sahni, & D. Grimaldi. 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the Early Eocene of India. *Proceedings of the National Academy of Sciences, U.S.A.* 107(43): 18360–18365.

Rutishauser, R., & P. Moline. 2005. Evo-devo and the search for homology (“sameness”) in biological systems. *Theory in Biosciences* 124(2): 213–241.

Sakagami, S.F. 1978. *Tetragonula* stingless bees of the continental Asia and Sri Lanka (Hymenoptera, Apidae). *Journal of the Faculty of Science, Hokkaido University, Series VI, Zoology* 21(2): 165–247.

Sakagami, S.F., D.W. Roubik, & R. Zucchi. 1993. Ethology of the robber stingless bee, *Lestrimelitta limao* (Hymenoptera: Apidae). *Sociobiology* 21(3): 237–277.

Saunders, W.B., R.H. Mapes, F.M. Carpenter, & W.C. Elsik. 1974. Fossiliferous amber from the Eocene (Claiborne) of the Gulf Coastal Plain. *Geological Society of America Bulletin* 85(6): 979–984.

Schmidt, A.R., U. Kaulfuss, J.M. Bannister, V. Baranov, C. Beimforde, N. Bleile, A. Borkent, A. Busch, J.G. Conran, M.S. Engel, M. Harvey, E.M. Kennedy, P.H. Kerr, E. Kettunen, A.P. Kiecksee, F. Lengeling, J.K. Lindqvist, M. Maraun, D.C. Mildenhall, V. Perrichot, J. Rikkinen, E.-M. Sadowski, L.J. Seyfullah, F. Stebner, J. Szwedo, P. Ulbrich, & D.E. Lee. 2018. Amber inclusions from New Zealand. *Gondwana Research* 56: 135–146.

Schultz, T.R., M.S. Engel, & M. Prentice. 1999. Resolving conflict between morphological and molecular evidence for the origin of eusociality in the corbiculate bees (Hymenoptera: Apidae): A hypothesis-testing approach. *University of Kansas Natural History Museum Special Publication* 24: 125–138.

Schultz, T.R., M.S. Engel, & J.S. Ascher. 2001. Evidence for the origin of eusociality in the corbiculate bees (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 74(1): 10–16.

Schwarz, H.F. 1948. Stingless bees (Meliponidae) of the Western Hemisphere. *Lestrimelitta* and the following subgenera of *Trigona*: *Trigona*, *Paratrigona*, *Schwarziana*, Parapartamona, *Cephalotrigona*, *Oxytrigona*, *Scaura*, and *Mourella*. *Bulletin of the American Museum of Natural History* 90: i–xviii, 1–546, +8 pls.

Shanas, S., & P. Faseeh. 2019. A new subgenus and three new species of stingless bees (Hymenoptera: Apidae: Apinae: Meliponini) from India. *Entomon* 44 (1): 33–48.

Shi, G., S. Dutta, S. Paul, B. Wang, & F.M.B. Jacques. 2014. Terpenoid compositions and botanical origins of Late Cretaceous and Miocene amber from China. *PLoS ONE* 9(10): e111303 [1–8].

Shorthouse, D.P. 2010. SimpleMappr, an online tool to produce publication-quality point maps [program and documentation]. Online resource [http://www.simplemappr.net; last accessed 22 July 2021].

Silvestri, F. 1902. Contribuzione alla conoscenza dei Meliponidi del Bacino del Rio de La Plata. *Rivista di Patologia Vegetale* 10(5–12): 121–174, +3 pls. [i–iii].

Simon, E. 1879. Études arachnologiques. 10^{e} Mémoire (1). XVI. Essai d'une classification des *Galéodes*, remarques synonymiques et description d'espèces nouvelles ou mal connues. *Annales de la Société Entomologique de France, 5^{e} Série* 9: 93–154.

Simon, E. 1880. Descriptions de deux nouveaux genres de l'ordre des Solifugae. *Annales de la Société Entomologique de France, 5^{e} Série* 10: 399–402.

Sklenarova, K., D. Chesters, & L. Bocak. 2013. Phylogeography of poorly dispersing net-winged beetles: A role of drifting India in the origin of Afrotropical and Oriental fauna. *PLoS ONE* 8(6): e67957 [1–11].

Smith, F. 1854. *Catalogue of Hymenopterous Insects in the Collection of the British Museum. Part II. Apidae*. Taylor and Francis; London, UK; [i]+199–465 pp., +6 pls. [vii–xii].

Smith, F. 1863. Descriptions of Brazilian honey bees belonging to the genera *Melipona* and *Trigona*, which were exhibited, together with samples of their honey and wax, in the Brazilian Court of the International Exhibition of 1862. *Transactions of the Entomological Society of London, Third Series* 1(6): 497–512, +1 pl. [xx].

Smith, J.P., T.A. Heard, M. Beekman, & R. Gloag. 2017. Flight range of the Australian stingless bee *Tetragonula carbonaria* (Hymenoptera: Apidae). *Austral Entomology* 56 (1): 50–53.

Solórzano Kraemer, M.M., X. Delclòs, M.E. Clapham, A. Arillo, D. Peris, P. Jäger, F. Stebner, & E. Peñalver. 2018. Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. *Proceedings of the National Academy of Sciences, U.S.A.* 115(26): 6739–6744.

Solórzano-Kraemer, M.M., X. Delclòs, M.S. Engel, & E. Peñalver. 2020. A revised definition for copal and its significance for palaeontological and Anthropocene biodiversity-loss studies. *Scientific Reports* 10: 19904 [1–12].

Stilwell, J.D., A. Langendam, C. Mays, L.J.M. Sutherland, A. Arillo, D.J. Bickel, W.T. De Silva, A.H. Pentland, G. Roghi, G.D. Price, D.J. Cantrill, A. Quinney, & E. Peñalver. 2020. Amber from the Triassic to Paleogene of Australia and New Zealand as exceptional preservation of poorly known terrestrial ecosystems. *Scientific Reports* 10: 5703 [1–11].

Tosi, A. 1896. Di un nuovo genere di Apiaria fossile nell'ambra di Sicilia (*Meliponorytes succini* – *M. sicula*). *Rivista Italiana di Paleontologia* 2(6): 352–356, +1 pl.

Quarles van Ufford, A., & M. Cloos. 2005. Cenozoic tectonics of New Guinea. *AAPG* [*American Association of Petroleum Geologists*] *Bulletin* 89(1): 119–140.

Wang, B., G. Shi, C.-P. Xu, R.A. Spicer, V. Perrichot, A.R. Schmidt, K. Feldberg, J. Heinrichs, C. Chény, H. Pang, X.-Y. Liu, T.-P. Gao, Z.-X. Wang, A. Ślipiński, M.M. Solórzano-Kraemer, S.W. Heads, M.J. Thomas, E.-M. Sadowski, J. Szwedo, D. Azar, A. Nel, Y. Liu, J. Chen, Q. Zhang, Q.-Q. Zhang, C.-H. Luo, T.-T. Yu, D. Zheng, H.-C. Zhang, & M.S. Engel. 2021. The mid-Miocene Zhangpu biota reveals an outstandingly rich rainforest biome in East Asia. *Science Advances* 7(18): eabg0625 [1–7].

Wappler, T., & M.S. Engel. 2003. The middle Eocene bee faunas of Eckfeld and Messel, Germany (Hymenoptera, Apoidea). *Journal of Paleontology* 77(5): 908–921.

Wappler, T., T. De Meulemeester, A.M. Aytekin, D. Michez, & M.S. Engel. 2012. Geometric morphometric analysis of a new Miocene bumble bee from the Randeck Maar of southwestern Germany (Hymenoptera: Apidae). *Systematic Entomology* 37(4): 784–792.

Wappler, T., C.C. Labandeira, M.S. Engel, R. Zetter, & F. Grímsson. 2015. Specialized and generalized pollen-collection strategies in an ancient bee lineage. *Current Biology* 25(23): 3092–3098.

Wikramanayake, E., E. Dinerstein, C.J. Loucks, D.M. Olson, J. Morrison, J. Lamoreux, M. McKnight, & P. Hedao. 2002. *Terrestrial Ecoregions of the Indo-Pacific: A Conservation Assessment*. Island Press; Washington, D.C.; xxix+643 pp.

Wille, A. 1959. A new fossil stingless bee (Meliponini) from the amber of Chiapas, Mexico. *Journal of Paleontology* 33(5): 849–852, +1 pl.

Wille, A. 1979. Phylogeny and relationships among the genera and subgenera of the stingless bees (Meliponinae) of the world. *Revista de Biología Tropical* 27(2): 241–277.

Wille, A. 1983. Biology of the stingless bees. *Annual Review of Entomology* 28: 41–64.

Wille, A., & L.C. Chandler. 1964. A new stingless bee from the Tertiary amber of the Dominican Republic (Hymenoptera; Meliponini). *Revista de Biología Tropical* 12(2): 187–195.

Wille, A., & C.D. Michener. 1973. The nest architecture of stingless bees with special reference to those of Costa Rica (Hymenoptera, Apidae). *Revista de Biología Tropical* 21(Suplemento 1): 1–278.

Yokoyama, Y., A. Purcell, K. Lambeck, & P. Johnston. 2001. Shore-line reconstruction around Australia during the Last Glacial Maximum and Late Glacial Stage. *Quaternary International* 83–85: 9–18.

Zhang, J.-F. 1989. *Fossil Insects from Shanwang, Shandong, China*. Shandong Science and Technology Publishing House; Jinan, China; [i]+459 pp.

Zhang, J.-F. 1990. New fossil species of Apoidea (Insecta: Hymenoptera). *Acta Zootaxonomica Sinica* 15(1): 83–91.

Zheng, D., G. Shi, S.R. Hemming, H.-C. Zhang, W.-M. Wang, B. Wang, & S.-C. Chang. 2019. Age constraints on a Neogene tropical rainforest in China and its relation to the Middle Miocene Climatic Optimum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 518: 82–88.

ZooBank: urn:lsid:zoobank.org:pub:3637F70F-42FC-461E-82B3-A847752A071A

APPENDIX

Emendations to the classification of Meliponini (Apinae): The genera *Axestotrigona*, *Nannotrigona*, *Asperplebeia*, *Plebeia*, *Schwarziana*, and *Trigona*, with keys to the African fauna and *Plebeia*-group genera

Michael S. Engel

The classification of Meliponini has improved significantly over the last 15 years, with considerable stability provided by the judicious application of both morphological and molecular data (*e.g.*, Rasmussen & Cameron, 2010; Ramírez *et al.*, 2010; Melo, 2016, 2021; Rasmussen *et al.*, 2017). Various emendations to the classification are provided here in what is hoped might be a further step toward a complete and satisfactory classification of the tribe. These names are made available here so that they may be used herein as well as in forthcoming treatments. Refer to table 2 for an outline of the classification as here conceived.

SYSTEMATICS

Tribe Meliponini Lepeletier de Saint Fargeau
Subtribe Hypotrigonina Engel

The classification of African Meliponini employed herein (Table 2 and section on Hypotrigonitae, *vide supra*), differs in various ways from those in the literature (*e.g.*, Eardley, 2004; Michener, 2007). Accordingly, a key is provided to the genera and subgenera as they are conceived here, with the proposal of a new subgenus within *Axestotrigona*. To make the key as easy to use as possible, images are provided to all of the genera as they are circumscribed here given that they are not as often figured in the literature as are Neotropical stingless bees: *Liotrigona s.str*. (Figs. 65, 69, 72, 76, 77, 84), *Liotrigona* (*Cleptotrigona*) (Figs. 67, 70, 73, 80, 81, 85), *Hypotrigona* (Figs. 66, 71, 74, 78, 79, 86), *Dactylurina* (Figs. 68, 75, 82, 83, 87), *Plebeina* (Figs. 88–93), *Meliponula* (Figs. 94, 98, 102, 109, 113), *Plebeiella* (Figs. 95, 99, 103, 112), *Meliplebeia s.str*. (Figs. 96, 100, 104, 106, 107, 110, 114), *Meliplebeia* (*Apotrigona*) (Figs. 97, 101, 105, 108, 111, 115), *Axestotrigona* (Figs. 116–121).

Key to Genera and Subgenera of African Meliponini
(worker caste; modified from Michener, 2007)

1. Forewing length less than 3.5 mm; hind wing without closed cells, veins closing radial and cubital cells, if visible at all, clear and unpigmented; forewing with 2Rs, 1rs-m, and 2rs-m almost always completely absent, thus indications of submarginal cells absent (Figs. 69–71); at least distal part of second cubital cell (= subdiscoidal cell) of forewing undefined or defined by completely unpigmented vein traces (Figs. 69–71); vein 2M of forewing terminating without bend at about position of anterior end of 1m-cu (*i.e.*, 3M absent), which, however, is absent or spectral (Figs. 69–71) 2

Figures 65–68. Lateral habitus of workers of African genera. **65.** *Liotrigona* (*Liotrigona*) *mahafalya* Brooks & Michener. **66.** *Hypotrigona gribodoi* (Magretti). **67.** *L.* (*Cleptotrigona*) *cubiceps* (Friese). **68.** *Dactylurina schmidti* (Stadelmann).

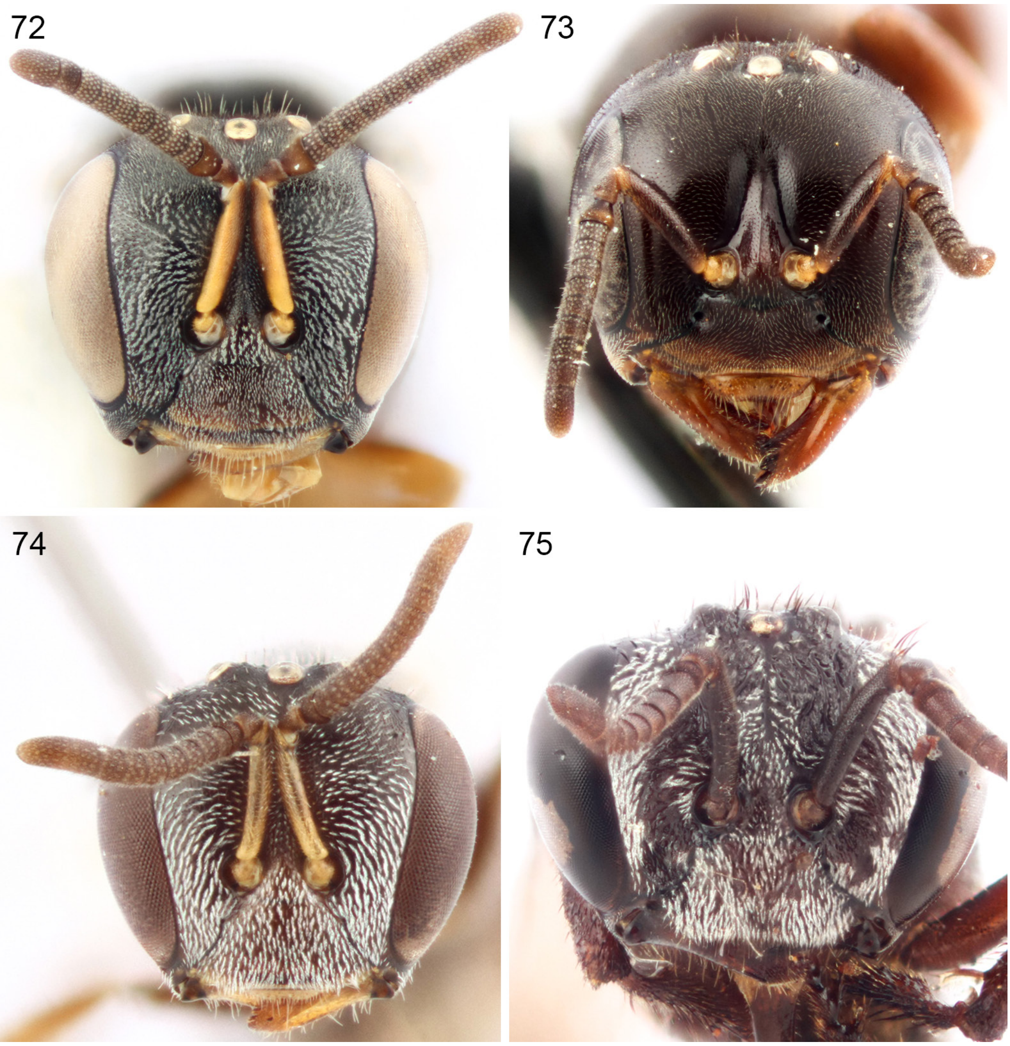
—. Forewing length about 4 mm or more; hind wing commonly with radial and cubital cells closed by at least weakly brownish nebulous veins (*e.g.*, Fig. 112); forewing with 2Rs and 1rs-m usually weakly indicated, first submarginal cell thus usually recognizable (Figs. 92, 112–115, 120); second cubital cell of forewing completely indicated, at least by faint veins (Figs. 92, 112–115, 120); vein M of forewing extending at least slightly beyond position of anterior end of 1m-cu and angulate at end of that crossvein (*i.e.*, 3M distinct from 2M, with at least tubular to nebulous stub), which is usually at least faintly visible (Figs. 92, 112–115, 120) 4

2(1). Distal part of prolateral surface of metatibia flat or concave, margined by long setae, forming corbicula (Figs. 76, 78, 82, 90, 106, 108, 109, 117); penicillum present (*e.g.*, Figs. 110, 111); clypeus twice as wide as long or less (Figs. 72, 74) 3

—. Prolateral surface of metatibia convex, without corbicula (Fig. 80); penicillum absent (Fig. 80); clypeus much more than twice as wide as long (Fig. 73) .... *Liotrigona* (*Cleptotrigona*) Moure

3(2). Superior distal angle of metatibia forming distinct angle (Figs. 76, 77); mesoscutum and mesoscutellum smooth and shining (Fig. 84); gonostyli much longer than broad, flat, adjacent or separated by less than one gonostylar diameter, without setae but with gonotrichia .... *Liotrigona* (*Liotrigona*) Moure, *s.str*.

Figures 69–71. Forewings of workers of minute African genera. **69.** *Liotrigona* (*Liotrigona*) *mahafalya* Brooks & Michener. **70.** *L.* (*Cleptotrigona*) *cubiceps* (Friese). **71.** *Hypotrigona gribodoi* (Magretti).

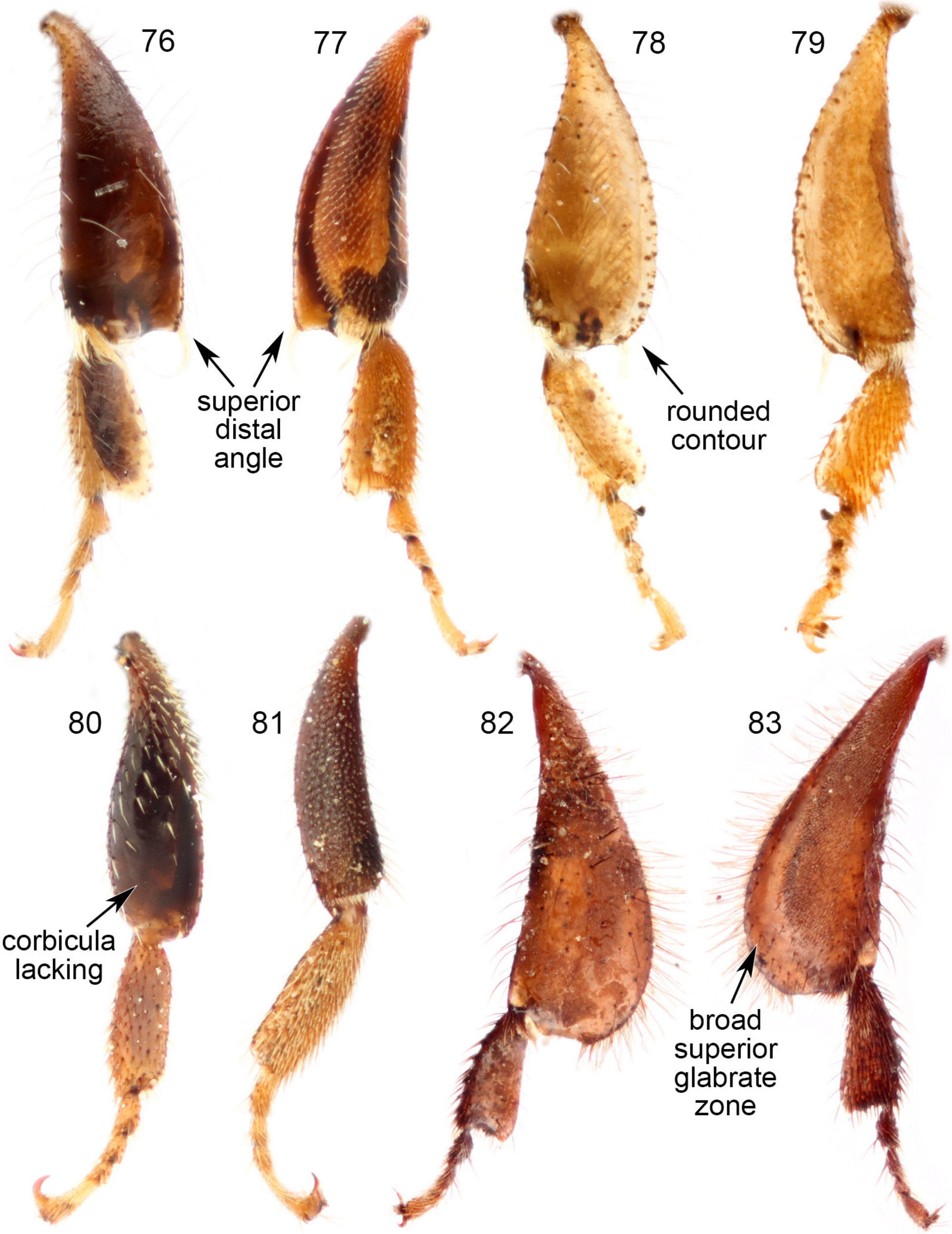


Figures 72–75. Faces of workers of African genera. **72.** *Liotrigona* (*Liotrigona*) *mahafalya* Brooks & Michener. **73.** *L.* (*Cleptotrigona*) *cubiceps* (Friese). **74.** *Hypotrigona gribodoi* (Magretti). **75.** *Dactylurina schmidti* (Stadelmann).

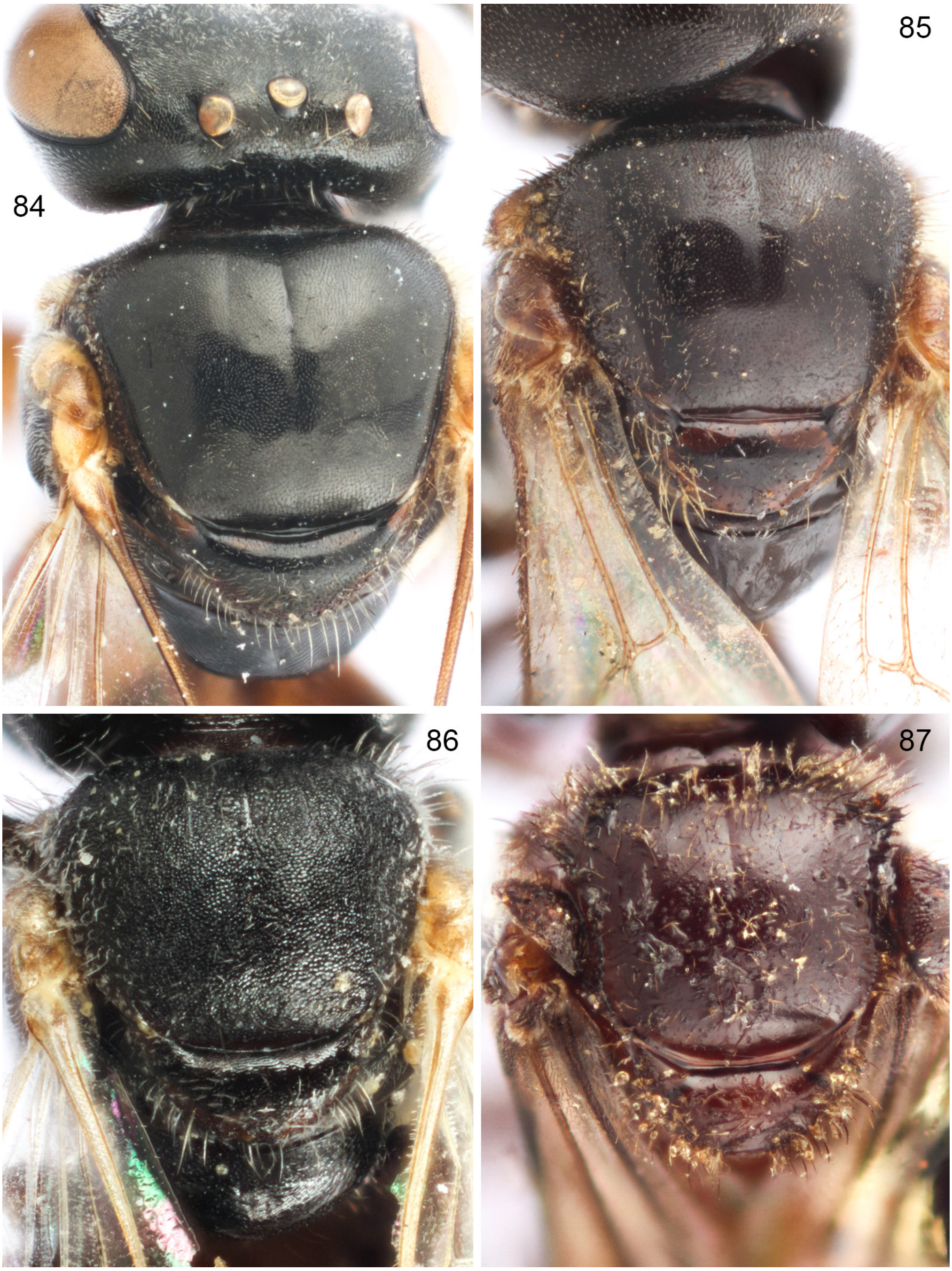
—. Superior distal angle of metatibia a rounded contour (Figs. 78, 79); mesoscutum and mesoscutellum matte, microalveolate to imbricate (Fig. 86); gonostyli minute, tuberculiform, separated by several gonostylar diameters, with setae but without gonotrichia .... *Hypotrigona* Moure

4(1). Retrolateral surface of metatibia with depressed upper marginal glabrate area narrow (much less than half as wide as broad area with keirotrichia) or absent (Figs. 91, 107, 118), keirotrichia extending to or close to margin; first metasomal segment broader than long (Fig. 68) 5

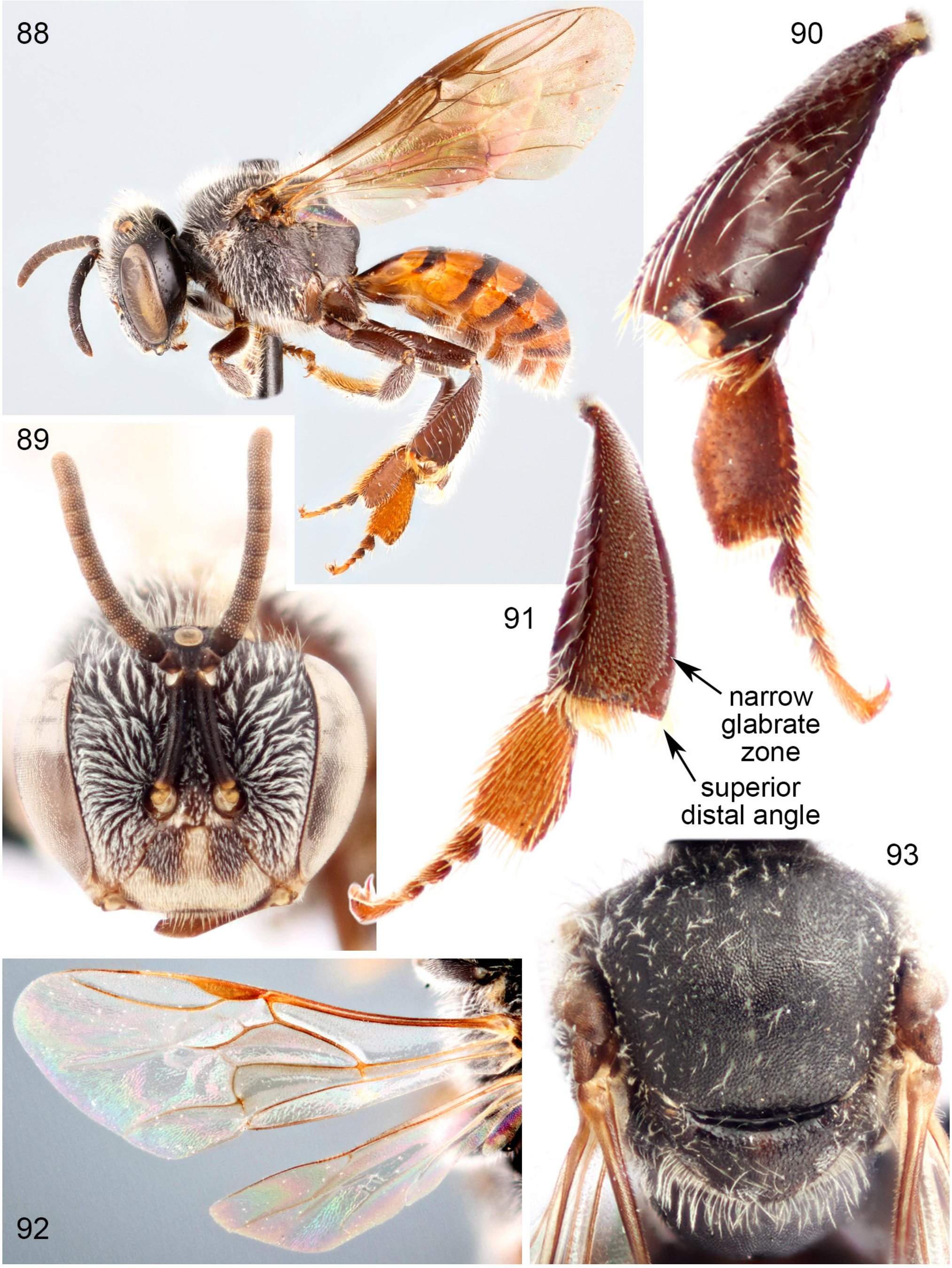
—. Retrolateral surface of metatibia with strongly depressed, shining, superior marginal glabrate area nearly as broad apically as longitudinal median keirotrichiate plateau (Fig. 83), and about half as wide as keirotrichiate plateau midway of metatibial length; first metasomal segment longer than broad (Fig. 68) .... *Dactylurina* Cockerell



Figures 76–83. Metatibia and metatarsi of workers of African genera. **76.** Prolateral view of *Liotrigona* (*Liotrigona*) *mahafalya* Brooks & Michener. **77.** Retrolateral view of *L.* (*L.*) *mahafalya*. **78.** Prolateral view of *Hypotrigona gribodoi* (Magretti). **79.** Retrolateral view of *H. gribodoi*. **80.** Prolateral view of *L.* (*Cleptotrigona*) *cubiceps* (Friese). **81.** Retrolateral view of *L.* (*C.*) *cubiceps*. **82.** Prolateral view of *Dactylurina schmidti* (Stadelmann). **83.** Retrolateral view of *D. schmidti*.



Figures 84–87. Mesosomal dorsa of workers of African genera. **84.** *Liotrigona* (*Liotrigona*) *mahafalya* Brooks & Michener. **85.** *L.* (*Cleptotrigona*) *cubiceps* (Friese). **86.** *Hypotrigona gribodoi* (Magretti). **87.** *Dactylurina schmidti* (Stadelmann).



Figures 88–93. Worker of *Plebeina armata* (Magretti). **88.** Lateral habitus. **89.** Facial view. **90.** Prolateral view of metatibia and metatarsus. **91.** Retrolateral view of metatibia and metatarsus. **92.** Wing venation. **93.** Mesosomal dorsum.

Figures 94–97. Lateral habitus of workers of African genera. **94.** *Meliponula bocandei* (Spinola). **95.** *Plebeiella lendliana* (Friese). **96.** *Meliplebeia* (*Meliplebeia*) *beccarii* (Gribodo). **97.** *M.* (*Apotrigona*) *nebulata* (Smith).

5(4). Metatibia rather spoon-shaped, superior distal angle rounded but with coarse, amber-colored to blackish bristles (superior parapenicillum) (Figs. 106, 108, 109, 117); sting stylet distinct, acute 6

—. Metatibia slender, triangular with distinct superior distal angle supporting long, pale setae (not especially coarse) (Fig. 90); sting stylet a mere rounded convexity .... *Plebeina* Moure

6(5). Propodeal profile with slanting dorsal portion rounding onto vertical portion; corbicula occupying more than distal half of metatibia (Figs. 106, 108, 117); metasomal terga at least partly shining [apical reflexed process of sternum VI of male longer than body of sternum] 7

—. Propodeal profile largely vertical; corbicula occupying less than distal half of metatibia (Fig. 109); metasomal terga dull, minutely sculptured [apical reflexed process of sternum VI of male short and rounded] .... *Meliponula* Cockerell

7(6). Head and mesosoma without yellow markings (Figs. 116, 119); retrolateral surface of metatibia without well-defined, shining, depressed superior margin (Fig. 118), although keirotrichiate area does not reach margin at least distally [Genus *Axestotrigona* Moure, *s.l.*] 8

Figures 98–101. Faces of workers of African genera. **98.** *Meliponula bocandei* (Spinola). **99.** *Plebeiella lendliana* (Friese). **100.** *Meliplebeia* (*Meliplebeia*) *beccarii* (Gribodo). **101.** *M.* (*Apotrigona*) *nebulata* (Smith).

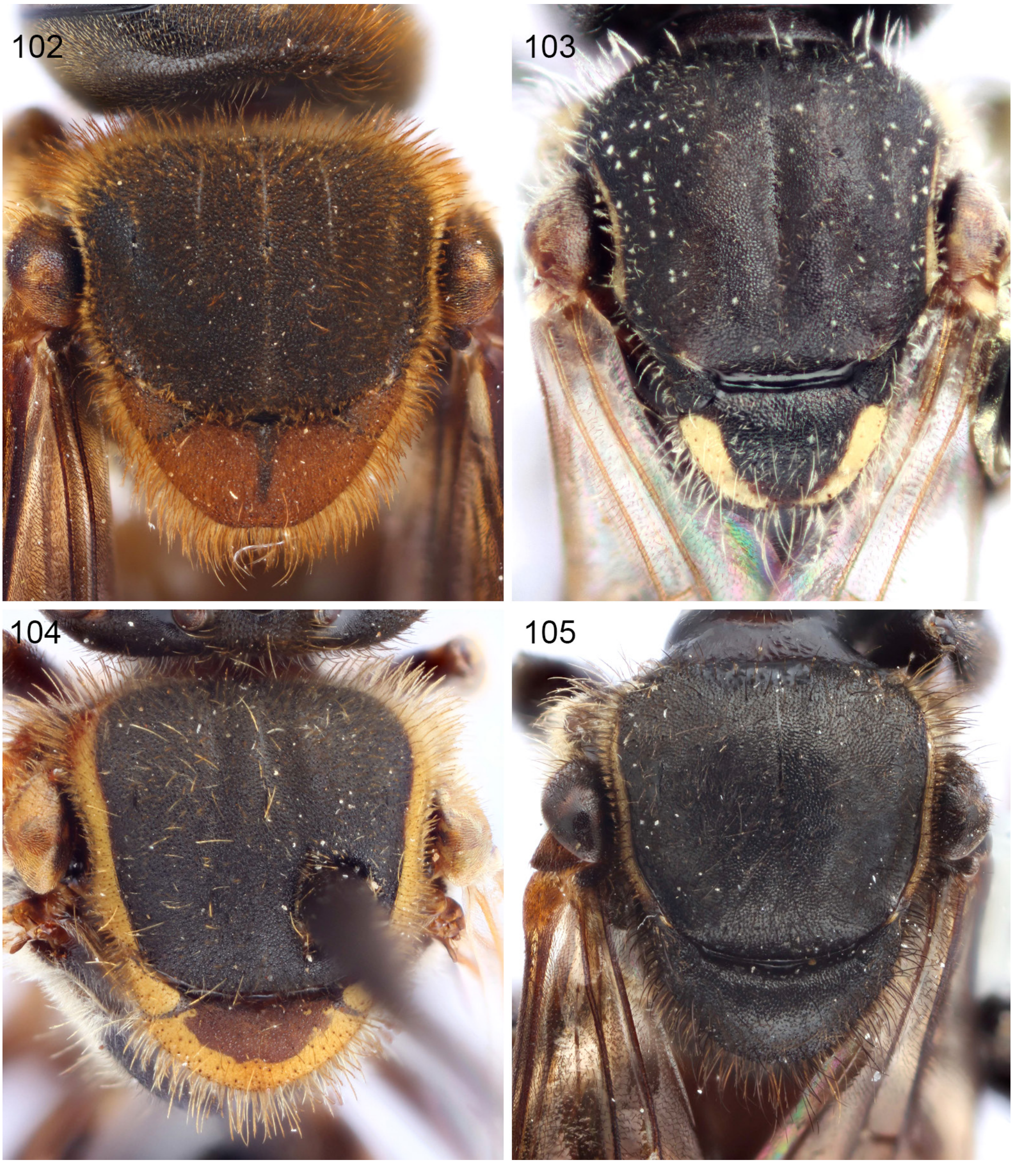
—. Head and mesosoma with yellow markings (Figs. 95, 97, 99–101, 103–105); retrolateral surface of metatibia with shining superior margin (*e.g.*, Fig. 107), at least slightly depressed 9

8(7). Basal area of propodeum finely tessellate to microalveoate, sometimes faintly so and appearing nearly smooth, and laterally setose (sometimes lateral patches of setae sparse and wispy or may be difficult to discern in worn individuals or those with considerable pitch on the body) (Fig. 121); wing membranes hyaline clear to lightly infuscate (parchment-colored) or ferruginous (Figs. 116, 120) .... *Axestotrigona* Moure, *s.str.*

—. Basal area of propodeum glabrous and smooth; wing membranes darkly infumate throughout .... *Atrichotrigona* Engel, n. subgen.

9(7). Basal area of propodeum pubescent [Genus *Meliplebeia* Moure, *s.l.*] 10

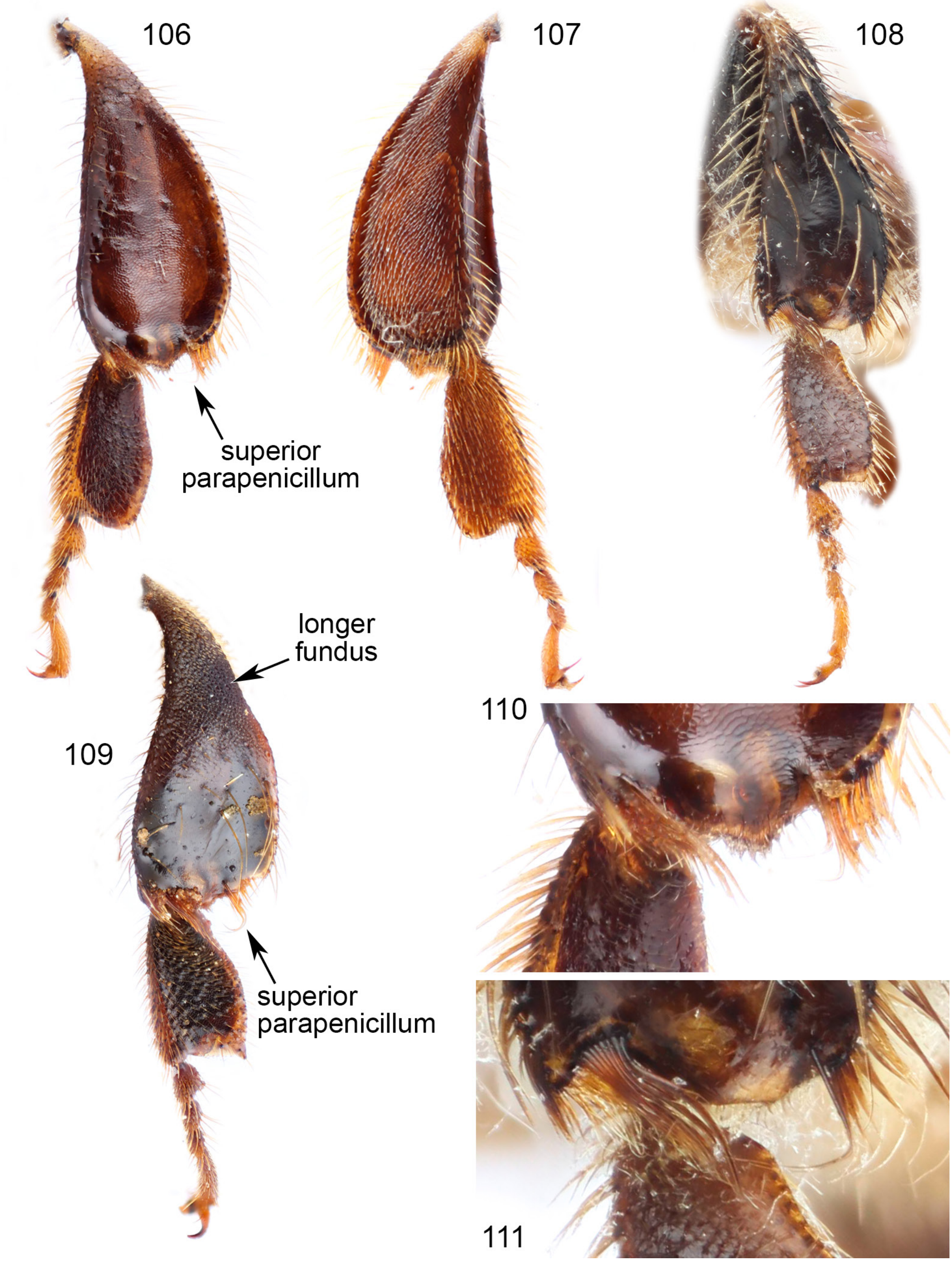
—. Basal area of propodeum glabrous .... *Plebeiella* Moure



Figures 102–105. Mesosomal dorsa of workers of African genera. **102.** *Meliponula bocandei* (Spinola). **103.** *Plebeiella lendliana* (Friese). **104.** *Meliplebeia* (*Meliplebeia*) *beccarii* (Gribodo). **105.** *M.* (*Apotrigona*) *nebulata* (Smith).

10(9). Mesoscutum tessellate (Fig. 104); mandibular teeth small; scape as long as antennal-ocellar distance (Fig. 100); basal vein (1M) slightly distad 1cu-a (Fig. 114); superior parapenicillum well developed (Figs. 106, 107, 110) .... *Meliplebeia* Moure, *s.str*.

—. Mesoscutum punctate (Fig. 105); mandibular teeth strong; scape shorter than antennal-ocellar distance (Fig. 101); basal vein (1M) slightly basad 1cu-a (Fig. 115); superior parapenicillum scarcely definable (Fig. 111) ..... *Apotrigona* Moure



Figures 106–111. Metatibiae and metatarsi workers of African genera. **106.** Prolateral view of *Meliplebeia* (*Meliplebeia*) *beccarii* (Gribodo). **107.** Retrolateral view of *M.* (*M.*) *beccarii*. **108.** Prolateral view of *M.* (*Apotrigona*) *nebulata* (Smith). **109.** Prolateral view of *Meliponula bocandei* (Spinola). **110.** Detail of metatibial apex (prolateral) of *M.* (*M.*) *beccarii*. **111.** Detail of metatibial apex (prolateral) of *M.* (*A.*) *nebulata*.

Figures 112–115. Wing venation of workers of African genera. **112.** *Plebeiella lendliana* (Friese). **113.** *Meliponula bocandei* (Spinola). **114.** *Meliplebeia* (*Meliplebeia*) *beccarii* (Gribodo). **115.** *M.* (*Apotrigona*) *nebulata* (Smith).

Figures 116–121. Worker of *Axestotrigona* (*Axestotrigona*) *togoensis* (Stadelmann). **116.** Lateral habitus. **117.** Prolateral view of metatibia and metatarsus. **118.** Retrolateral view of metatibia and metatarsus. **119.** Dorsal view of head and mesosoma. **120.** Wing venation. **121.** Posterior view of mesosoma; note wispy lateral pubescence on basal area of propodeum.

Genus *Axestotrigona* Moure

The genus *Axestotrigona* comprises six species found throughout sub-Saharan Africa, and consists of typically small to moderate-sized bees (5–8 mm in length). Although originally established as a genus (Moure, 1961), Michener (1990, 2007) relegated the group to a subgenus of a significantly expanded *Meliponula*, recasting this group to include all of those African taxa in which the metatibia was broadly spatulate in form. Recent phylogenetic work, however, has demonstrated the Michener's circumscription of *Meliponula* renders the group polyphyletic (Rasmussen & Cameron, 2010). Rasmussen *et al*. (2017) transferred *Axestotrigona* to an expanded *Meliplebeia* in order to resolve the polyphyly resulting from inclusion in *Meliponula*, but such an arrangement renders the broader circumscription of *Meliplebeia* challenging. Therefore, we follow Moure's (1961) original circumscription of the genus and as sister to a clade comprising *Meliplebeia s.l.* (Rasmussen & Cameron, 2010) (Table 2). Within the genus there are two distinct groups, here treated as subgenera.

Atrichotrigona Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:D1D7622B-83E4-4065-8343-0A07AF388C52

TYPE SPECIES: *Trigona cameroonensis* Friese, 1900.

DIAGNOSIS: The subgenus includes two distinctive species that lack the wispy lateral setae otherwise present on the basal area of the propodeum in typical *Axestotrigona*. In addition to being glabrous, the basal area of the propodeum is smooth and polished rather than finely tessellate to microalveoate in the nominate subgenus. The wing membranes are characteristically darkly infumate throughout rather than clear, somewhat ferruginous, or parchment colored as is found in the remaining species. Lastly, the species of this subgenus are slightly larger than those of the nominate group, with body lengths over 7 mm and forewings (including tegula over 7.8 mm, whereas the latter are typically 5.0–6.5 mm with forewings (including tegula) 5.5–6.7 mm.

ETYMOLOGY: The new subgeneric name is a combination of the Greek alpha privativum, *a*– (ᾰ–, indicating negation or opposite), *trikhós* (*τρῐχός*, meaning, "hairy"), and the generic name *Trigona* [*tri*– (*τρῐ*–, meaning, "three") and *gōnía* (*γωνία*, meaning, "corner" or "angle")]. The gender of the name is feminine.

INCLUDED SPECIES: Aside from the type species, the subgenus includes *Axestotrigona simpsoni* Moure.

Subtribe Meliponina Lepeletier de Saint Fargeau
Infratribe Meliponitae Lepeletier de Saint Fargeau
Clan *Trigona*
Plebeia Genus Group

The *Plebeia* genus group is a large and diverse lineage of Neotropical stingless bees, and currently includes four clades (Rasmussen & Cameron, 2010) (Table 2). The *Tetragonisca* clade comprises *Tetragonisca* Moure, *Frieseomelitta* Ihering, *Duckeola* Moure, and *Trichotrigona* Camargo & Moure, although the last three could be united as subgenera of a single genus. The *Scaura* clade includes only the genus *Scaura* Schwarz and its two subgenera. Should future studies continue to indicate that *Scaura s.str.* is paraphyletic to *Schwarzula* Moure (*e.g*., Rasmussen & Cameron, 2010), then these two should be united and no subgenera recognized. The *Nannotrigona* clade comprises *Nannotrigona* Cockerell and *Schwarziana* Moure. Lastly, the *Plebeia* clade — *Plebeia* Schwarz, *Friesella* Moure, *Lestrimelitta* Friese, *Plectoplebeia* Melo, and *Asperplebeia* n. gen. — is one of the most challenging groups among New World Meliponini, with many difficult to distinguish species in *Plebeia* and potential intergradations between this genus and *Plectoplebeia* (Engel, in press-c). A key encompassing the entire group as it is currently conceived has been lacking and so one is presented here in an attempt to aid the identification of these bees.

Key to Genera and Subgenera of *Plebeia* Genus Group
(worker caste; partly emended and expanded from Silveira *et al*., 2002; Michener, 2007)

1. Prolateral surface of metatibia flat or concave apically, forming corbicula, proventral margin gently convex to concave, differing from retromarginal contour; penicillum present; rastellum variable; first flagellomere shorter than combined lengths of second and third flagellomeres 2

—. Prolateral surface of metatibia convex, without corbicula, proventral margin convex like retromarginal contour; penicillum absent; rastellum consisting of tapering setae; first flagellomere nearly as long as combined lengths of second and third flagellomeres .... *Lestrimelitta* Friese

2(1). Anterior margin of mesoscutellum with shining, longitudinal, V- or U-shaped median depression opening anteriorly into mesoscutal-mesoscutellar fossa; posterior margin of mesoscutellum notched or emarginate medially; preoccipital carina present, extending far down each side of head; integument of head and mesosoma, or at least mesoscutellum, with coarse, cribriform punctation [Genus *Nannotrigona* Cockerell, *s.l.*] 3

—. Anterior margin of mesoscutellum without shining, longitudinal, median depression; posterior margin of mesoscutellum entire; preoccipital carina absent or weakly indicated only by transverse dorsal section posterior to vertex; integument of head and mesosoma with fine, often scattered, punctation 4

3(2). Mesoscutum and mesoscutellum with dense, coarse, cribriform punctures (Fig. 122); larger bees, head width more than 1.6 mm .... *Nannotrigona* Cockerell, *s.str.*

—. Mesoscutum sparsely punctate, integument between punctures shining, contrasting denser, coarser punctation of mesoscutellum (Fig. 123); smaller bees, head width less than 1.6 mm .... *Lispotrigona* Gonzalez & Engel, n. subgen.

4(2). Retrolateral surface of metatibia with strongly depressed superior glabrate zone, superior glabrate zone at least apically about as broad as keirotrichiate zone 5

—. Retrolateral surface of metatibia with depressed superior glabrate zone narrow, much less than half as wide as keirotrichiate zone, or absent, keirotrichia extending to or close to margin 8

5(4). Retrolateral surface of metabasitarsus without basal sericeous area 6

—. Retrolateral surface of metabasitarsus with basal sericeous area .... *Tetragonisca* Moure

6(5). Compound eyes bare; rastellum strongly developed 7

—. Compound eyes setose; rastellum reduced to tapering setae .... *Trichotrigona* Camargo & Moure

7(6). Posterior margin of vertex elevated as strong, setose ridge between summits of compound eyes; superior distal angle of metatibia acute .... *Duckeola* Moure

Figures 122–123. Mesosomal dorsum of workers of *Nannotrigona* Cockerell. **122.** *Nannotrigona* (*Nannotrigona*) *perilampoides* (Cresson). **123.** *N.* (*Lispotrigona*) *schultzei* (Friese).

—. Posterior margin of vertex not elevated; superior distal angle of metatibia broadly rounded .... *Frieseomelitta* Ihering

8(4). Metabasitarsus thickened, prolateral surface swollen, nearly as broad as or broader than metatibia, bristles of inferior retrolateral margin curved apically; yellow maculation absent; rastellum nearly occupying full length of metatibial apical margin [Genus *Scaura* Schwarz, *s.l.*] 9

—. Metabasitarsus not thickened, prolateral surface flat, much narrower than metatibia; bristles of inferior retrolateral margin straight; yellow maculation present; rastellum occupying two-thirds or less of metatibial apical margin 10

9(8). Metabasitarsus as wide as or wider than metatibia; malar space shorter than flagellar diameter; gena in profile narrower than compound eye; mandible virtually edentate .... *Scaura* Schwarz, *s.str*.

—. Metabasitarsus narrower than metatibia; malar space as long as flagellar diameter; gena in profile broader than compound eye; mandible with two denticles .. .. *Schwarzula* Moure

10(8). Head and mesosoma largely smooth and shining between scattered small setiferous punctures, rarely granulose-microrugulose and more matte; mesepisternum with at least some simple erect setae among plumose setae 11

—. Head and mesosoma with large, dense punctation or integument matte and microreticulate with indistinct punctures; mesepisternum with erect setae always plumose or minutely branched 14

11(10). Clypeo-ocular distance at base of clypeus 2× torular diameter or less; scape distinctly shorter than torulocellar distance; metatibia shorter, length 2.2–2.5× maximum width, with apical proventral margin comparatively straight; mesoscutellum width about 2× medial length; r-rs 0.5× length Rs+M or frequently less; malar space less than 0.5× flagellar diameter, often linear; smaller bees 12

—. Clypeo-ocular distance at base of clypeus 2.5× torular diameter or more; scape as long as or slightly longer than torulocellar distance; metatibia long, length 2.6–2.8× maximum width, with apical proventral margin curved; mesoscutellum width about 1.9× medial length; r-rs 0.6× length or more of Rs+M; malar space 0.25–0.65× flagellar diameter; larger bees .... *Plectoplebeia* Melo

12(11). Mesoscutum generally matte owing to finely microrugulose-granulose sculpture resulting from dense, coarse, shallow punctures (Figs. 124, 125) .... *Asperplebeia* Engel, n. gen.

—. Mesoscutum shining and smooth, punctures small to minute and distinctly separated, often widely so (Figs. 126, 127) [Genus *Plebeia* Schwarz, *s.l.*] 13

13(12). Forewing 2Cu a faint nebulous trace, weakening apically and disappearing by wing margin; minute bees, 2–3.5 mm in length ..... *Nanoplebeia* Engel, n. subgen.

—. Forewing 2Cu terminating on wing margin as a dark brown to brown tubular vein or nebulous trace, no weaker at terminus than on remigium; small bees, typically 3.5 mm or greater in length .... *Plebeia* Schwarz, *s.str.*

14(10). Head and mesosoma with conspicuous yellow maculation; erect sternal setae predominantly plumose; moderate-sized bees, body length over 5 mm [Genus *Schwarziana* Moure, *s.l.*] 15

—. Head and mesosoma with exceptionally small areas of yellow maculation; erect sternal setae simple; smaller bees, body length less than 4 mm ... *Friesella* Moure

15(14). Integument without metallic reflections; mesoscutum matte, integument microreticulate, with punctures indistinct 16

—. Integument with weak metallic reflections; mesoscutum shining, punctures distinct and dense .... *Mourella* Schwarz

16(15). Malar space shorter than flagellar diameter; mesepisternal setae long, longer than protibial width, and dense, sometimes obscuring integument .... *Schwarziana* Moure, *s.str.*

—. Malar space as long as flagellar diameter; mesepisternal setae short, shorter than protibial width, and sparser .... *Chapadapis* Engel, n. subgen.

Genus *Nannotrigona* Cockerell

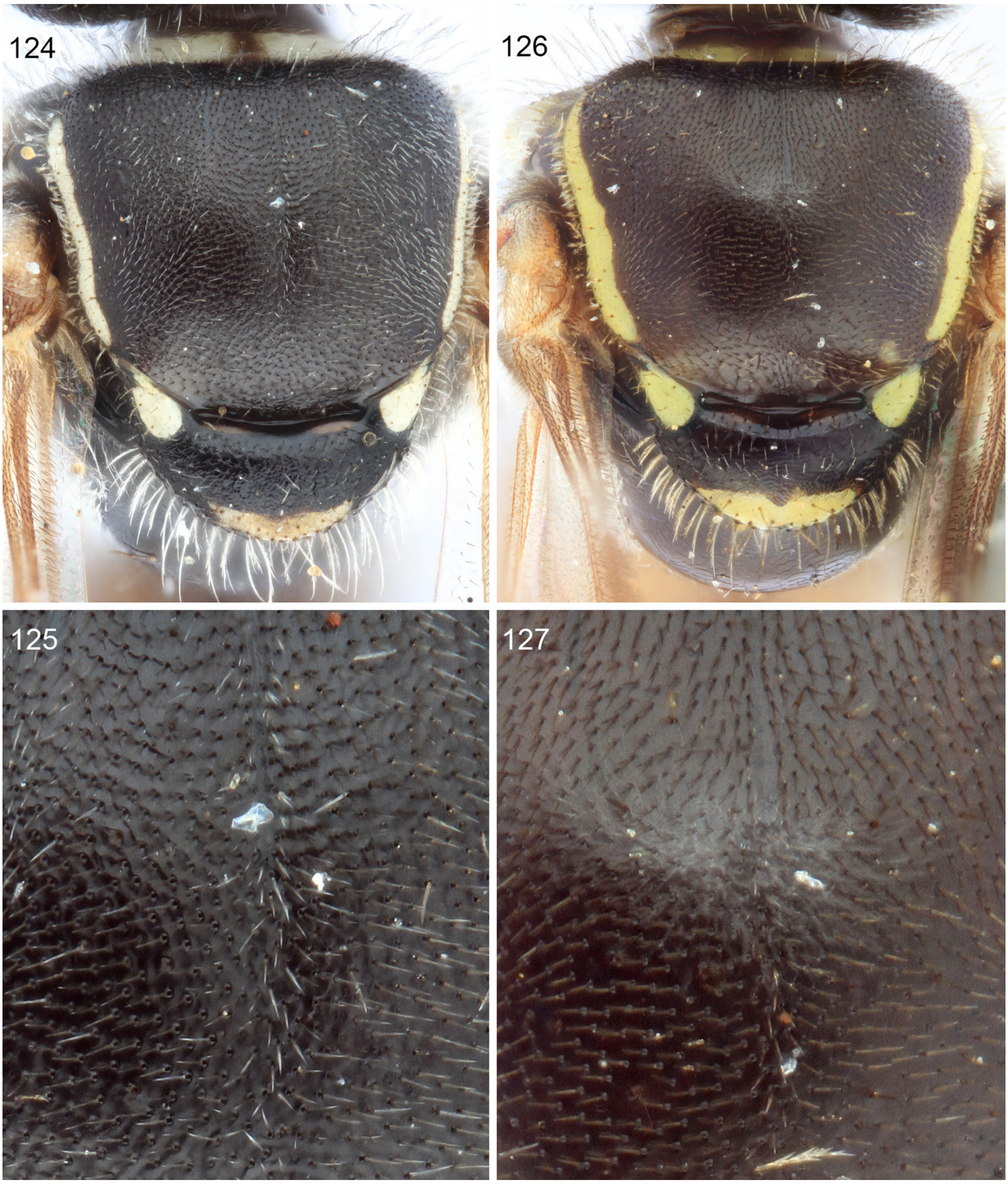
The genus *Nannotrigona* Cockerell comprises 14 species found from northern Mexico to southern Peru, Bolivia, Paraguay, and southeastern Brazil. The genus is one of the more distinctive of New World Meliponini owing to the combination of a shining, mediolongitudinal depression anteriorly on the mesoscutellum (Figs. 122, 123), a strong preoccipital carina, and a dense, coarse, cribriform punctation on the mesoscutellum (Figs. 122, 123), and often on the head and mesoscutum as well. Within the genus there are two distinctive groups (Rasmussen & Gonzalez, 2017), here treated as subgenera.

Lispotrigona V.H. Gonzalez & Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:8D632CB5-27FB-4BAC-AA9C-4A6495D278F0

Type species: *Trigona schultzei* Friese, 1901.

Diagnosis: This subgenus is equivalent to the *dutrae*-species group of Rasmussen & Gonzalez (2017) and consists of small bees, with head widths less than 1.6 mm



Figures 124–127. Mesosomal dorsa of workers of *Asperplebeia*, new genus, and *Plebeia* Schwarz. **124.** Mesosomal dorsum of *Asperplebeia moureana* (Ayala), new combination. **125.** Detail of mesoscutal disc of *A. moureana*. **126.** Mesosomal dorsum of *Plebeia* (*Nanoplebeia*) *minima* (Gribodo). **127.** Detail of mesoscutal disc of *P.* (*N.*) *minima*.

(versus larger than this in the nominate subgenus). Unlike typical species of *Nannotrigona*, the species of the new subgenus have the mesoscutum sparsely punctate and the integument shining between the punctures (Fig. 123). This sculpturing contrasts with the denser, coarser, cribriform punctation of the mesoscutellum. In the nominate subgenus the punctation of the mesoscutum and mesoscutellum are both dense, coarse, and cribriform Fig. 122).

Etymology: The new subgeneric name is a combination of the Greek *líspos* (*λῐ́σπος*, meaning, "polished") and the generic name *Trigona*. The gender of the name is feminine.

Included species: Aside from the type species, the subgenus includes *Nannotrigona* (*Lispotrigona*) *dutrae* (Friese).

Asperplebeia Engel, new genus

ZooBank: urn:lsid:zoobank.org:act:AB56D1E5-AF86-4E4E-8ACC-66CF54B54F5C

Type species: *Plebeia moureana* Ayala, 1999.

Diagnosis: This genus includes particularly small *Plebeia*-like bees, with total body lengths approximately 2.6–4.1 mm. Most notably, the integument of the mesoscutum and mesoscutellum is generally matte and finely granular or microrugulose with comparatively coarser punctures (Figs. 124, 125). By contrast, in *Plebeia* Schwarz the integument of the mesoscutum and mesoscutellum is noticeably shiny and typically smooth with widely spaced, minute punctures (Figs. 126, 127). Otherwise, the genus shares most traits with *Plebeia*, including the keirotrichiate zone on the retrolateral surface of the metatibia extending nearly to the retrodorsal margin. The surface of the mesoscutellum is gently and weakly convex, and posteriorly overhangs the metanotum and the basalmost margin of the propodeum. Currently, the genus is known from Mexico to Costa Rica, but likely also occurs further south.

Etymology: The new genus-group name is a combination of the Latin terms *asper* (meaning, "rough" or "coarse") and *plēbēia* (meaning, "commoner"), in reference to the roughened and matte mesoscutum relative to *Plebeia*. The gender of the name is considered to be feminine.

Included species: Aside from the type species, *Asperplebeia moureana* (Ayala), the genus includes *A. tica* (Wille), both new combinations.

Genus *Plebeia* Schwarz

Nanoplebeia Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:ED35E46F-94FA-4996-A0D4-694F57FFE766

Type species: *Trigona minima* Gibodo, 1893.

Diagnosis: This group includes particularly small species of *Plebeia*, with total body lengths approximately 2–3.5 mm. In most characters they are otherwise identical with the nominate subgenus, although in the forewing 2Cu is frequently a faint nebulous trace, weakening apically and disappearing by the wing margin. In typical *Plebeia* the vein is more prominently developed, often a brown to dark brown nebulous vein that extends across the remigium and terminates at the wing margin. In these species the mesoscutellum projects over the metanotum and the suture with the propodeum, but does not extend further. In *Plebeia s.str*. the extent to which the meoscutellum is extended is more variable and sometimes scarcely overhangs the metanotum or may more distinctly extend over the base of the propodeum.

Etymology: The new genus-group name is a combination of the Latin terms *nānus* (meaning, "dwarf") and *plēbēia* (meaning, "commoner"). The gender of the name is considered to be feminine.

INCLUDED SPECIES: The subgenus currently includes *Plebeia franki* (Friese), *P. margaritae* Moure, *P. minima* (Gribodo), and at least four undescribed species (Engel, in press-d).

Genus *Schwarziana* Moure

Schwarziana Moure is a distinctive group of stingless bees that nest in the ground. The group was included in *Plebeia* by Michener (1990, 2007), where it was considered a subgenus, although *Mourella* Schwarz was removed and placed into synonymy with *Plebeia s.str.* (an arrangement not followed here as *Mourella* is considered a distinct subgenus of *Schwarziana*). Five species are recognized in three subgenera, two of which are monotypic.

Chapadapis Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:1D3425ED-2F27-4092-9AD4-34CBA7BDD2DB

TYPE SPECIES: *Schwarziana chapadensis* Melo, 2015.

DIAGNOSIS: This subgenus includes a single species that generally resembles those species of *Schwarziana s.str.*, but can be distinguished by the longer malar space, which is about as long as the flagellar diameter, and by the sparser and shorter mesepisternal setae, which are shorter than the protibial width (Melo, 2015). Like *Schwarziana s.str.*, *Chapadapis* lacks metallic reflections and has a generally matte mesoscutum, with indistinct punctures and a microreticulate integumental sculpture. The subgenus is currently endemic to Chapada dos Veadeiros of Goiás, Brazil.

ETYMOLOGY: The new subgeneric name is a combination of chapada, referring to the plateaus of the Brazilian Highlands, in reference to the Chapada dos Veadeiros, and *apis* (Latin, meaning, "bee"). The gender of the name is feminine.

Trigona Genus Group

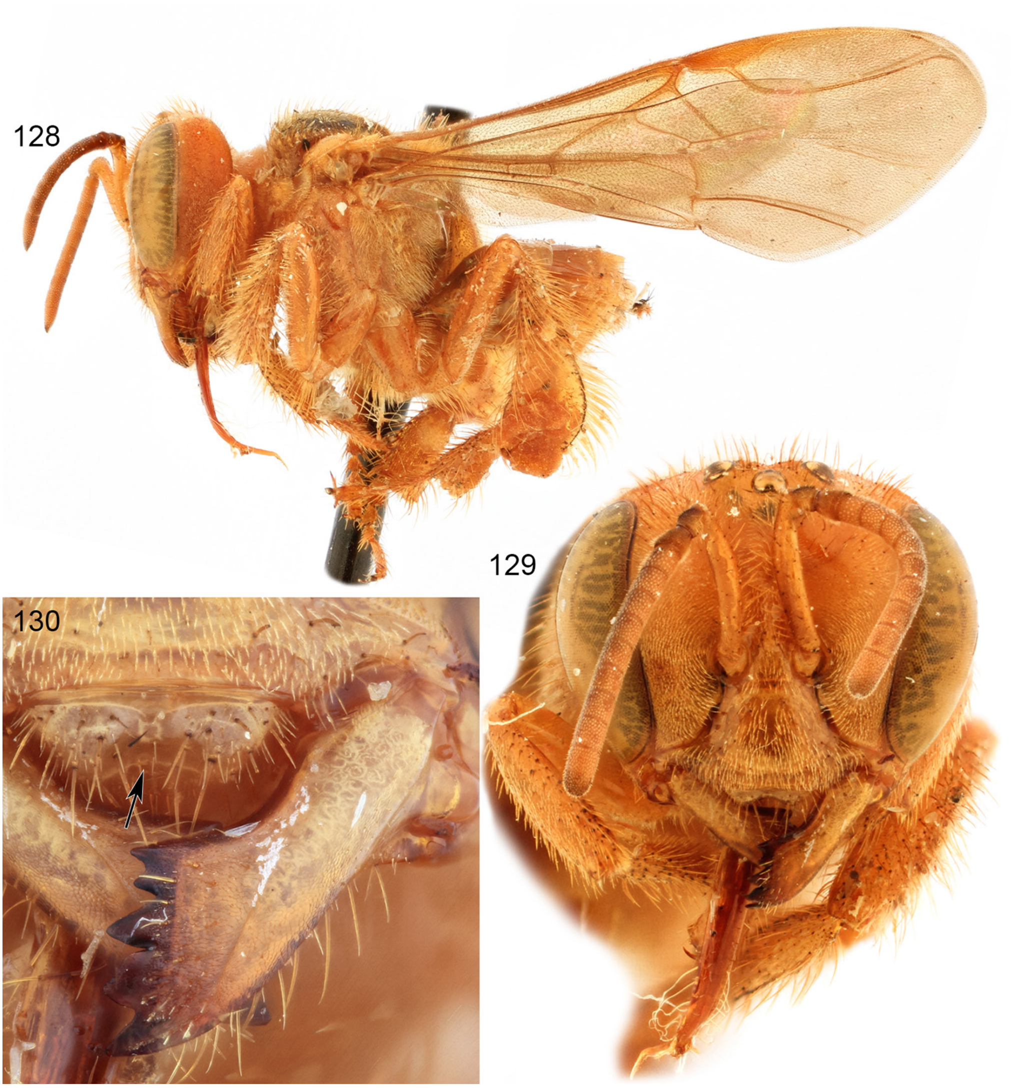
Genus *Trigona* Jurine

This is perhaps one of the more familiar groups of Neotropical bees and also one of the most varied in terms of biology. Some species are not uncommonly encountered and can be quite defensive of their nests if approached, effectively repeling intruders from their perimeter. Although only 30 species are currently described, there are perhaps just as many awaiting description, including cryptic species lumped under *Trigona amalthea* (Olivier) and other comparatively common and widespread species.

Key to Subgenera of *Trigona*

(worker caste)

1. Mandible with four teeth 2
—. Mandible with five teeth (Figs. 130, 147) 3
2(1). Labrum simple, surface gently and evenly convex; wings dichroic, proximally infuscate, apically whitish (*e.g.*, Fig. 136); pterostigma yellowish brown; scape black .... *Aphaneuropsis* Engel, n. subgen.



Figures 128–130. Worker of *Trigona* (*Aphaneura*) *pallens* (Fabricius). **128.** Lateral habitus. **129.** Facial view. **130.** Detail of labrum and mandibular dentition; arrow shows mediolongitudinal furrow resulting in bigibbous labrum.

—. Labrum bigibbous, with pronounced mediolongitudinal furrow (*e.g.*, Fig. 130); wings uniformly fuscous; pterostigma brown to dark brown; scape lighter ventrally, light brown to yellowish brown .... *Koilotrigona* Engel, n. subgen.

3(1). Metatibia with distinct corbicula on apical prolateral surface (corbicular surface concave) (Fig. 132), superior distal angle present (Fig. 132), retromarginal fringe setae abundant (Fig. 132) 4

—. Metatibia without defined corbicula on apical prolateral surface (corbicular surface not concave) (Fig. 131), superior distal margin rounded (Fig. 131), retromarginal fringe setae less numerous (Fig. 131) ..... *Necrotrigona* Engel, n. subgen.

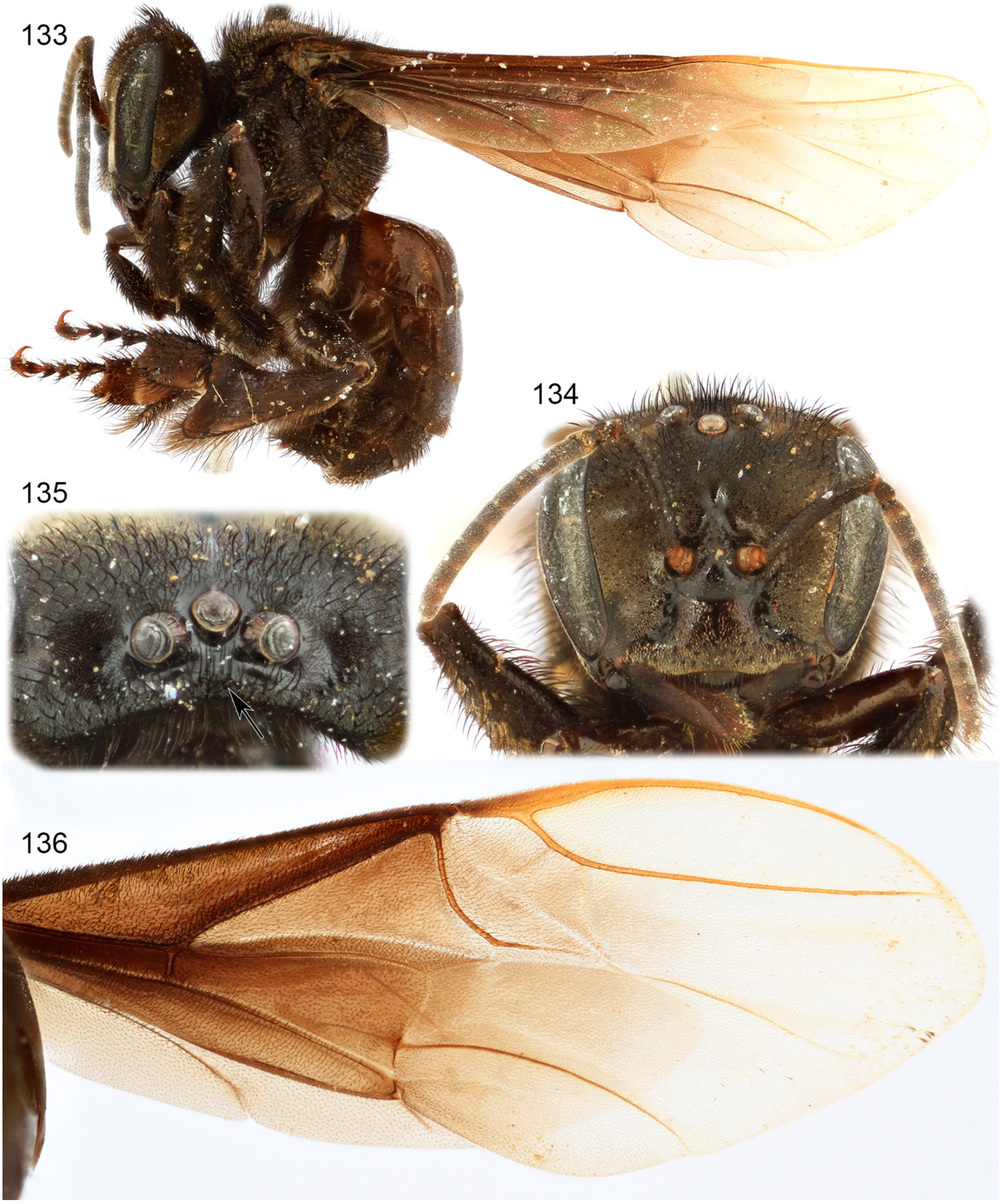
Figures 131–132. Prolateral surfaces of metatibiae and metatarsi of workers of *Trigona* Jurine. **131.** *Trigona* (*Necrotrigona*) *hypogea* Silvestri. **132.** *T.* (*Dichrotrigona*) *dimidiata* Smith.

4(3). Labrum simple, surface gently and evenly convex; vertex with distinct postocellar ridge (Figs. 135, 138, 139, 144–148); integument entirely dark brown to black (Figs. 133, 134, 138, 144, 145, 147) (except entirely orange in *T. dallatorreana* Friese) 5

—. Labrum bigibbous, with mediolongitudinal furrow (Fig. 130) (furrow somewhat weak in *T. williana* Friese); vertex without postocellar ridge (Fig. 129), or ridge quite weak; integument largely yellowish orange (Figs. 128, 129) (head, mesoscutum, and parts of pleura sometimes largely black but clypeus and antenna always yellowish to yellowish orange) .... *Aphaneura* Gray

5(4). Wing membrane not as below, if slightly lighter apically, then transition gradual across wing length; metatibial width variable, sometimes comparatively narrow 6

—. Wing membrane strikingly dichroic, proximally darkly infuscate, apically whitish (Figs. 133, 136); metatibia broad apically, with broadly rounded retromarginal contour (Fig. 133) .... *Dichrotrigona* Engel, n. subgen.



Figures 133–136. Worker of *Trigona* (*Dichrotrigona*) *dimidiata* Smith. **133.** Lateral habitus. **134.** Facial view. **135.** Vertex; arrow indicates postocellar ridge. **136.** Forewing.

6(5). Small bees, head width 2.5 mm or less; forewing (including tegula) length less than 6.5 mm; metatibia narrow, retromarginal contour comparatively straight until apical fifth 7

—. Larger bees, head width typically 2.5 mm or greater, rarely as small as 2.45 mm (in some *T. corvina* Cockerell), forewing (including tegula) length 6.9 mm or greater; metatibia broader, typically with broadly rounded retromarginal contour .... *Trigona* Jurine, *s.str*.

7(6). Apical fundal surface of metatibia near corbicula with abundant minute, fine, appressed setae (Figs. 140, 141); scape with prominent, thick, black bristles along length, such bristles often as long as scape diameter (Figs. 145, 149); clypeus in profile with numerous, erect, black bristles; distance from median ocellus to postocellar ridge about ocellar diameter (Fig. 146); smaller bees, intertegular distance 1.35 mm or less .... *Nostotrigona* Engel, n. subgen.

—. Apical fundal surface of metatibia near corbicula with minute, fine, appressed setae either lacking or exceedingly sparse (Figs. 142, 143); scape without thick bristles, with fine, lighter setae, such setae shorter than scape diameter (Fig. 147, 150); clypeus in profile with a few short, fine setae, without black bristles; distance from median ocellus to postocellar ridge less than ocellar diameter (Fig. 148); larger bees, interegular distance 1.4 mm or greater .... *Ktinotrofia* Engel, n. subgen.

Aphaneuropsis Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:8B67997E-43D5-432E-8C5F-8E155232B3E4

Type species: *Centris cilipes* Fabricius, 1804.

Diagnosis: This group includes those species of *Trigona* with four teeth that build temporary support pillars in the nest as well as regular horizontal brood combs (*cf. Koilotrigona, infra*). The subgenus is characterized by the following combination of traits: integument entirely dark brown to black; forewing membrane dichroic, proximally infuscate, apically whitish; mandible quadridentate; labrum simple, surface gently and evenly convex; vertex with distinct postocellar ridge (ridge absent or weak in *Aphaneura* Gray); distance from median ocellus to postocellar ridge subequal to ocellar diameter; metatibia with distinct corbicula, with retromarginal fringe setae abundant.

Etymology: The new subgeneric name is a combination of *Aphaneura* Gray [*aphanḗs* (*ἀφᾰνής*, meaning, "unseen") and *neûron* (*νεῦρον*, meaning, "nerve")] and the Greek *ópsis* (*ὄψῐς*, meaning, "appearance"). The gender of the name is feminine.

Included species: Aside from the type species, the subgenus includes *T. lacteipennis* Friese, *T. mazucatoi* Almeida, and *T. pellucida* Cockerell.

Koilotrigona Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:7BD0BD04-5095-40E9-A1CF-F0AA922E47DF

Type species: *Trigona fulviventris* Guérin-Méneville, 1844.

Diagnosis: Like *Aphaneuropsis* (*supra*), this genus has four teeth but builds permanent support pillars in the nest and irregular horizontal brood combs. The subgenus is characterized by the following combination of traits: integument entirely dark brown to black, although metasoma sometimes orange to reddish orange (*i.e.*, *T. fulviventris*); forewing membrane uniformly infumate; mandible quadridentate; labrum bigibbous, with pronounced mediolongitudinal furrow; vertex with distinct postocellar ridge; distance from median ocellus to postocellar ridge an ocellar diameter or less; metatibia with distinct corbicula, with retromarginal fringe setae abundant.

Etymology: The new subgeneric name is a combination of the Greek *koílos* (*κοίλος*, meaning, "hollow" or "concave") and *Trigona*. The gender of the name is feminine.

Included species: In addition to the type species, the subgenus currently includes *T. braueri* Friese and *T. guianae* Cockerell.

Figures 137–139. Worker of *Trigona* (*Trigona*) *silvestriana* (Vachal). **137.** Lateral habitus. **138.** Facial view. **139.** Vertex; arrow indicates postocellar ridge.

Necrotrigona Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:8EE70210-E246-4033-BFD3-2B14B2015983

Type species: *Trigona hypogea* Silvestri, 1902.

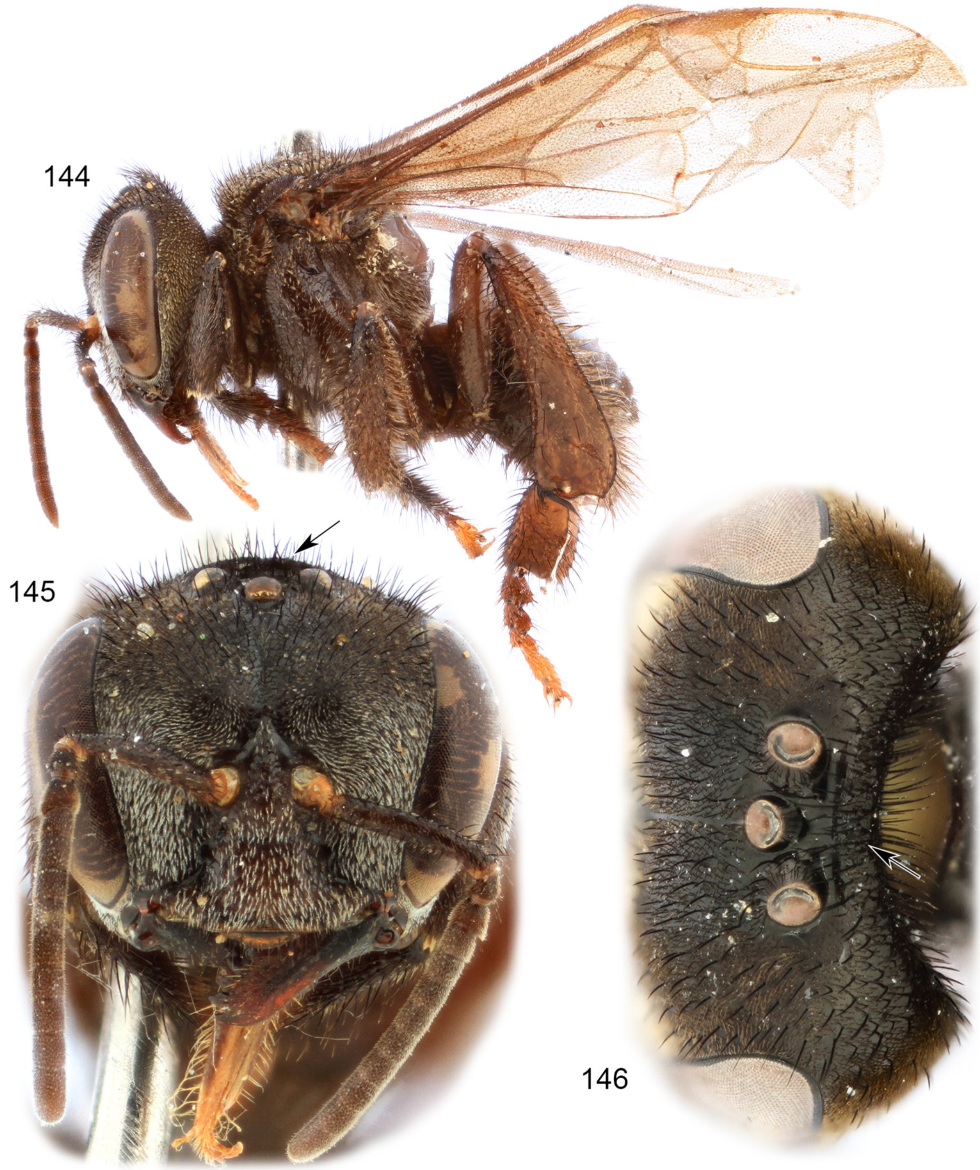
Diagnosis: This group includes the obligate necrophages. The subgenus is characterized by the following combination of traits: integument entirely dark brown to black; forewing membrane hyaline and typically lightly infumate, particularly proximally, sometimes slightly lighter apically; mandible quinquedentate; labrum simple, surface gently and evenly convex; vertex with distinct postocellar ridge; distance from

Figures 140–143. Metatibiae of workers of *Trigona* Jurine. **140.** *Trigona* sp. **141.** Detail of 140 showing abundant minute setae on fundus. **142.** *Trigona* (*Ktinotrofia*) *albipennis* Almeida. **143.** Detail of 142 showing sparse minute setae on fundus.

median ocellus to postocellar ridge subequal to ocellar diameter; metatibia without defined corbicula, superior distal angle rounded, penicillum absent, retromarginal fringe setae sparse (Fig. 131) .

ETYMOLOGY: The new subgeneric name is a combination of the Greek *nekrós* (*νεκρός*, meaning, "dead") and *Trigona*. The gender of the name is feminine.

INCLUDED SPECIES: Aside from the type species, the subgenus includes *T. crassipes* (Fabricius) and *T. necrophaga* Camargo & Roubik.



Figures 144–146. Worker of *Trigona* (*Nostotrigona*) *recursa* Smith. **144.** Lateral habitus. **145.** Facial view; arrow indicates postocellar ridge. **146.** Vertex; postocellar ridge.

Dichrotrigona Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:9CB27106-700C-4CF2-B502-FA35E1338C2B

Type species: *Trigona dimidiata* Smith, 1854.

Diagnosis: This subgenus is superficially similar to *Aphaneuropsis* in the dichroic pattern of wing coloration (Figs. 133, 136), but most readily differs in the five mandibular teeth, among other characters. The subgenus is characterized by the following combination of traits: integument entirely dark brown to black; forewing membrane dichroic, proximally infuscate, apically whitish (Figs. 133, 136); mandible quinqueden-

Figures 147–148. Worker of *Trigona* (*Ktinotrofia*) *albipennis* Almeida. **147.** Facial view. **148.** Vertex.

tate; labrum simple, surface gently and evenly convex; vertex with distinct postocellar ridge (Figs. 134, 135); distance from median ocellus to postocellar ridge an ocellar diameter or less (Fig. 135); metatibia with distinct corbicula, with retromarginal fringe setae abundant.

ETYMOLOGY: The new subgeneric name is a combination of the Greek *díkhrōs* (*δίχρως*, meaning, "bicolored") and *Trigona*. The gender of the name is feminine.

INCLUDED SPECIES: Aside from the type species, the subgenus currently includes *T. sesquipedalis* Almeida and *T. venezuelana* Schwarz.

Nostotrigona Engel, new subgenus

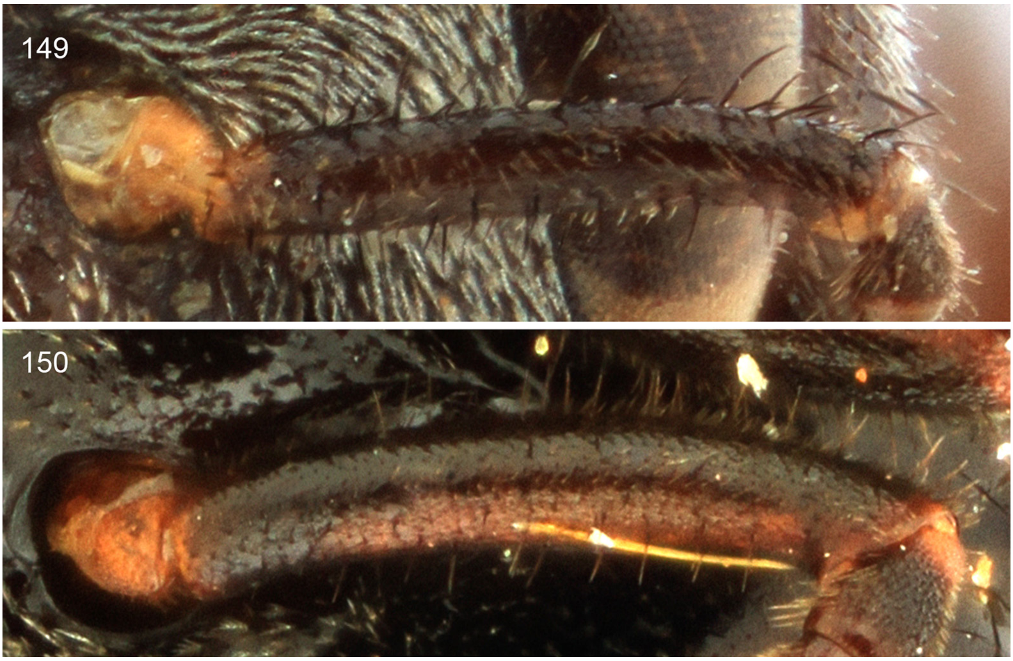
ZooBank: urn:lsid:zoobank.org:act:CE166A96-B187-41BA-8E40-CD70FCA2ADDE

TYPE SPECIES: *Trigona recursa* Smith, 1863.

DIAGNOSIS: This group includes the smallest species of *Trigona* and is generally similar to the hemipterophilic species of *Ktinotrofia* (*vide infra*). The subgenus can generally be characterized by the following combination of traits: integument entirely dark brown to black (Fig. 144); forewing membrane hyaline clear to faintly infumate or parchment-colored; mandible quinquedentate; labrum simple, surface gently and evenly convex; clypeus in profile with numerous erect bristles; scape with prominent, thick, black bristles, such bristles typically as long as scape diameter (sometimes even slightly longer) (Fig. 149); vertex with distinct postocellar ridge (Figs. 145, 146); distance from median ocellus to postocellar ridge equal to ocellar diameter (Fig. 146); metatibia with distinct corbicula, with retromarginal fringe setae abundant.

ETYMOLOGY: The new subgeneric name is a combination of the Greek *nóstos* (*νόστος*, meaning, "returning") and *Trigona*. The gender of the name is feminine.

INCLUDED SPECIES: In addition to the type species, the subgenus includes *T. permodica* Almeida.



Figures 149–150. Worker scapes of *Trigona* Jurine. **149.** *Trigona* (*Nostotrigona*) *recursa* Smith. **150.** *T.* (*Ktinotrofia*) *albipennis* Almeida.

Ktinotrofia Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:94837C5A-59EE-4D4E-B1FA-44CF5BD63BD4

Type species: *Trigona fuscipennis* Friese, 1900.

Diagnosis: This group includes those obligately hemipterophilic species of *Trigona*. The subgenus is characterized by the following combination of traits: integument entirely dark brown to black; forewing membrane hyaline clear to lightly infumate; mandible quinquedentate; labrum simple, surface gently and evenly convex; clypeus in profile without numerous erect bristles; scape with fine, fuscous setae, such setae shorter than scape diameter (Fig. 150); vertex with distinct postocellar ridge (Figs. 147, 148); distance from median ocellus to postocellar ridge less than ocellar diameter (Fig. 148); metatibia with distinct corbicula, with retromarginal fringe setae abundant.

Etymology: The new subgeneric name is a combination of the Greek *ktinotrofía* (*κτηνοτροφία*), meaning, "animal husbandry", and refers to the obligate hemipterophily of these species. The gender of the name is feminine.

Included species: In addition to the type species, the subgenus includes *T. albipennis* Almeida.

JM Journal of Melittology

A Journal of Bee Biology, Ecology, Evolution, & Systematics

The *Journal of Melittology* is an international, open access journal that seeks to rapidly disseminate the results of research conducted on bees (Apoidea: Anthophila) in their broadest sense. Our mission is to promote the understanding and conservation of wild and managed bees and to facilitate communication and collaboration among researchers and the public worldwide. The *Journal* covers all aspects of bee research including but not limited to: anatomy, behavioral ecology, biodiversity, biogeography, chemical ecology, comparative morphology, conservation, cultural aspects, cytogenetics, ecology, ethnobiology, history, identification (keys), invasion ecology, management, melittopalynology, molecular ecology, neurobiology, occurrence data, paleontology, parasitism, phenology, phylogeny, physiology, pollination biology, sociobiology, systematics, and taxonomy.

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.

Journal of Melittology is registered in ZooBank (www.zoobank.org), and archived at the University of Kansas and in Portico (www.portico.org).

http://journals.ku.edu/melittology
ISSN 2325-4467