AMERICAN MUSEUM NOVITATES

Number 3888, 33 pp. December 14, 2017

A New Genus of Eastern Hemisphere Stingless Bees (Hymenoptera: Apidae), with a Key to the Supraspecific Groups of Indomalayan and Australasian Meliponini

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ABSTRACT

A new genus of stingless bees (Apinae: Meliponini) is described and figured from Indonesia (Sulawesi), known from a single species previously placed in *Geniotrigona* Moure. Based on recent phylogenetic studies, *Trigona* (*Geniotrigona*) *incisa* Sakagami and Inoue renders *Geniotrigona* polyphyletic and is more closely related to *Lepidotrigona* Moure. The species is transferred to *Wallacetrigona* Engel and Rasmussen, new genus, and differentiated from *Geniotrigona* proper as well as all other meliponines occurring in Sundaland, Wallacea, and Sahul (Australinea). The new genus occurs east of the Wallace Line and separate from the distribution of *Geniotrigona*, which is otherwise restricted to Sundaland, but *Wallacetrigona* is presently not known beyond the Weber Line. A hierarchical classification of Indomalayan and Australasian stingless bees is tabulated and a revised key to the genera and subgenera provided, as well as an appendix tabulating the species and synonyms. The following new combinations are established: *Wallacetrigona incisa* (Sakagami and Inoue), *Homotrigona* (*Lophotrigona*) *canifrons* (Smith), *Homotrigona* (*Odontotrigona*) *haematoptera* (Cockerell), *Homotrigona* (*Tetrigona*) *apicalis* (Smith), *H.* (*T.*) *binghami* (Schwarz), *H.* (*T.*) *melanoleuca* (Cockerell), *H.* (*T.*) *peninsularis* (Cockerell), and *H.* (*T.*) *vidua* (Lepeletier de Saint Fargeau).

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 ISSN 0003-0082

INTRODUCTION

Bees are attractive insects that mostly visit flowers and secure pollination of plants (Michener, 2007). While most species live a solitary life, with a single female establishing and providing for the nest, some species of bees live in large perennial colonies where they store food as honey, known to humans since prehistory. While honey bees (species of *Apis* Linnaeus) are well-known for their honey products, the much larger, and more diverse, group of tropical and subtropical bees, the stingless bees (Apinae: Corbiculata: Meliponini) have regionally also played important roles as honey producers (e.g., Nogueiro-Neto, 1953; Cortopassi-Laurino et al., 2006; Heard, 2016), particularly in the Americas where no native honey bees cooccurred with humans (*Apis* occurred in the New World only prior to the Pliocene: Engel et al., 2009). There are about 500 species of stingless bees known, and the classification of this highly diverse group of pantropical bees comprises one of the greatest challenges among the diversifications of corbiculate apines.

The Indomalayan/Australasian clade of stingless bees (as defined by Rasmussen and Cameron, 2010), was traditionally treated as belonging to a single genus, *Trigona* Jurine (e.g., Schwarz, 1937). Schwarz (1939) was the first to propose two subgenera from the region, *Heterotrigona* Schwarz and *Lepidotrigona* Schwarz. The remaining stingless bee taxa were at the time placed in either the New World or Afrotropical (then) subgenera of *Trigona*: *Tetragona* Lepeletier and Audinet-Serville or *Hypotrigona* Cockerell. Finally, in 1961 Moure proposed a series of 11 genera that took into consideration the distinctiveness and diversity of the known Indomalayan/Australasian fauna (Moure, 1961). Two additional higher-level groups were proposed as *Trigonella* Sakagami and Moure (in Sakagami, 1975), replaced later as *Sundatrigona* Inoue and Sakagami (1993), and *Papuatrigona* Michener and Sakagami (1990). While the names were available, they were only reluctantly accepted and major works dealing with the classification, such as Michener (1990, 2007), refrained from removing the majority of the taxa from the New World genus of *Trigona*. Instead, they were merged into a restricted subset of subgenera within the otherwise New World genus *Trigona*. Recently, however, a phylogenetic study focused on the Old World fauna (Rasmussen and Cameron, 2007), and a comprehensive taxonomic catalog of the region (Rasmussen, 2008), emphasized the need to diverge from tradition and adopt a revised classification, closer in line to that advocated by Moure (1961), that more adequately reflected the inferred evolutionary relationships among these distinctive clades. In the study by Rasmussen and Cameron (2007), a distinct species originally described as *Trigona* (*Geniotrigona*) *incisa* Sakagami and Inoue from Sulawesi (Sakagami and Inoue, 1989) (fig. 1A) rendered the genus *Geniotrigona* Moure polyphyletic. *Geniotrigona incisa* was recovered with significant support as sister to *Lepidotrigona*. As the genus *Lepidotrigona* is morphologically and behaviorally distinct based on the unique plumose or scalelike setae along the mesoscutal margins (Schwarz, 1939) and oviposition rituals (Sakagami and Yamane, 1987), it was undesirable to accommodate *G. incisa* within that genus. Morphologically, *G. incisa* appeared only superficially related to other members of *Geniotrigona* and based on priority it was thus suggested that a new supraspecific name for *G. incisa* was needed (Rasmussen and Cameron, 2007, 2010).

Here we provide the description of the new stingless bee genus from Indonesia (Sulawesi) along with revised keys to the genera and subgenera of Indomalayan and Australasian Meliponini. An appendix is provided with a synonymic list of the Indomalayan stingless bees arranged according to the hierarchical organization of the genera and subgenera as used herein (table 1).

MATERIAL AND METHODS

Specimens of pertinent species were examined in the collections of the Division of Invertebrate Zoology, American Museum of Natural History, New York (AMNH); the Claus Rasmussen Collection, Aarhus University, Denmark (CRCD); California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, California (CSCA); and the Division of Entomology, University of Kansas Natural History Museum, Lawrence (SEMC), and included representatives of all currently recognized supraspecific groups of Indomalayan and Australasian stingless bees. Standard, translingual typographic symbols for sex and caste are employed in reporting specimens examined: ♀, for reproductive female (= queen caste); ♂, for reproductive male (= drone caste of highly eusocial species); ☿, for sterile or nonreproductive female (= worker caste). Morphological terminology is adapted from Engel (2001) and Michener (2007), while the general format used for the descriptions is augmented from those provided by Moure (1961) and Sakagami (1975). Terms for the various stages of vein development and reduction follow those of Mason (1986). Greek letters are used herein to denote proximal or distal subsections of the individual vein abscissae of 1Cu. The forewing 1Cu extends from the divergence of M from Cu to the placement of 1m-cu, distal of which Cu then angles toward the posterior wing margin as 2Cu. Depending on the position of 1cu-a, 1Cu may at times be divided into two subsections (i.e., when 1cu-a is antefurcal the vein is simply 1Cu, but if 1cu-a is postfurcal and meets 1Cu, then 1Cu may be segregated into a proximal and apical portion). Sharkey and Wharton (1997) advocated using "1Cua" and "1Cub" to distinguish between these two units when 1Cu is subdivided by 1cu-a, thereby preserving the homology of the entire abscissae of 1Cu and 2Cu more broadly. We agree with this scheme although have preferred the use of Greek letters: 1Cuα for the proximal section and 1Cuβ for the distal section. Such usage avoids any potential confusion with the lowercase Roman letters for crossveins (e.g., 1cu-a) or the broader entomological system for distinguishing between anterior and posterior sectors of longitudinal veins (e.g., CuA). Contrary to some other usage, however, we have not restricted the numbering of abscissae to proximal, middle, and distal, and used additional numbering, particularly in relation to the abscissae of Rs and M. Microphotography was done by J.C.T. with the aid of an Infinity K-2 long-distance lens attached to a Canon EOS 7 digital camera, and the images then edited, cropped, arranged, and labeled in Adobe Photoshop by M.S.E. The descriptions are provided to enhance our understanding of general patterns among Indomalayan and Australasian bees, patterns that form the foundation for broader evolutionary interpretations (Grimaldi and Engel, 2007), as well as modernize the circumscription of taxa within the region (Gonzalez et al., 2013).

TABLE 1. Hierarchical supraspecific classification of Old World stingless bees (Meliponini) as outlined in Engel (in prep.), with number of currently recognized species indicated (numbers tabulated from the synonymic checklist of the Indomalayan and Australasian species summarized in the appendix and from Eardley, 2004, and Eardley and Urban, 2010, for the African fauna). Daggers (†) indicate extinct taxa.

Heterotrigona Clade	
Heterotrigona Genus Group	
Genus *Tetragonula* Moure, 1961	
Subgenus *Tetragonula* Moure, 1961	31
Subgenus *Tetragonilla* Moure, 1961	4
Genus *Heterotrigona* Schwarz, 1939	
Subgenus *Heterotrigona* Schwarz, 1939	3
Subgenus *Platytrigona* Moure, 1961	5
Subgenus *Sahulotrigona* Engel and Rasmussen, 2017	2
= *Pacificotrigona* Tadauchi et al., 1998, nomen nudum	
Subgenus *Sundatrigona* Inoue and Sakagami, 1993	2
= *Trigonella* Sakagami and Moure in Sakagami, 1975	
Genus *Papuatrigona* Michener and Sakagami, 1990	1
Genus *Lepidotrigona* Schwarz, 1939	12
Genus *Wallacetrigona* Engel and Rasmussen, n. gen.	1
Genus *Geniotrigona* Moure, 1961	2
Homotrigona Genus Group	
Genus *Homotrigona* Moure, 1961	
Subgenus *Tetrigona* Moure, 1961	5
Subgenus *Homotrigona* Moure, 1961	4
Subgenus *Odontotrigona* Moure, 1961	1
Subgenus *Lophotrigona* Moure, 1961	1
Hypotrigona Clade	
Meliponula Genus Group	
Genus *Meliplebeia* Moure, 1961	
Subgenus *Axestotrigona* Moure, 1961	6
Subgenus *Apotrigona* Moure, 1961	1
Subgenus *Meliplebeia* Moure, 1961	4
Subgenus *Plebeiella* Moure, 1961	2
Genus *Dactylurina* Cockerell, 1934	2
Genus *Meliponula* Cockerell, 1934	1
Genus *Plebeina* Moure, 1961	1
Hypotrigona Genus Group	
Genus *Hypotrigona* Cockerell, 1934	4
Genus †*Kelneriapis* Sakagami, 1978	1
= †*Kelnermelia* Moure in Moure and Camargo, 1978	
Genus †*Liotrigonopsis* Engel, 2001	1
Genus *Liotrigona* Moure, 1961	
Subgenus *Liotrigona* Moure, 1961	12
Subgenus *Cleptotrigona* Moure, 1961	1
Genus *Austroplebeia* Moure, 1961	5
Genus *Lisotrigona* Moure, 1961	3
Genus *Pariotrigona* Moure, 1961	1
Clade incertae sedis	
Genus †*Exebotrigona* Engel and Michener, 2013	1
Genus †*Meliponorytes* Tosi, 1896	2

SYSTEMATICS

Tribe Meliponini Lepeletier de Saint Fargeau

Wallacetrigona Engel and Rasmussen, new genus

Type species: *Trigona* (*Geniotrigona*) *incisa* Sakagami and Inoue, 1989.

Diagnosis: The genus *Wallacetrigona* is most similar to *Geniotrigona* (see below), in which its type species was initially placed. The genus can be distinguished from *Geniotrigona* by the narrowly concave emargination (= interdental incision) separating the two preapical teeth (broadly concave interdental incision in *Geniotrigona*); the absence of a strongly elevated ridge posteriorly on the vertex (present in *Geniotrigona*); the presence of a deep, U- or V-shaped concave incision medially on the posterior border of the vertex (absent in all other Indomalayan and Australasian taxa); the absence of a dense covering of short, plumose setae on the mesoscutum (present in *Geniotrigona*); the apical metasomal terga with short, scattered plumose setae amid longer, erect, black setae (plumose setae of *Geniotrigona* longer); keirotrichiate zone of metatibial inner surface about as broad as or slightly broader than posterior glabrate zone, and subequal to the length of the apical glabrate zone.

Description: Workers of moderate size, forewing length approximately 7.0–8.0 mm; integument fairly shiny (fig. 1A), smooth, with scattered microscopic punctures (some of which are setigerous) giving appearance of fine imbrication or tessellation on face (fig. 2A), gena, and apical margins of metasomal terga, but otherwise without distinctive sculpturing; integumental maculation absent; with fine, minute, plumose pubescence on face and clypeus and fine, plumose pubescence on mesosoma particularly numerous on metanotum, metepisternum, and propodeal lateral surfaces but not greatly obscuring integument; apical metasomal terga without dense, elongate, apically plumose setae (such setae present in *Geniotrigona*).

Head as broad as mesosoma, with face broader than compound eye length (fig. 2A); vertex with faint depression immediately posterior to ocelli and with faint transverse ridge before occipital border but never elevated above level of ocelli (figs. 3A, 3B) (vertex with depression immediately posterior to ocelli and with posterior border greatly elevated as ridge above ocelli in frontal view in *Geniotrigona*: figs. 2C, 6A, 6B), with deep, concave, medial notch along border with rounded preoccipital ridge (immediately posterior to median ocellus), notch approximately 0.3× ocellar diameter (notch shallow, narrow, and scarcely evident in *Geniotrigona*); ocelloccipital distance slightly greater than one ocellar diameter; interocellar distance approximately 2.5× ocellar diameter; ocellocular distance 2.5× ocellar diameter; scape longer than torulocellar distance; second flagellomere longer than first, second and third flagellomeres subequal in length; second through 10th flagellomeres each longer than wide; intertorular distance a little less than one-half torulorbital distance; upper torular ("alveolar" in the terminology of Moure, 1961, and Sakagami, 1975) tangent at about facial midlength; frontal carina present but faint; inner orbit of compound eye weakly concave in upper third; gena slightly broader than compound eye in profile, posterior border rounded; malar area elongate, nearly twice as long as flagellar diameter (figs. 2A, 3A, 3B); labrum flat, large, wider than long, apical margin medially concave; mandible bidentate, teeth well defined and incised (i.e., interdental spaces dis-

FIGURE 1. Lateral habitus of workers. **A.** *Wallacetrigona incisa* (Sakagami and Inoue). **B.** *Geniotrigona thoracica* (Smith). **C.** *G. lacteifasciata* (Cameron).

tinct) (fig. 3C) (but not broadly concavely incised, i.e., with interdental spaces deep, as in *Homotrigona* Moure), interdental incision between first and second preapical teeth (teeth of the pollex sensu Michener and Fraser, 1978) angulate (fig. 3C) (broadly orthogonal or concave in *Geniotrigona*: fig. 6D); galea with longitudinal rows of long, erect, apically hooked, brightly colored setae; first and second labial palpomeres with numerous, elongate, strongly apically wavy but simple setae (see also Michener and Roubik, 1993) (similar to those setae present in *Geniotrigona*: figs. 2D, 6C).

Mesoscutum with median sulcus weakly impressed; notauli short and scarcely evident; parapsidal lines short, length less than ocellar diameter, and weakly impressed. Mesoscutellum short, ending at profile of metanotum and not overhanging propodeum, rounded, swollen in profile, with shining transverse depression along mesoscuto-mesoscutellar sulcus. Propodeum declivitous, with shallow change in slope between basal area and posterior surface; basal area smooth, glabrous, and shining; propodeal spiracle elongate, 8× as long as wide.

Forewing extending beyond apex of metasoma (fig. 1A), with 2Rs, 1rs-m, 1m-cu, apical half 3M, 4M, apical half 1Cuβ, 2Cu, 3Cu, and 2cu-a indicated by brownish nebulous traces and fenestrae demarcated by white spectral lines on otherwise infuscate wing membrane (fig. 3D); membrane with dark brown microtrichia; prestigma short, scarcely longer than anterior

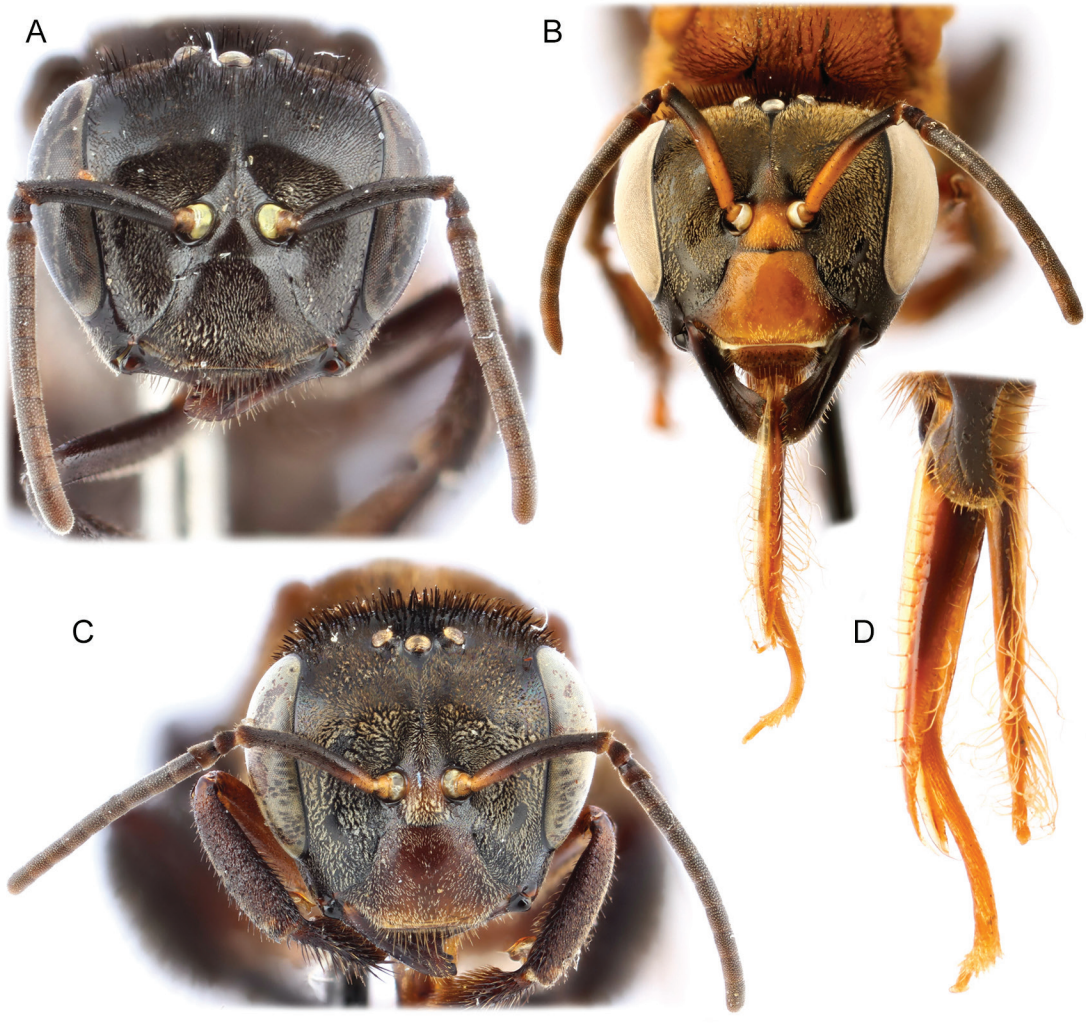

FIGURE 2. Facial views and mouthparts of workers. **A.** Facial view of *Wallacetrigona incisa* (Sakagami and Inoue). **B.** Facial view of *G. lacteifasciata* (Cameron). **C.** Facial view *Geniotrigona thoracica* (Smith). **D.** Lateral view of extended mouthparts of *G. lacteifasciata*, note erect, hooked setae of galea and wavy setae of basal labial palpomeres.

width of 1Rs; pterostigma slender; marginal cell slightly less than 4× as long as maximum breadth, separated from wing apex by slightly more than its maximum width, with apex narrowly open, opening less than one-fifth maximum marginal cell width, with nebulous, angled, appendiculate apex to 4Rs; 1M basad 1cu-a (1M either basad or confluent with 1cu-a in *Geniotrigona*), thus short 1Cuα present, 1Cuα shorter than 1cu-a; submarginal angle (i.e., anterior angle between 1Rs and Rs+M), nearly orthogonal; M obtusely angled at 1m-cu (i.e., angle between 2M and 3M); 3M tubular in basal half, then nebulous; 2Rs angulate; 1rs-m straight; r-rs about as long as 3Rs. Hind wing with 8–9 distal hamuli; radial and cubital cells closed by nebulous veins.

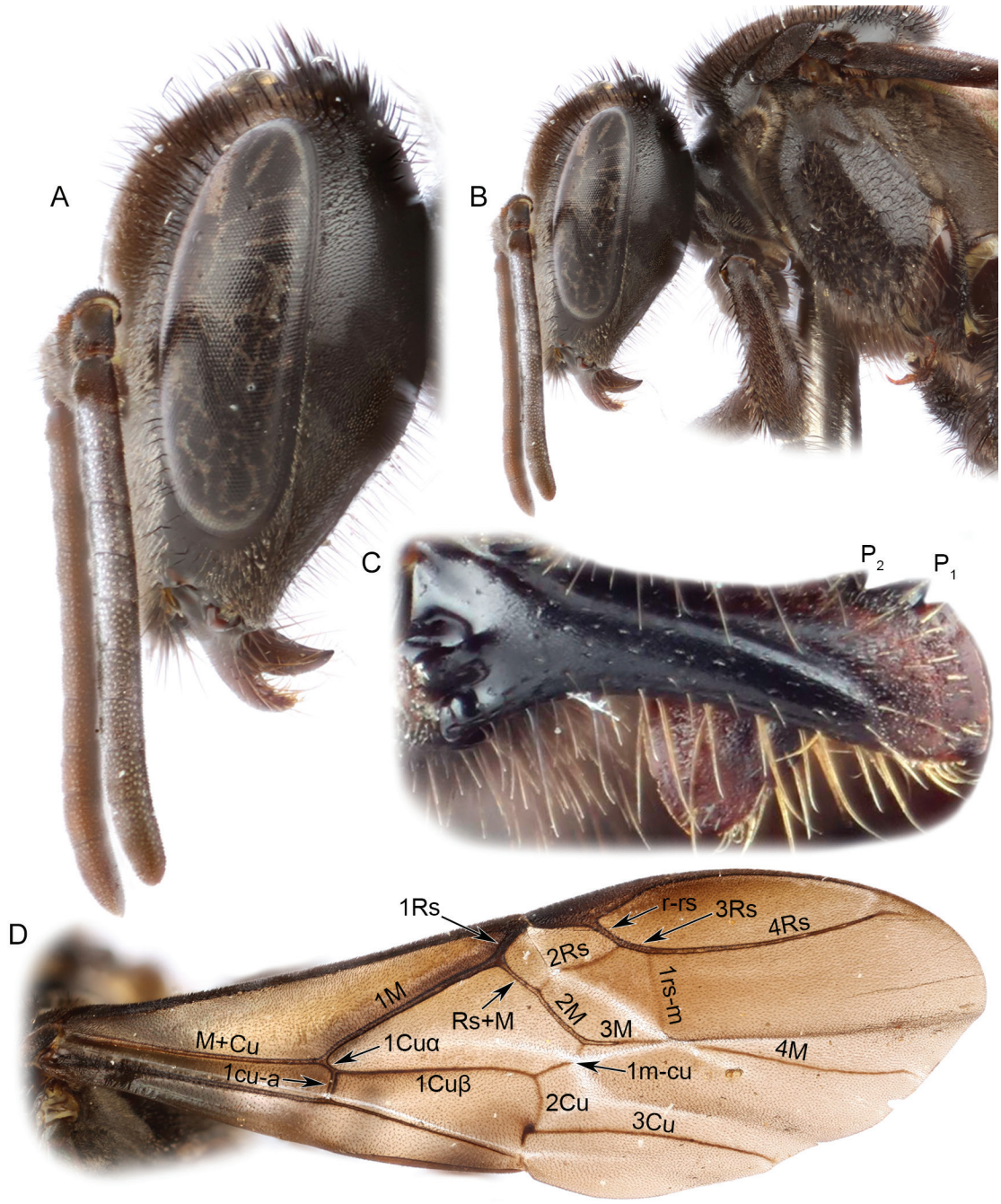

FIGURE 3. Morphological details of *Wallacetrigona incisa* (Sakagami and Inoue), worker caste. **A.** Head in profile. **B.** Head and anterior mesosoma in profile. **C.** Mandible outer surface, with preapical teeth (P_1 and P_2) labeled. **D.** Forewing with prominent veins and crossveins labeled.

FIGURE 4. Metatibiae and metatarsi of workers. **A.** Outer surface of *Wallacetrigona incisa* (Sakagami and Inoue). **B.** Inner surface of *W. incisa*. **C.** Outer surface of *Geniotrigona thoracica* (Smith). **D.** Inner surface of *G. thoracica*.

Metatibia slightly less than 3× as long as greatest width, elongate clavate (figs. 4A, 4B); posterior margin gently recurved with subangulate distal angle (fig. 4B) (recurved with rounded distal angle in *Geniotrigona*: figs. 4C, 4D), setae along posterior margin and upper outer surface mostly plumose; outer surface weakly concave apically, with corbicula occupying apical third (fig. 4A); apical margin transverse; inner surface with narrow, elevated keirotrichiate zone and broad subglabrous zone (figs. 4B, 5A), with abrupt clivulus[4]; keirotrichiate zone about as broad as or slightly broader than posterior glabrate zone (figs. 4B, 5A) (narrower than posterior glabrate zone in *Geniotrigona*: figs. 4D, 5B), width of keirotrichiate zone subequal to length of apical glabrate zone (figs. 4B, 5A) (greater than length of apical glabrate zone in *Geniotrigona*: figs. 4D, 5B); penicillus and rastellar comb present, each composed of stiff setae. Metabasitarsus lightly concave and trapezoidal, with posterior margin arched, distal angle not projecting (figs. 4A, 4B, 5A); outer surface with small basal posterior fimbriate field; inner surface with short basal sericeous area (figs. 4B, 5A).

[4] The term *clivulus* is introduced here (from Latin, diminutive form of *clivus*, meaning "sloping incline") to refer to the slope between the elevated keirotrichiate plateau and the posterior glabrate zone. The condition of the clivulus varies between a gentle slope between these two surfaces in *Lepidotrigona* and *Papuatrigona* to an abrupt precipice in most Eastern Hemisphere genera.

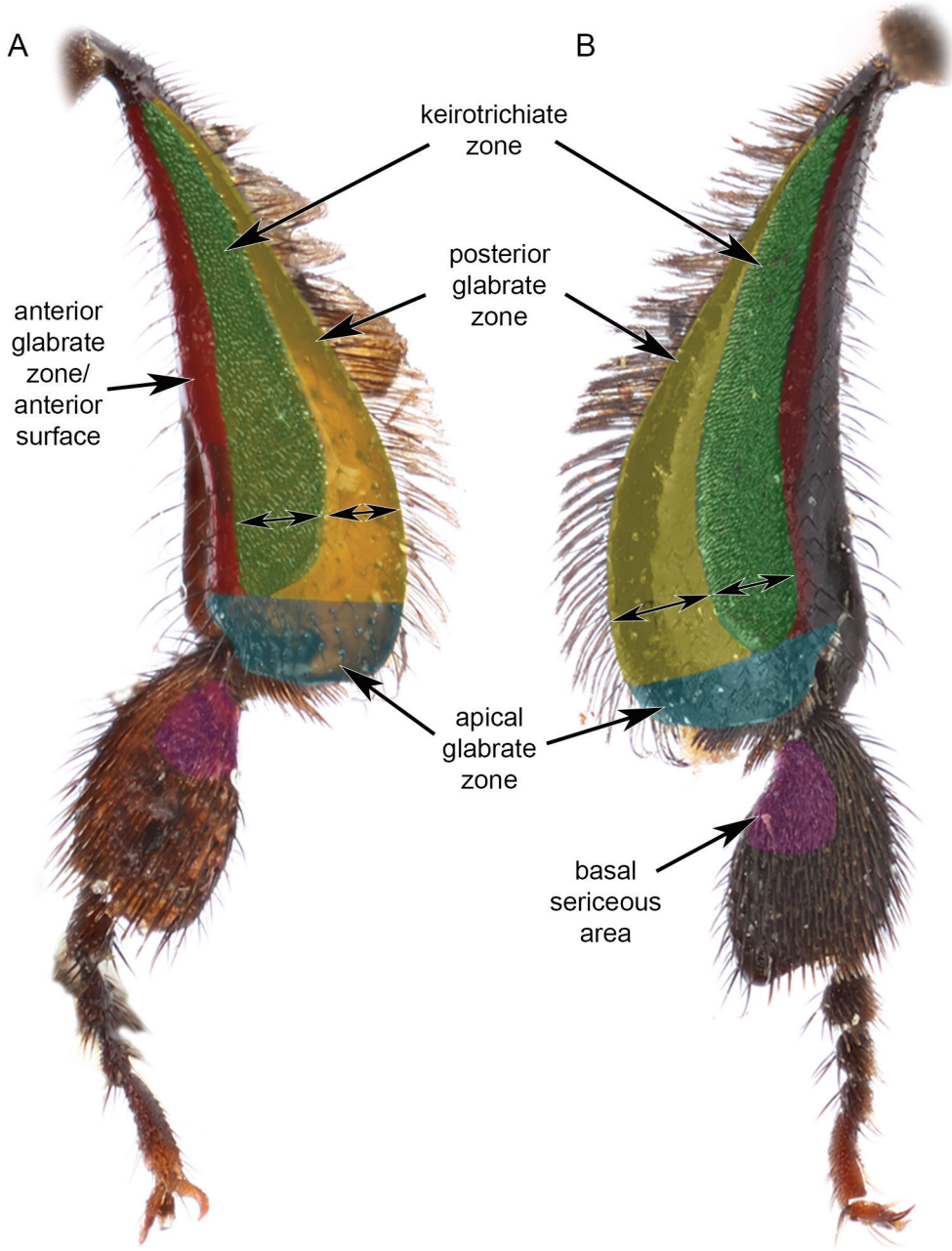

FIGURE 5. Inner surfaces of worker metatibiae and metarsi, with prominent zones and areas colored and labeled (green = keirotrichiate zone; yellow = posterior glabrate zone; red = lower glabrate zone blending into anterior surface; pink = basal sericeous area). **A.** *Wallacetrigona incisa* (Sakagami and Inoue). **B.** *Geniotrigona thoracica* (Smith).

Metasoma narrow, with first metasomal tergum smooth and shining, second through fourth terga largely smooth and shining except narrow apical marginal zones microscopically punctate; apical half of fifth and entire postgradular surface of sixth terga with short, plumose setae intermixed amid stiff, erect, black setae, plumose setae distinctly shorter than thicker erect, black setae and not densely covering integument (such setae as long as or longer than black setae, apically plumose, and dense in *Geniotrigona*).

Etymology: The generic name honors Alfred Russel Wallace (1823–1913), an intrepid and early explorer of the Indomalayan insect fauna and coauthor with Charles R. Darwin (1809–1882) of the theory of evolution. The gender of the name is feminine.

Included species: Presently the genus is understood to only include the type species, *Wallacetrigona incisa* (Sakagami and Inoue), new combination, from Indonesia (Sulawesi), east of the important faunal boundary known as the Wallace Line (and part of the biogeographic area known as Wallacea).

Wallacetrigona incisa (Sakagami and Inoue), new combination

Figures 1A, 2A, 3, 4A, 4B, 5A, 11E

Trigona (*Geniotrigona*) *incisa* Sakagami and Inoue, 1989: 605.
Geniotrigona incisa (Sakagami and Inoue); Rasmussen, 2008: 11.

Material examined (n = 22♀♀): **INDONESIA: Sulawesi:** 8♀♀, Indonesia: Central Sulawesi, 8 km N Sedoa, Kec. [Kecamatan] Lore Utara [North Lore District], Kab. Poso [Kabupaten Poso, a.k.a. Poso Regency], 1500 m, XI-10-1995 [10 November 1995], G.W. Otis, ex: at honey bait [120.29°, -1.22°] (SEMC); 12♀♀, Indonesia: Central Sulawesi, 8 km N Sedoa, Kec. [Kecamatan] Lore Utara [North Lore District], Kab. Poso [Kabupaten Poso, a.k.a. Poso Regency], 1500 m, XI-10-1995, G.W. Otis, ex: at honey bait [120.29°, -1.22°] (CRCD); 2♀♀, Indonesia: C. Sulawesi, Kamarora, Survey Site 12, Waterfall, 24 ix 1996 [24 September 1996], 800m, G.W. Otis [55 km SE of Palu, 120.14°, -1.22°] (CRCD).

Additional localities: Although we have not examined specimens from the following localities in Sulawesi, the following were reported by Sakagami and Inoue (1989): N. Celebes [North Sulawesi], Minahasa [Peninsula], Modoinding [124.45°, 0.80°]; C. Celebes, Todyamboe [Tojambu, actually South Sulawesi], 900 m [120.10°, -2.93°]; Sulawesi, Sulteng, Kab. Poso [Kabupaten Poso, a.k.a. Poso Regency, Central Sulawesi], Wuasa [120.29°, -1.42°]; Central Sulawesi, Lore Lindu National Park [120.19°, -1.47°]; Gn. [Gunung] Tokosa [Central Sulawesi], 2100–2200 m [120.04°, -1.35°]; Lake Tambing [in Poso Regency, Central Sulawesi], Mal. Trap 5 [Malaise trap 5], swamp [120.31°, -1.33°]. According to J.S. Ascher (pers. comm.), an additional specimen is present in the Essig Museum of Entomology, University of California, Berkeley: [South] Sulawesi, Latimojong, along aqueduct, 1350 m, 9 Aug 2016, Pete Obovski [120.10°, -3.40°].

FIGURE 6. Morphological details of *Geniotrigona thoracica* (Smith), worker caste. **A.** Head in profile. **B.** Head and anterior mesosoma in profile. **C.** Oblique view of lower face, with mouthparts extended to show hooked galeal setae and wavy setae ventrally on basal labial palpomeres. D. Mandible outer surface, with preapical teeth (P_1 and P_2) labeled.

Genus *Geniotrigona* Moure

Geniotrigona Moure, 1961: 212. Type species: *Trigona thoracica* Smith, 1857, by original designation.

Diagnosis: The genus *Geniotrigona* is distinctive among Indomalayan Meliponini owing to the combination of its large size; elongate malar space (more than twice diameter of the third flagellomere) (figs. 1B, 1C, 2B, 2C, 6A, 6B); short mesoscutellum; short, declivitous propodeum; distinctively raised ridge posteriorly on the vertex (figs. 1B, 6A, 6B); and comparatively short, dense, plumose setae that largely obscure the integument on the mesosoma. It is most similar to the new genus described above, but can be distinguished by those features outlined there (above).

Included species: Presently, the genus includes two species: *Geniotrigona thoracica* (Smith) and *G. lacteifasciata* (Cameron).

Key to Species of *Geniotrigona*

1.Anterior corners of mesoscutum covered in golden, brushlike setae; wings markedly bicolored (Malaysia: Sabah, Sarawak; Indonesia: West Kalimantan) . . . . . *G. lacteifasciata* (Cameron)

–Anterior corners of mesoscutum covered in dark brown, brushlike setae; wings weakly bicolored (Thailand, Laos, Vietnam, Singapore, Malaysia, Indonesia: Sumatra). . . . . *G. thoracica* (Smith)

Geniotrigona thoracica (Smith)

Figures 1B, 2C, 4C, 4D, 5B, 6

Trigona thoracica Smith, 1857: 50.
Melipona thoracica (Smith); Dalla Torre, 1896: 584.
Trigona ambusta Cockerell, 1918: 387. Synonymy vide Schwarz (1939).
Trigona thoracica variety *ambusta* (Cockerell); Schwarz, 1937: 327.
Trigona (*Tetragona*) *thoracica* Smith; Schwarz, 1939: 104.
Geniotrigona thoracica (Smith); Moure, 1961: 212.
Trigona (*Geniotrigona*) *thoracica* Smith; Sakagami, 1975: 56.
Trigona (*Heterotrigona*) *thoracica* Smith; Michener, 1990: 126.

Material examined (n = 98♀♀, 10♂♂): **MALAYSIA: Kedah:** 1♀, Malay Penin. [Malay Peninsula], Kedah, Alor Setar, Gunong Keriang, April 1, 1928 (AMNH); **Pahang:** 1♀, Frasers Hill, F.M.S. [Federated Malay States], 30.ix.29 [30 September 1929], N.C.E. Miller (AMNH); 1♀, Malay Penin. [Malay Peninsula], Pahang, F.M.S. [Federated Malay States], Jerantut, Datu Dalan [?], March 19, 1927 (AMNH); **Perak:** 1♀, Malaya, Maxwell Gardens, Taiping Hills, 3300 ft., 12.xi.1931 [12 November 1931], H.T. Pagden (AMNH); **Selangor:** 2♀♀, Malaysia: Selangor, Kepong, 9-VIII-2004, H.R. Hepburn, ex: caught on flowers (SEMC); 3♀♀, Malaysia: Selangor, Phoon Chun Guan, March 1980, R9, Azhar P.C. Guan (SEMC); 7♀♀, Malaysia: Selangor, Kepong, Sept. 1976, S. Appanah (SEMC); 2♀♀,

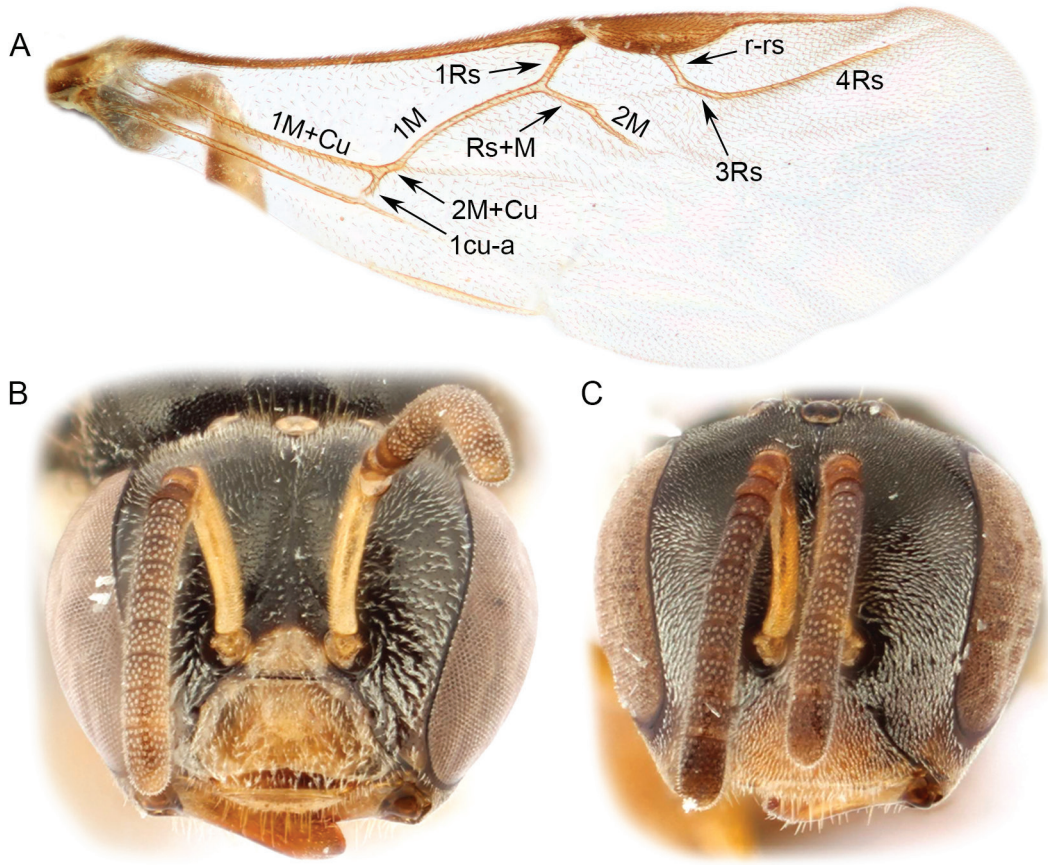

FIGURE 7. Anatomical details of the minute genera of Indomalayan Meliponini. **A.** Forewing of *Lisotrigona carpenteri* Engel, with pertinent veins and crossveins labeled. **B.** Facial view of *L. carpenteri*. **C.** Facial view of *Pariotrigona pendleburyi* (Schwarz).

Malaysia, W. Selangor, Serdaag, 1983, on Brazil nut (SEMC); 1♀, Malaya, Bukit Kutu [peak near Kuala Kubu], 30.i.1930 [30 January 1930], H.T. Pagden, 3485 ft. (AMNH); **Kuala Lumpur:** 18♀♀, Malaysia: Kepong Forest Res. Inst., 18 October 1975, Rudolf Jander (SEMC); 1♀, Malay Penin. [Malay Peninsula], ex: Coll. Agr. Dept. Kuala Lumpur, April 23, 1909 (AMNH); **Johor:** 1♀, Malaysia: Johor, 15.3 km W. Sedili Besar, 16 Oct 1986, John W. Wenzel (SEMC); **Malacca:** 1♀, Malacca, Kuala Kubu [it is unclear which locality Buttel-Reepen is referring to as "Kuala Kubu" is in Selangor, we have merely listed it as it appears on his label], 3.1912 [March 1912], Butt.-Reep. [Buttel-Reepen] (AMNH); **SINGAPORE:** 14♀♀, Singapore, Bukit Timah, 12 Oct 1986, J.W. Wenzel (SEMC); **THAILAND: Sisaket:** 1♀, Thailand, Sisaket, Huai Thap Than Distr., 25.iii.2004, S. Thummajitsakul (SEMC); **Prachuap Khiri Khan:** 2♀♀, Thailand, Prachuap Khiri Khan, Thap Sakae Distr., 12.ii.2006, S. Thum-

majitsakul (SEMC); 7♀♀, Thailand: Prachuap Khiri Khan Prov., Huai Yang waterfall, 25 km SW Prachuap Khiri Khan, 27 January 1993, S. Boongird, C. Michener (SEMC); 6♀♀, Thailand: Prachuabkirikan Prov., Huay Yang Waterfall, 30.iii.2004, S. Boongird (SEMC); 1♀, Thailand, Thap-Sakae, 2.9.76 [2 September 1976], Pauly rec, composit, radiee, blanche (CRC); **Ranong:** 1♀, S. Thailand, hills above hot springs, 29.4.08 [29 April 2008], Ranong, Ranong Prov., Hans Bänziger leg. (SEMC); 8♀♀, Thailand: Ranong Prov., Muang Distr., 9–13 Nov 2002, Samnuk [sic: Somnuk] Boongird (SEMC); 3♂♂, Thailand, Ngao, A. Muang, Ranong, 16.12.03 [16 December 2003], [S. Boongird] (SEMC); **Surat Thani:** 2♀♀, Thailand, Surat Thani, Chaiya Distr., 20.x.2003, S. Thummajitsakul (SEMC); **Phang Nga:** 2♀♀, Thailand, Phang Nga Prov., Khao Sok National Park, between Takua Pa and Khao Mok, March 2000, D.R. Smith (SEMC); **Krabi:** 5♀♀, Thailand: Krabi Prov., Owluk Distr., 8–15 Nov 2002, Samnuk [sic: Somnuk] Boongird (SEMC); 7♂♂, Thailand: Krabi Prov., Khoa Phanom Distr., 13.v.2004, S. Boongird (SEMC); **Songkhla:** 4♀♀, Ban Prakamp, Song Kalo Prov. [Songkhla Province], vii.18.28 [18 July 1928], Siam [Thailand] (AMNH); **INDONESIA: North Sumatra (Sumatera Utara):** 4♀♀, O. Sumatra [Ost Sumatra], [illegible], 7.1932 [July 1932] (AMNH); **South Sumatra (Sumatera Selatan):** 1♀, S. Sumatra [South Sumatra], Kedaton, 150 m, 28 Maart 1937 [28 March 1937], J.v.d. Vecht (AMNH); 1♀, Z. Sumatra [Zuid Sumatra], Ranau [Lake Ranau], 24.viii.33 [24 August 1933], H.R.A. Miller (AMNH).

Geniotrigona lacteifasciata (Cameron)

Figures 1C, 2B, 2D, 11D

Trigona lacteifasciata Cameron, 1902: 131.
Trigona borneënsis Friese, 1933a: 46. Synonymy vide Schwarz (1939).
Trigona thoracica variety *lacteifasciata* Cameron; Schwarz, 1937: 317.
Trigona thoracica variety *borneënsis* Friese; Schwarz, 1937: 328.
Geniotrigona lacteifasciata (Cameron); Moure, 1961: 213.

Material examined (n = 21♀♀): **MALAYSIA: Sabah (Borneo):** 1♀, Malaysian Borneo: Sabah, Kampung Bam Bam (20 km SW of Tenom), 06-VIII-2009 [6 August 2009], R.S. Hepburn (SEMC); 2♀♀, Malaysia: Sabah (Borneo), Penampang Distr., Crocker Range, Kipandi Butterfly Park, 720 m, 5°52'20"N, 116°14'53"E, 15.x.2011 [15 October 2011], M. Hauser and S. Gaimari (SEMC, CSCA); 10♀♀, Malaysia, Sabah, near Sek. Keb. Labang, at the Sapulut River, 20–27.vii.2005 [20–27 July 2005], 300 m, Claus Rasmussen leg. (CRCD); 1♀, Sabah, Babagon, 7.vii.1968 [7 July 1968], P.J.L. Roche (SEMC); 1♀, Sabah, Sandakan, 3.viii.1985 [3 August 1985], C.G. Roche (SEMC); 1♀, Sabah, Sepilok F.R., 14.vii.1968 [14 July 1968], C.G. Roche (SEMC); **Sarawak (Borneo):** 1♀, Lundu, Sarawak, April 1913 (AMNH); **INDONESIA: West Kalimantan:** 4♀♀, Borneo, Sanggau [Sanggau Regency], 24.7.32 [24 July 1932] (AMNH).

Key to Indomalayan and Australasian Genera and Subgenera of Meliponini (based on worker caste)

Given the introduction of a new genus along with the significant alteration of the generic classification (e.g., Rasmussen, 2008) since Michener's (2007) recent key to the fauna, we provide here a new dichotomous identification key to the genera and subgenera as conceived herein.

1. Forewing length less than 3 mm, wing venation greatly reduced (fig. 7) and posterior margin of metatibia without plumose setae; hind wing without closed cells, veins closing radial and cubital cells, if visible at all, clear and unpigmented (spectral); forewing with 2Rs and 1rs-m almost always completely absent, thus without indication of submarginal cells (fig. 7); at least distal part of second cubital cell of forewing undefined or defined completely by unpigmented spectral vein traces (i.e., at least 2Cu and 3Cu absent or spectral); vein M of forewing terminating without bend at about position of anterior end of 1m-cu which, however, is absent (i.e., 3M lacking) 2

–Forewing length typically over 4 mm, wing venation typically not greatly reduced for Meliponini, but if minute and with some wing reduction, then posterior margin of metatibia with plumose setae intermixed with simple setae; hind wing typically with radial and cubital cells closed by at least weakly brownish nebulous veins; forewing with one or two submarginal cells usually weakly indicated by nebulous traces of 2Rs and 1rs-m (fig. 3D), first submarginal cell usually recognizable; second cubital cell of forewing completely indicated by at least faint nebulous veins (i.e., 2Cu present); vein M of forewing usually extending at least slightly beyond position of 1m-cu and angular at apex of tubular portion of vein (i.e., 3M present) (fig. 3D), the stub of which is usually at least faintly visible 3

2. Malar space shorter than flagellar diameter (fig. 7B); inner margins of compound eyes converging below (fig. 7B); worker gonostylus with many minute setae, in addition to setae along outer and distal margins (India; Vietnam; Laos; Cambodia; Thailand; Malaysia: Sarawak, Sabah; Indonesia: Sumatra). . . . . *Lisotrigona* Moure

–Malar space almost one-fifth as long as compound eye, much longer than flagellar diameter (fig. 7C); inner margins of compound eyes nearly parallel (fig. 7C); worker gonostylus with setae but without minute setae (Thailand; Malaysia: West Malaysia, Sarawak, Sabah; Brunei; Indonesia: Sumatra). . . . . *Pariotrigona* Moure

3. Head and mesosoma without distinct maculation; inner surface of metatibia with strong longitudinal keirotrichiate ridge above which is a broad, depressed shining marginal area . . . 4

–Mesoscutellum and usually face and mesoscutum with well-developed yellow maculation (figs. 8A, 8B); inner surface of metatibia with keirotrichiate area broad, nearly reaching posterior margin of metatibia (figs. 8C, 8D) (Australia; Papua New Guinea; Indonesia: Irian Jaya [West Papua]). . . . . *Austroplebeia* Moure

4. Setae along posterior margin of worker metatibia and males entirely simple, or some plumose only on apical one-fifth or one-sixth of margin; keirotrichiate median zone of inner surface of metatibia separated from shining posterior marginal zone by gentle slope 5

–Setae along posterior margin of worker metatibia and some males partly plumose; elevated keirotrichiate median zone of inner surface of metatibia separated from shining posterior marginal zone by abrupt slope. 6

5.Mesoscutum margined with whitish, densely plumose (scalelike) setae (fig. 9A); head and mesosoma dull, with minute close punctures (fig. 9A); propodeal dorsum finely reticulate (fig. 9C); posterior margin of worker metatibia without plumose setae (fig. 9E); (Indomalaya [Sundaland]). . . . . *Lepidotrigona* Moure

–Mesoscutum without conspicuous plumose setae (fig. 9B); head and mesosoma shining, although with minute, rather close punctures (fig. 9B); propodeal dorsum smooth, shining; posterior margin of worker metatibia with plumose setae among bristles on apical one-fifth or one-sixth of margin (Indonesia: Irian Jaya [West Papua]; Papua New Guinea) . . . . . *Papuatrigona* Michener and Sakagami

6.Mesoscutellum short, only slightly projecting over metanotum (best seen in profile, fig. 11A); malar area variable, typically as long as diameter of diameter of third flagellomere or greater but sometimes approximately 0.5–0.75× diameter of third flagellomere; vein M of forewing bent at trace of 1m-cu, sometimes present only as minute stub beyond bend (e.g., fig. 3D). 7

–Mesoscutellum well projected posteriorly, extending over propodeum as far as posterior propodeal angle (change in slope between basal area and posterior surface) (best seen in profile, fig. 11B); malar area linear or at least narrower than 0.5× diameter of third flagellomere; vein M of forewing straight and ending at or shortly after 1m-cu (fig. 10) (*Tetragonula* Moure, s.l.). 10

7.Malar space less than 2× diameter of third flagellomere. 8

–Malar space 2× or greater diameter of third flagellomere (figs. 2, 3A, 3B, 6A, 6B). 9

8.Mandible unidentate or bidentate, teeth small (*Heterotrigona* Schwarz, s.l.). 11

–Mandible bidentate, teeth large, deeply incised, i.e., interdental spaces deep (fig. 9D) (*Homotrigona* Moure, s.l.). 14

9.Vertex with deep depression and elevated ridge rising above level of ocelli (figs. 6A, 6B), posteriorly without deep, concave, medial notch; mesoscutum with dense covering of short, plumose setae amid scattered erect, black setae; apical metasomal terga with dense, long, apically plumose setae amid erect, black setae, with plumose setae at least as long as black setae (fig. 11D); keirotrichiate zone of metatibial inner surface narrower than posterior glabrate zone, and greater than length of apical glabrate zone (figs. 4C, 4D, 5B) (Myanmar; Cambodia; Thailand; Singapore; Malaysia: West Malaysia, Sarawak, Sabah; Indonesia: Kalimantan, Sumatra). . . . . *Geniotrigona* Moure

–Vertex without strongly elevated ridge, with faint transverse depression and ridge posterior to ocelli (fig. 3A), posteriorly with deep, concave medial incision (fig. 11E); mesoscutum without dense covering of short, plumose setae amid scattered erect, black setae; apical metasomal terga with short, scattered plumose setae amid longer, erect, black setae; keirotrichiate zone of metatibial inner surface about as broad as or slightly broader than posterior glabrate zone, and subequal to length of apical glabrate zone (figs. 4A, 4B, 5A) (Indonesia: Sulawesi). . . . . *Wallacetrigona*, n. gen.

10. Scape shorter than torulocellar distance; about five distal hamuli; posterior contour of metatibia slightly convex, with distal angle subangulate; penicillus usually composed of soft setae (India to Australia and Solomon Islands) . . . . . *Tetragonula* Moure, s.str.
–Scape at least as long as torulocellar distance; six distal hamuli; posterior contour of metatibia distinctly convex and distal angle rounded almost without angulation; penicillus composed of stiff setae (Cambodia; Vietnam; Laos; Myanmar; Thailand; Malaysia: West Malaysia, Sarawak, Sabah; Brunei; Indonesia: Sumatra, Kalimantan) . . . . . *Tetragonilla* Moure
11. Basal area of propodeum largely or entirely glabrous, at most with wispy apicolateral patches of setae. 12
–Basal area of propodeum entirely pubescent (fig. 11C), or with a small medial glabrous patch (in *H. hobbyi* (Schwarz)) (Indonesia: Irian Jaya [West Papua, Papua], Moluccas; Papua New Guinea) . . . . . *Platytrigona* Moure
12. Basal vein (1M) of forewing basad 1cu-a 13
–Basal vein (1M) of forewing distad 1cu-a (Indonesia [Papua]; Papua New Guinea) . . . . . *Sahulotrigona* Engel and Rasmussen
13. Posterior glabrate zone of metatibial inner surface apically broader than keirotrichiate zone; forewing length more than 5.5 mm (Thailand; Singapore; Malaysia: West Malaysia, Sarawak, Sabah; Brunei; Indonesia: Java, Sumatra, Kalimantan). . . . . *Heterotrigona* Schwarz, s.str.
–Posterior glabrate zone of metatibial inner surface apically narrower than or at most as broad as keirotrichiate zone; forewing length less than 6.0 mm (Singapore; Malaysia: West Malaysia, Sarawak; Indonesia: Sumatra). . . . . *Sundatrigona* Inoue and Sakagami
14. Basal sericeous area of metabasitarsus present; clypeus approximately 2× broader than long 15
–Basal sericeous area of metabasitarsus absent; clypeus short, at least 2.5× broader than long (Thailand; Laos; Singapore; Vietnam; Cambodia; Indonesia: Sumatra, Kalimantan; Brunei; Malaysia: West Malaysia, Sarawak; Myanmar) . . . . . *Homotrigona* Moure, s.str.
15. Basal area of propodeum smooth and glabrous; vertex not elevated posterior to ocelli 16
–Basal area of propodeum pubescent; vertex elevated posterior to ocelli (Thailand; Malaysia: West Malaysia, Sarawak, Sabah; Singapore; Indonesia: Sumatra, Kalimantan; Myanmar; Sri Lanka; Australia) . . . . . *Lophotrigona* Moure
16. Malar space as long as flagellar diameter; clypeus with a transverse row of erect setae along apical margin; metabasitarsus 2× as long as wide (Cambodia; Malaysia: Sarawak, Sabah, West Malaysia; Brunei; Myanmar; Indonesia: Sumatra, West Timor, Kalimantan; East Timor; Thailand; Laos; Vietnam) . . . . . *Tetrigona* Moure
–Malar space about as long as 1.5× flagellar diameter; clypeus with erect black setae scattered over entire surface; metabasitarsus less than 1.5× as long as wide (Malaysia: Sarawak, Sabah; Brunei) . . . . . *Odontotrigona* Moure

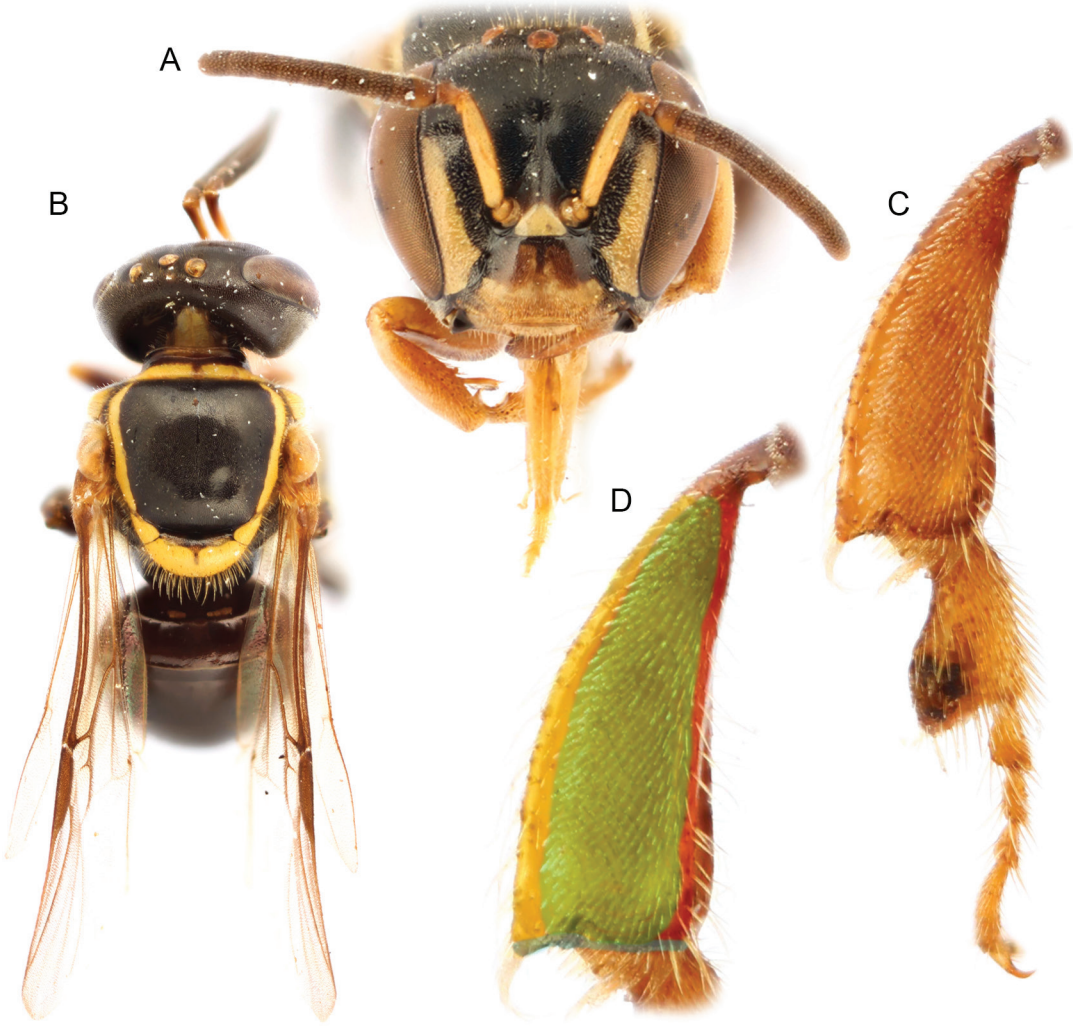

FIGURE 8. Anatomical details of *Austroplebeia cincta* (Mocsáry). **A.** Facial view. **B.** Dorsal view. **C.** Inner surface of metatibia and metatarsus. **D.** Inner surface of metatibia colored using the same scheme as presented in figure 5.

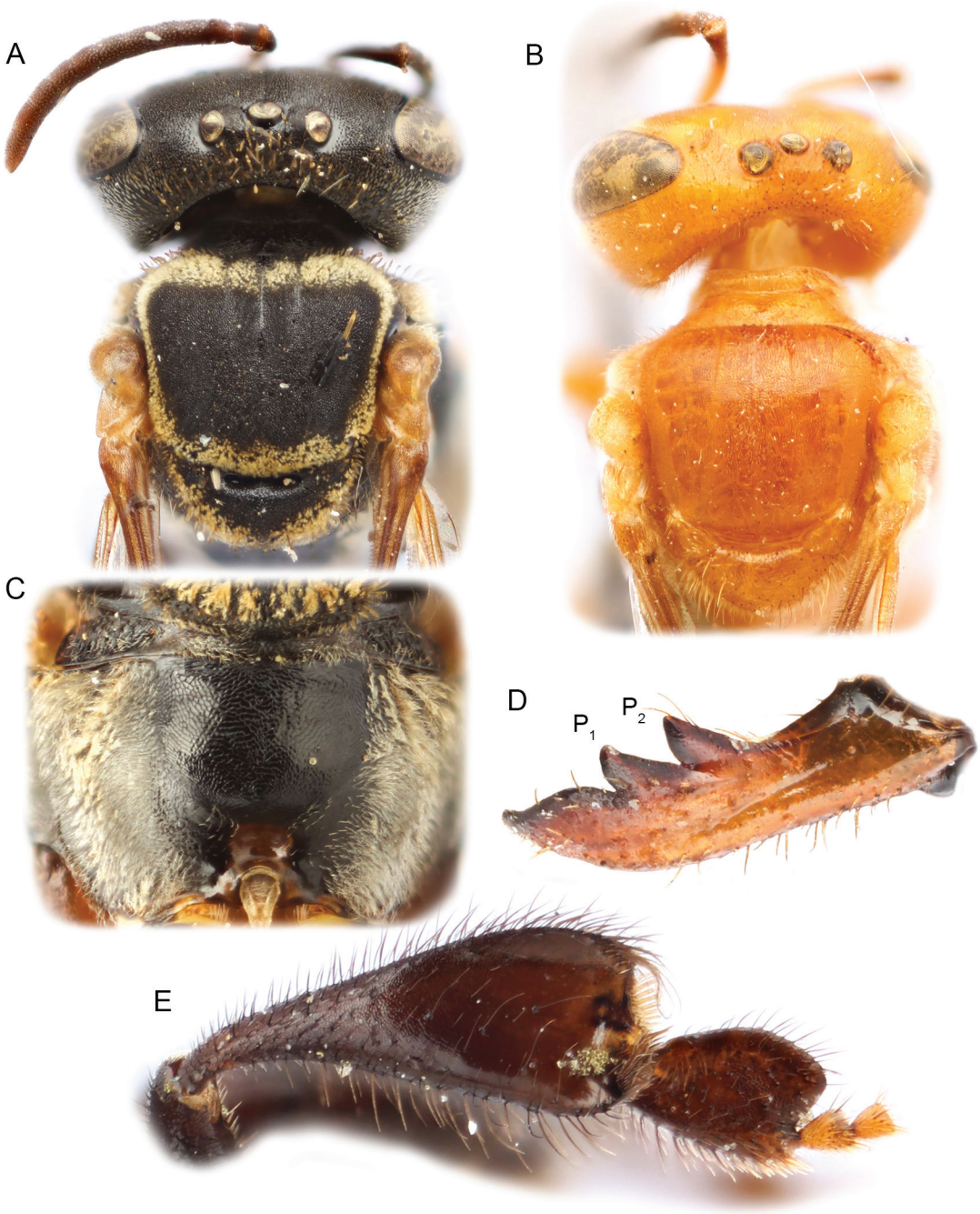

FIGURE 9. Anatomical details of various genera of Indomalayan and Australasian genera of Meliponini. **A.** Dorsal view of head and mesosoma of *Lepidotrigona terminata* (Smith). **B.** Dorsal view of head and mesosoma of *Papuatrigona genalis* (Friese). **C.** Propodeum of *L. terminata*. **D.** Mandible of *Homotrigona* (*Homotrigona*) *fimbriata* (Smith). **E.** Outer surface of metatibia, metabasitarsus, and two further metatarsomeres of *L. doipaensis* (Schwarz).

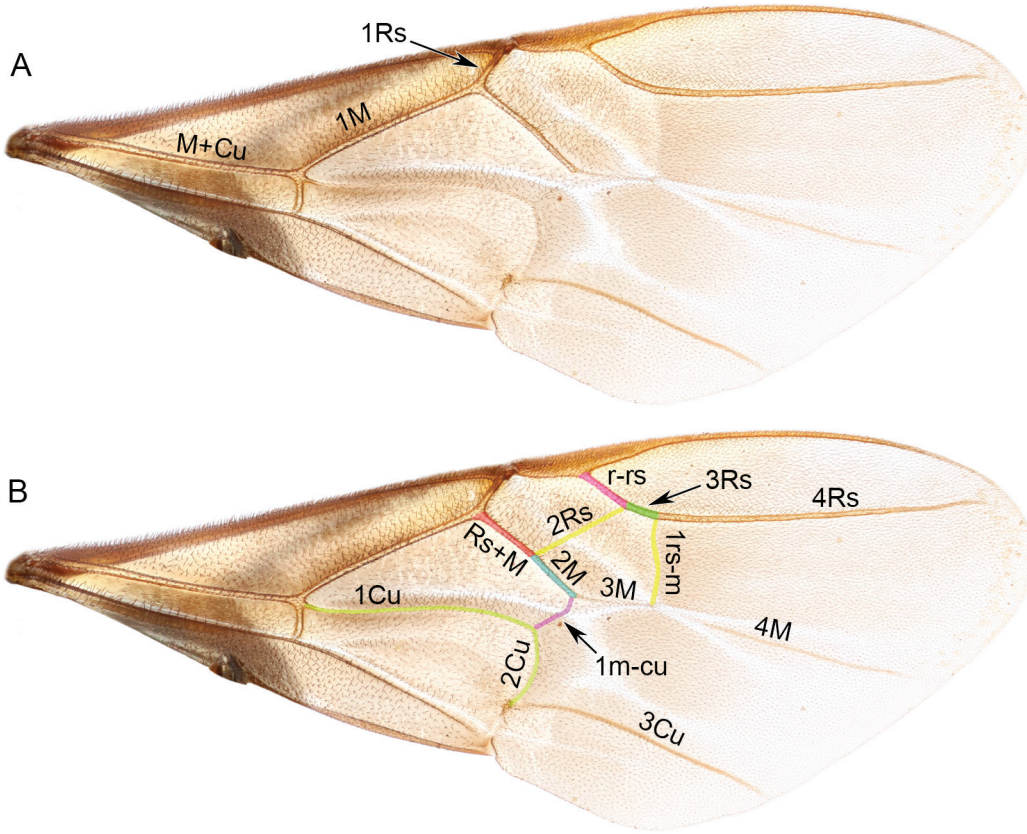

FIGURE 10. Forewing venation of *Tetragonula* (*Tetragonilla*) *atripes* (Smith). **A.** Unadulterated wing with pertinent veins labeled. **B.** Wing with particular sectors of veins and crossveins colored to highlight homologous portions and positions of nebulous and spectral traces.

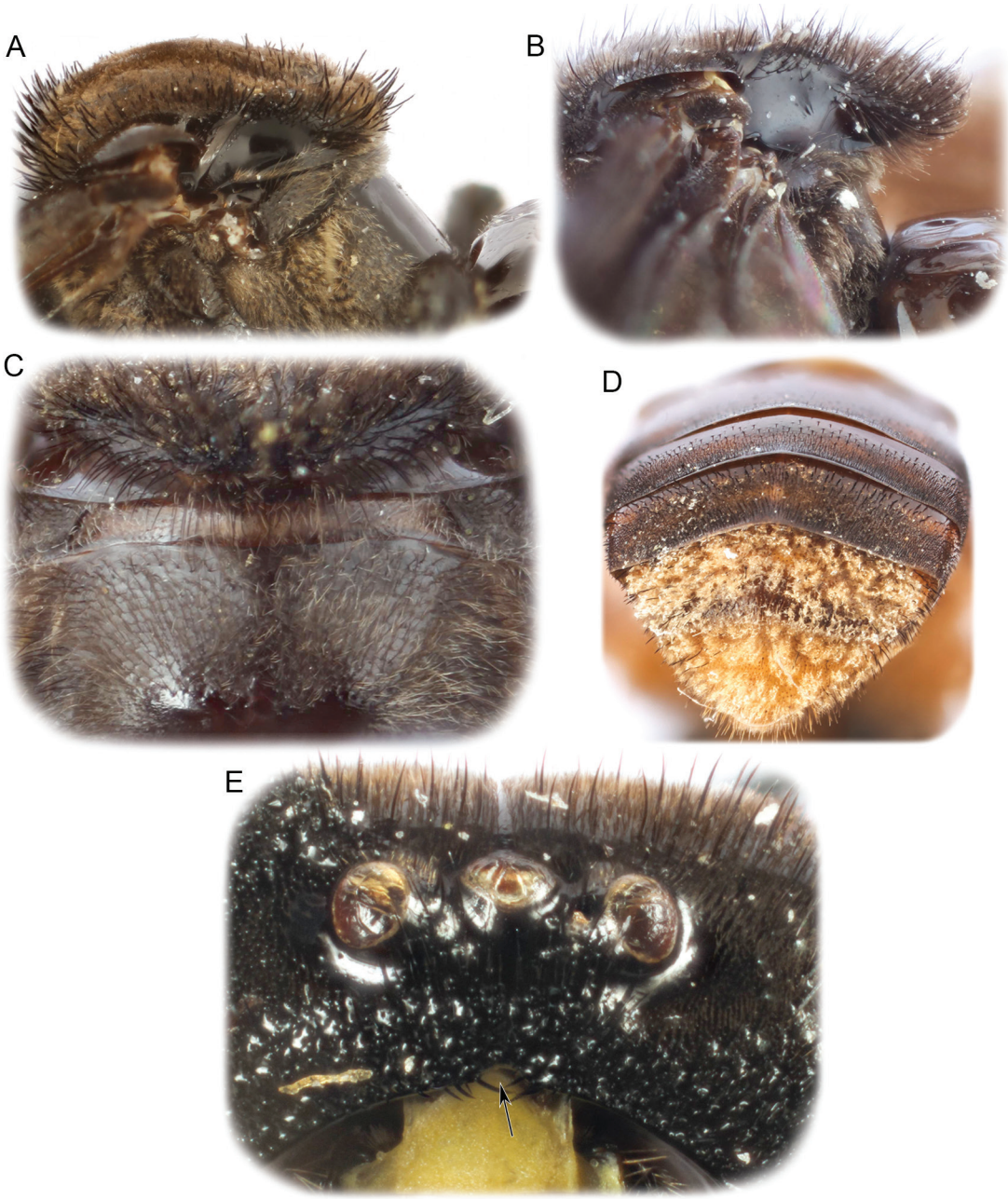

FIGURE 11. Anatomical details of various genera of Indomalayan and Australasian genera of Meliponini. **A.** Profile of upper mesosoma of *Heterotrigona* (*Heterotrigona*) *itama* (Cockerell). **B.** Profile of upper mesosoma of *Tetragonula* (*Tetragonilla*) *collina* (Smith). **C.** Propodeum of *Homotrigona* (*Lophotrigona*) *canifrons* (Smith). **D.** Metasomal apex of *Geniotrigona lacteifasciata* (Cameron). **E.** Ocellar triangle and medial vertex of *Wallacetrigona incisa* (Sakagami and Inoue), with arrow indicating posterior, medial, U-shaped incision.

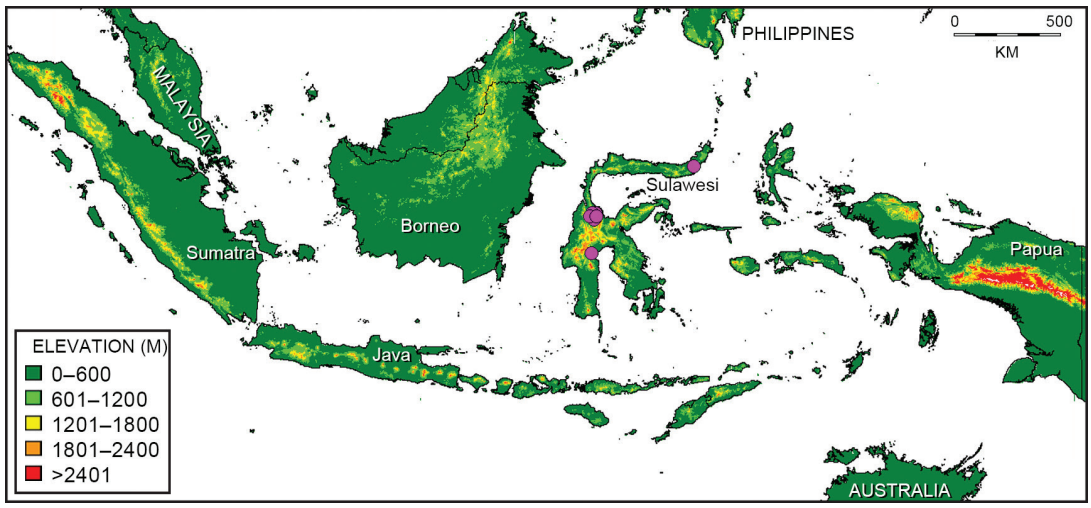

FIGURE 12. Collection localities of individuals of *Wallacetrigona incisa* (Sakagami and Inoue) in Indonesia (Sulawesi). Specimens are those either examined here or reported in the literature (refer to text). The species is apparently restricted to mountainous areas of Sulawesi as all localities are at elevations above 800 m.

DISCUSSION

The classification of stingless bees has made tremendous strides during the last 20 years (table 2), although there remains significant challenges. Recognizing their diversity is merely the first step toward properly assessing their classification, and we have here emphasized both the hidden diversity in the Eastern Hemisphere as well as the importance of the Wallace Line for the stingless bees of the region (e.g., Vane-Wright, 1991). At present, *Wallacetrigona incisa* is known only from Sulawesi, where it has been captured at localities ranging from 800–2200 m (fig. 12). While the Australasian fauna of stingless bees is rather species poor compared to the Indomalayan fauna (Dollin et al., 1997, 2015; Rasmussen, 2008), *Wallacetrigona* is the third endemic genus/subgenus of stingless bees to be reported from the easternmost range of meliponines, the others being *Austroplebeia* Moure and *Heterotrigona* (*Papuatrigona*). Species of *Tetragonula* and *Lepidotrigona* are also found east of the Wallace Line, but not near the diversity known from the island of Borneo or continental Southeast Asia. Extensive sampling of stingless bees throughout the Sunda Islands, Wallacea, and the western limits of the Sahul is needed to clarify the biogeographic limits and history of these lineages. In addition, considerable effort is needed to resolve species circumscriptions for groups such as *Tetragonula* where numerous, presumably cryptic species exist, sometimes distinguishable more by morphometrics and biology than clear demarcations among workers. It is hoped that by providing an easier means for identifying monophyletic genera and subgenera among the fauna there shall be a growing number of melittologists investigating the bees of the Indomalayan and Australasian regions. A tremendous interest in local stingless bees is already seen from the increase in beekeepers and producers of the highly appraised and valued "kelulut" honey produced by meliponines, likely including *W. incisa*.

TABLE 2. Comparison of current generic/subgeneric classification for Old World stingless bees (Meliponini) to equivalents in three prior classificatory schemata (order of taxa as presented in table 1). Daggers indicate extinct taxa. Note that Rasmussen (2008) did not cover the African fauna.

System accepted herein	Moure (1961)	Michener (2000, 2007)	Rasmussen (2008)
Tetragonula (*Tetragonula*)	*Tetragonula*	*Trigona* (*Heterotrigona*)	*Tetragonula*
Tetragonula (*Tetragonilla*)	*Tetragonilla*	*Trigona* (*Heterotrigona*)	*Tetragonilla*
Heterotrigona (*Heterotrigona*)	*Heterotrigona*	*Trigona* (*Heterotrigona*)	*Heterotrigona*
Heterotrigona (*Platytrigona*)	*Platytrigona*	*Trigona* (*Heterotrigona*)	*Platytrigona*
Heterotrigona (*Sahulotrigona*)	—	*Trigona* (*Heterotrigona*)	*Platytrigona*
Heterotrigona (*Sundatrigona*)	—	*Trigona* (*Heterotrigona*)	*Sundatrigona*
Papuatrigona	—	*Trigona* (*Papuatrigona*)	*Papuatrigona*
Lepidotrigona	*Lepidotrigona*	*Trigona* (*Lepidotrigona*)	*Lepidotrigona*
Wallacetrigona	*Geniotrigona*	*Trigona* (*Heterotrigona*)	*Geniotrigona*
Geniotrigona	*Geniotrigona*	*Trigona* (*Heterotrigona*)	*Geniotrigona*
Homotrigona (*Tetrigona*)	*Tetrigona*	*Trigona* (*Heterotrigona*)	*Tetrigona*
Homotrigona (*Homotrigona*)	*Homotrigona*	*Trigona* (*Homotrigona*)	*Homotrigona*
Homotrigona (*Odontotrigona*)	*Odontotrigona*	*Trigona* (*Heterotrigona*)	*Odontotrigona*
Homotrigona (*Lophotrigona*)	*Lophotrigona*	*Trigona* (*Heterotrigona*)	*Lophotrigona*
Meliplebeia (*Axestotrigona*)	*Axestotrigona*	*Meliponula* (*Axestotrigona*)	—
Meliplebeia (*Apotrigona*)	*Apotrigona*	*Meliponula* (*Meliplebeia*)	—
Meliplebeia (*Meliplebeia*)	*Meliplebeia*	*Meliponula* (*Meliplebeia*)	—
Meliplebeia (*Plebeiella*)	*Plebeiella*	*Meliponula* (*Meliplebeia*)	—
Dactylurina	*Dactylurina*	*Dactylurina*	—
Meliponula	*Meliponula*	*Meliponula* (*Meliponula*)	—
Plebeina	*Plebeina*	*Plebeina*	—
Hypotrigona	*Hypotrigona*	*Hypotrigona*	—
†*Kelneriapis*	—	†*Kelneriapis*	—
†*Liotrigonopsis*	—	†*Liotrignopsis*	—
Liotrigona (*Liotrigona*)	*Liotrigona*	*Liotrigona*	—
Liotrigona (*Cleptotrigona*)	*Lestrimelitta* (*Cleptotrigona*)	*Cleptotrigona*	—
Austroplebeia	*Austroplebeia*	*Austroplebeia*	*Austroplebeia*
Lisotrigona	*Lisotrigona*	*Lisotrigona*	*Lisotrigona*
Pariotrigona	*Pariotrigona*	*Pariotrigona*	*Pariotrigona*
†*Exebotrigona*	—	—	—
†*Meliponorytes*	—	†*Meliponorytes*	—

ACKNOWLEDGMENTS

We are grateful to Gard W. Otis and Alain Pauly for providing some of the specimens used as part of this study, to John S. Ascher for providing an additional specimen record, and to Sydney A. Cameron for discussing the implications of the initial molecular work that suggested the distinctiveness of the taxon. The manuscript received helpful input from Jerome G. Rozen, Jr., and an anonymous reviewer. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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APPENDIX

Synonymic Checklist of Indomalayan-Australasian Meliponini

The following list summarizes the currently recognized species within the genera and subgenera of stingless bees occurring in the Indomalayan and Australasian regions. The species are arranged according to the organization of the genera given in the present work (table 1). Currently valid names are indicated in boldface, with known synonyms listed, and asterisks identify the type species for the genus-group taxa.

Genus *Austroplebeia* Moure, 1961

Austroplebeia ***australis*** (Friese, 1898)
= *Trigona cincta percincta* Cockerell, 1929a
= *Trigona cockerelli* Rayment, 1930
= *Trigona cockerelli ornata* Rayment, 1932
= *Trigona websteri* Rayment, 1932
Austroplebeia ***cassiae*** (Cockerell, 1910)*
= *Trigona symei* Rayment, 1932
Austroplebeia ***cincta*** (Mocsáry in Friese, 1898)
Austroplebeia ***essingtoni*** (Cockerell, 1905)
Austroplebeia ***magna*** Dollin, Dollin, and Rasmussen, 2015

Genus *Geniotrigona* Moure, 1961

Geniotrigona ***lacteifasciata*** (Cameron, 1902)
= *Trigona borneënsis* Friese, 1933a
Geniotrigona ***thoracica*** (Smith, 1857)*
= *Trigona ambusta* Cockerell, 1918

Genus *Heterotrigona* Schwarz, 1939

Subgenus *Heterotrigona* Schwarz, 1939

Heterotrigona (*Heterotrigona*) ***bakeri*** (Cockerell, 1919b)
Heterotrigona (*Heterotrigona*) ***erythrogastra*** (Cameron, 1902)
= *Trigona luteiventris* Friese, 1908 [1909]
= *Trigona sandacana* Cockerell, 1919a
Heterotrigona (*Heterotrigona*) ***itama*** (Cockerell, 1918)*
= *Trigona breviceps* Cockerell, 1919a

Subgenus *Platytrigona* Moure, 1961

Heterotrigona (*Platytrigona*) ***flaviventris*** (Friese, 1908 [1909])
Heterotrigona (*Platytrigona*) ***hobbyi*** (Schwarz, 1937)
Heterotrigona (*Platytrigona*) ***keyensis*** (Friese, 1901)
Heterotrigona (*Platytrigona*) ***lamingtonia*** (Cockerell, 1929a)
Heterotrigona (*Platytrigona*) ***planifrons*** (Smith, 1865)*

Subgenus *Sahulotrigona* Engel and Rasmussen, 2017

Heterotrigona (*Sahulotrigona*) ***atricornis*** (Smith, 1865)
Heterotrigona (*Sahulotrigona*) ***paradisaea*** Engel and Rasmussen, 2017*
= *Trigona* (*Pacificotrigona*) *okazawai* Tadauchi et al., 1998, nomen nudum
= *Trigona* (*Pacificotrigona*) *okazawai irianensis* Tadauchi et al., 1998, nomen nudum

Subgenus *Sundatrigona* Inoue and Sakagami, 1993

Heterotrigona (*Sundatrigona*) ***lieftincki*** (Sakagami and Inoue, 1987)

Heterotrigona (*Sundatrigona*) ***moorei*** (Schwarz, 1937)*

= *Trigona* (*Tetragona*) *matsumurai* Sakagami, 1959

Genus *Homotrigona* Moure, 1961

Subgenus *Homotrigona* Moure, 1961

Homotrigona (*Homotrigona*) ***aliceae*** (Cockerell, 1929b)

= *Trigona kusutkana* Dover, 1929

Homotrigona (*Homotrigona*) ***anamitica*** (Friese, 1909)

= *Trigona melanotricha* Cockerell, 1918

Homotrigona (*Homotrigona*) ***fimbriata*** (Smith, 1857)*

= *Melipona castanea* Bingham, 1903

= *Trigona flavistigma* Cameron, 1902

= *Trigona versicolor* Friese, 1908 [1909]

Homotrigona (*Homotrigona*) ***lutea*** (Bingham, 1897)

= *Trigona ferrea* Cockerell, 1929b

Subgenus *Lophotrigona* Moure, 1961

Homotrigona (*Lophotrigona*) ***canifrons*** (Smith, 1857)*, new combination

= *Trigona busara* Cockerell, 1918

Subgenus *Odontotrigona* Moure, 1961

Homotrigona (*Odontotrigona*) ***haematoptera*** (Cockerell, 1919a)*, new combination

= *Trigona haematoptera* variety *dulitae* Schwarz, 1937

Subgenus *Tetrigona* Moure, 1961

Homotrigona (*Tetrigona*) ***apicalis*** (Smith, 1857)*, new combination

= *Trigona hemileuca* Cockerell, 1929b

= *Trigona sericea* Friese, 1933b

Homotrigona (*Tetrigona*) ***binghami*** (Schwarz, 1937), new combination

Homotrigona (*Tetrigona*) ***melanoleuca*** (Cockerell, 1929b), new combination

Homotrigona (*Tetrigona*) ***peninsularis*** (Cockerell, 1927), new combination

Homotrigona (*Tetrigona*) ***vidua*** (Lepeletier de Saint Fargeau, 1836), new combination

Genus *Lepidotrigona* Schwarz, 1939

Lepidotrigona ***arcifera*** (Cockerell, 1929c)

= *Melipona tunneli* Pugh, 1947, nomen dubium et inquirendum

Lepidotrigona ***doipaensis*** (Schwarz, 1939)

Lepidotrigona ***flavibasis*** (Cockerell, 1929c)

Lepidotrigona ***hoozana*** (Strand, 1913)

Lepidotrigona ***javanica*** (Gribodo, 1891)

Lepidotrigona ***latebalteata*** (Cameron, 1902)

Lepidotrigona ***latipes*** (Friese, 1900)

Lepidotrigona ***nitidiventris*** (Smith, 1857)*

= *Trigona fulvopilosella* Cameron, 1908

Lepidotrigona ***palavanica*** (Cockerell, 1915)

Lepidotrigona ***terminata*** (Smith, 1878)

= *Trigona fulvomarginata* Cockerell, 1919b
Lepidotrigona ***trochanterica*** (Cockerell, 1920)
Lepidotrigona ***ventralis*** (Smith, 1857)
= *Trigona* (*Lepidotrigona*) *ventralis* form *nigribasis* Sakagami, 1975, nomen invalidum

Genus *Lisotrigona* Moure, 1961
Lisotrigona ***cacciae*** (Nurse, 1907)*
= *Trigona scintillans* Cockerell, 1920
= *Lisotrigona mohandasi* Jobiraj and Narendran, 2004, new synonym
= *Lisotrigona chandrai* Viraktamath and Sajan Jose, 2017, new synonym
= *Lisotrigona revanai* Viraktamath and Sajan Jose, 2017, new synonym
Lisotrigona ***carpenteri*** Engel, 2000
Lisotrigona ***furva*** Engel, 2000

Genus *Papuatrigona* Michener and Sakagami, 1990
Papuatrigona ***genalis*** (Friese, 1908 [1909])*

Genus *Pariotrigona* Moure, 1961
Pariotrigona ***pendleburyi*** (Schwarz, 1939)*
= *Trigona* (*Hypotrigona*) *pendleburyi* variety *klossi* Schwarz, 1939

Genus *Tetragonula* Moure, 1961
Subgenus *Tetragonilla* Moure, 1961
Tetragonula (*Tetragonilla*) ***atripes*** (Smith, 1857)*
Tetragonula (*Tetragonilla*) ***collina*** (Smith, 1857)
= *Trigona cambodiensis* Cockerell, 1926
Tetragonula (*Tetragonilla*) ***fuscibasis*** (Cockerell, 1920)
Tetragonula (*Tetragonilla*) ***rufibasalis*** (Cockerell, 1918)

Subgenus *Tetragonula* Moure, 1961
Tetragonula (*Tetragonula*) ***bengalensis*** (Cameron, 1897)
Tetragonula (*Tetragonula*) ***biroi*** (Friese, 1898)
Tetragonula (*Tetragonula*) ***carbonaria*** (Smith, 1854)
= *Trigona angophorae* Cockerell, 1912
Tetragonula (*Tetragonula*) ***clypearis*** (Friese, 1909)
= *Trigona wybenica* Cockerell, 1929d
Tetragonula (*Tetragonula*) ***dapitanensis*** (Cockerell, 1925)
Tetragonula (*Tetragonula*) ***davenporti*** (Franck in Franck et al., 2004)
Tetragonula (*Tetragonula*) ***drescheri*** (Schwarz, 1939)
Tetragonula (*Tetragonula*) ***fuscobalteata*** (Cameron, 1908)
= *Trigona erythrostoma* Cameron, 1908
= *Trigona pallidistigma* Cameron, 1908
= *Trigona atomella* Cockerell, 1919a
= *Trigona brevis* Friese, 1925, nomen nudum
= *Trigona pfeifferi* Friese, 1925

= *Trigona pygmaea* Friese, 1933b
Tetragonula (*Tetragonula*) ***geissleri*** (Cockerell, 1918)
= *Trigona confusella* Cockerell, 1919a
Tetragonula (*Tetragonula*) ***gressitti*** (Sakagami, 1978)
Tetragonula (*Tetragonula*) ***hirashimai*** (Sakagami, 1978)
Tetragonula (*Tetragonula*) ***hockingsi*** (Cockerell, 1929e)
Tetragonula (*Tetragonula*) ***iridipennis*** (Smith, 1854)*
Tetragonula (*Tetragonula*) ***laeviceps*** (Smith, 1857)
Tetragonula (*Tetragonula*) ***malaipanae*** Engel, Michener, and Boontop, 2017
Tetragonula (*Tetragonula*) ***melanocephala*** (Gribodo, 1893)
= *Trigona testaceinerva* Cameron, 1908
Tetragonula (*Tetragonula*) ***melina*** (Gribodo, 1893)
Tetragonula (*Tetragonula*) ***mellipes*** (Friese, 1898)
Tetragonula (*Tetragonula*) ***minangkabau*** (Sakagami and Inoue, 1985)
= *Trigona minangkabu* form *darek* Sakagami and Inoue, 1985, nomen invalidum et nudum
Tetragonula (*Tetragonula*) ***minor*** (Sakagami, 1978)
Tetragonula (*Tetragonula*) ***pagdeni*** (Schwarz, 1939)
Tetragonula (*Tetragonula*) ***pagdeniformis*** (Sakagami, 1978)
Tetragonula (*Tetragonula*) ***penangensis*** (Cockerell, 1919b)
Tetragonula (*Tetragonula*) ***praeterita*** (Walker, 1860)
Tetragonula (*Tetragonula*) ***reepeni*** (Friese, 1918)
= *Trigona latigenalis* Sakagami, 1978
Tetragonula (*Tetragonula*) ***ruficornis*** (Smith in Horne and Smith, 1870)
= *Melipona smithii* Bingham, 1897, nomen vanum
Tetragonula (*Tetragonula*) ***sapiens*** (Cockerell, 1911)
Tetragonula (*Tetragonula*) ***sarawakensis*** (Schwarz, 1937)
Tetragonula (*Tetragonula*) ***sirindhornae*** (Michener and Boongird, 2004)
Tetragonula (*Tetragonula*) ***testaceitarsis*** (Cameron, 1901)
= *Trigona testaceicornis* Cameron, 1901, lapsis calami
= *Trigona valdezi* Cockerell, 1918
Tetragonula (*Tetragonula*) ***zucchii*** (Sakagami, 1978)

Genus *Wallacetrigona* Engel and Rasmussen, herein
Wallacetrigona ***incisa*** (Sakagami and Inoue, 1989)*, new combination

Nomina dubia and unassociated nomina nuda
Melipona basimaculata Bingham, 1903, nomen dubium et inquirendum
Melipona khasiana Pugh, 1947, nomen nudum
Melipona pulla Illiger, 1806, nomen nudum
Melipona terrestris Pugh, 1947, nomen nudum
Trigona bismarkiana Tadauchi et al., 1998, nomen nudum
Trigona pallidicincta Cockerell, 1918, nomen dubium et inquirendum
Trigona wallacei Tadauchi et al., 1998, nomen nudum (a species of *Tetragonula* s.str.)

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