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Notes on Southeast Asian Stingless Bees of the Genus *Tetragonula* (Hymenoptera: Apidae), with the Description of a New Species from Thailand

MICHAEL S. ENGEL,[1] CHARLES D. MICHENER,[1,2] AND YUVARIN BOONTOP[3]

ABSTRACT

A new species of stingless bee (Apinae: Meliponini) is described from workers and two males recovered from nests in tree trunks in Kanchanaburi Province, Thailand. *Tetragonula* (*Tetragonula*) *malaipanae*, new species, resembles *T*. (*T*.) *laeviceps* (Smith), *T*. (*T*.) *pagdeni* (Schwarz), *T*. (*T*.) *testaceitarsis* (Cameron), and similar species, but is particularly similar to *T*. (*T*.) *drescheri* (Schwarz). Unlike *T*. *drescheri*, the new species lacks a defined black stripe on the underside of the metafemur, has the metatibia reddish brown to testaceous (rather than uniformly chestnut brown, and black with a yellow mark on the inner surface in *T*. *drescheri*). Characters of the uncommonly encountered *T*. (*T*.) *sarawakensis* (Schwarz) are also recorded.

INTRODUCTION

It is well known that the concentration of stingless bee (Apinae: Meliponini) diversity resides within South and Central America (Schwarz, 1948; Moure, 1951; Michener, 1990, 2007, 2013). Even so, Southeast Asia retains a remarkable and interesting fauna of diverse and often cryptically similar stingless bees (Moure, 1961; Sakagami, 1975, 1978; Sakagami and Inoue, 1985; Franck et al., 2004), including species with unique biologies generally diver-

[1] Division of Invertebrate Zoology, American Museum of Natural History; Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, University of Kansas.
[2] Deceased, 1 November 2015.
[3] Insect Taxonomy Group, Department of Agriculture, Bangkok.

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gent from those of other meliponines, such as the minute lachryphagous species of the genera *Lisotrigona* Moure and *Pariotrigona* Moure (Bänziger et al., 2009; Bänziger and Bänziger, 2010; Karunaratne et al., 2017). Most Asiatic Meliponini have traditionally been placed within the genus *Trigona* Jurine, with a broad circumscription and encompassing otherwise heterogeneous bees (e.g., Michener, 1990, 2007). However, as initially proposed by Moure (1961), further suggested by Michener (2000, 2007), and increasingly demonstrated by molecular and morphological studies (Rasmussen and Cameron, 2007, 2010), the Indo-Australian species of "*Trigona*" fall in a major clade independent from those of the true species of *Trigona* in the Neotropical Region.

The largest group of Indo-Australian "*Trigona*" has been placed in *Tetragonula* Moure, recognized in particular by the combined presence of a basal sericeous area on the inner metabasitarsal surface and the projection of the mesoscutellum over the propodeum (Moure, 1961; Sakagami, 1978). This group was characterized by Moure (1961) and Sakagami (1978), and has been treated as a subgenus of *Trigona* by Sakagami (1978), or as an outright genus by Moure (1961), Rasmussen (2008), Michener (2013), and the present authors. Michener (1990, 2000, 2007) united *Tetragonula* with several other groups under the name *Trigona* (*Heterotrigona* Schwarz), but because the species of *Tetragonula* are a readily recognized unit, that name was again used by Michener and Boongird (2004), albeit as a subgenus in *Trigona*. Here we regard *Tetragonula* as a genus, a practice consistent with the phylogenetic study of Rasmussen and Cameron (2007, 2010), the system proposed by Rasmussen, J.C. Thomas, and M.S.E. (in prep.), and in agreement with Rasmussen's (2008) checklist of Indo-Australian species of Meliponini.

The Asiatic species of *Tetragonula* were reviewed and characterized in considerable detail by Sakagami (1978), and then later extended for bicolorous species by Sakagami and Inoue (1985). The species of the genus are summarized in table 1. Many of them are similar to one another and often difficult to recognize, differing in minute aspects of coloration, size, and setation. In 2007 and 2008, several nests of a new species were found in the Thong Pha Phum District, Kanchanaburi Province, Thailand. We provide a characterization of the species here along with a few anecdotal notes on the occurrence of these nests in the hope of encouraging continued work on the biology of the species.

MATERIAL AND METHODS

Specimens were collected from nest entrances and flowers and were examined dry, mounted on points or pinned, with material deposited in the following institutional repositories:

AMNH Division of Invertebrate Zoology, American Museum of Natural History, New York (J.G. Rozen, Jr.)

BBSL Bee Biology and Systematics Laboratory, USDA-ARS, Utah State University, Logan (T.L. Griswold)

CNIN Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México, D.F., Mexico (I.A. Hinojosa-Díaz)
CSCA California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento (K. Williams)
DZUP Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil (G.A.R. Melo)
EMBT Entomological Museum Bangkok Thailand, Insect Taxonomy Group, Department of Agriculture, Bangkok (Y. Boontop)
FSCA Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Gainesville (E. Talamas)
ICNC Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santa Fé de Bogotá (F. Fernández)
KSMA King Saud Museum of Arthropods, Department of Plant Protection, King Saud University, Riyadh, Saudi Arabia (A.S. Alqarni)
KUEC Entomological Laboratory, Kyushu University, Fukuoka, Japan (O. Tadauchi)
LIPI Museum Zoologicum Bogoriense, Indonesian Institute of Sciences, Bogor, Indonesia (S. Kahono, P. Djunijanti).
NHML Department of Entomology, The Natural History Museum, London (D.G. Notton)
SANC South African National Collection of Insects, Pretoria (C.D. Eardley)
SEMC Division of Entomology (Snow Entomological Collection), University of Kansas Natural History Museum, Lawrence (M.S. Engel)
USNM Department of Entomology, National Museum of Natural History (United States National Museum), Smithsonian Institution, Washington, D.C. (B. Harris)
ZMHB Museum für Naturkunde der Humboldt-Universität, Berlin (M. Ohl)
ZISP Zoological Institute, Russian Academy of Sciences, St. Petersburg (Yu. Astafurova, S. Belokobylskij)

In reporting material examined, we have employed standard symbols for eusocial castes, specifically ♀ for the sterile female workers.

Morphological terminology generally follows that of Sakagami (1978), Engel (2001), and Michener (2007). Abbreviations used are: OD, ocellar diameter, used as a measurement of certain structures; and S, and T, respectively metasomal sternum and metasomal tergum, such that S6, for example, refers to the sixth metasomal sternum. Measurements were made with an ocular micrometer in an Olympus SZX12 stereomicroscope. In the description, mean values are provided with ranges from 20 workers indicated in parentheses and ranges for the two available males when the values differed between them. Measurements of the metatibial length and of the forewing diagonal (Sakagami's "WL2") from the base of vein M to the base of crossvein r-rs were made as illustrated by Sakagami (1978: figs. 1, 2). In the account of the worker caste, descriptive material placed in brackets represents observed variation among individuals in the type series.

TABLE 1. Hierarchical and synonymic checklist of species of *Tetragonula* Moure (Meliponini).

Genus *Tetragonula* Moure, 1961
- Subgenus *Tetragonula* Moure, 1961
  - *T. bengalensis* (Cameron, 1897)
  - *T. biroi* (Friese, 1898)
  - *T. carbonaria* (Smith, 1854)
    - = *Trigona angophorae* Cockerell, 1912
  - *T. clypearis* (Friese, 1908)
    - = *Trigona wybenica* Cockerell, 1929a
  - *T. dapitanensis* (Cockerell, 1925)
  - *T. davenporti* (Franck in Franck et al., 2004)
  - *T. drescheri* (Schwarz, 1939)
  - *T. 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, 1933
  - *T. geissleri* (Cockerell, 1918)
    - = *Trigona confusella* Cockerell, 1919a
  - *T. gressitti* (Sakagami, 1978)
  - *T. hirashimai* (Sakagami, 1978)
  - *T. hockingsi* (Cockerell, 1929b)
  - *T. iridipennis* (Smith, 1854)
  - *T. laeviceps* (Smith, 1857)
  - *T. malaipanae* Engel, Michener, & Boontop, n. sp.
  - *T. melanocephala* (Gribodo, 1893)
    - = *Trigona testaceinerva* Cameron, 1908
  - *T. melina* (Gribodo, 1893)
  - *T. mellipes* (Friese, 1898)
  - *T. minangkabau* (Sakagami & Inoue, 1985)
    - = *Trigona minangkabu* form *darek* Sakagami & Inoue, 1985, nomen invalidum et nudum
  - *T. minor* (Sakagami, 1978)
  - *T. pagdeni* (Schwarz, 1939)
  - *T. pagdeniformis* (Sakagami, 1978)
  - *T. penangensis* (Cockerell, 1919b)
  - *T. praeterita* (Walker, 1860)
  - *T. reepeni* (Friese, 1918)
    - = *Trigona latigenalis* Sakagami, 1978
  - *T. ruficornis* (Smith in Horne and Smith, 1870)
    - = *Melipona smithii* Bingham, 1897, nomen vanum
  - *T. sapiens* (Cockerell, 1911)
  - *T. sarawakensis* (Schwarz, 1937)
  - *T. sirindhornae* (Michener & Boongird, 2004)
  - *T. testaceitarsis* (Cameron, 1901)
    - = *Trigona testaceicornis* Cameron, 1901, lapsis calami
    - = *Trigona valdezi* Cockerell, 1918
  - *T. zucchii* (Sakagami, 1978)
- Subgenus *Tetragonilla* Moure, 1961
  - *T. atripes* (Smith, 1857)
  - *T. collina* (Smith, 1857)
    - = *Trigona cambodiensis* Cockerell, 1926
  - *T. fuscibasis* Cockerell, 1920
  - *T. rufibasalis* (Cockerell, 1918)

SYSTEMATICS

Genus *Tetragonula* Moure, 1961

Subgenus *Tetragonula* Moure, 1961

Tetragonula* (*Tetragonula*) *malaipanae, new species

Figures 1–3

Diagnosis: The species generally agrees with the subgeneric characterization as presented by Sakagami (1978). Worker dark but paler than *Tetragonula laeviceps* (Smith, 1857), *T. pagdeni* (Schwarz, 1939), and *T. pagdeniformis* (Sakagami, 1978) (figs. 1A, 1B), clypeus yellowish (fig. 1C), legs partly or wholly red brown or testaceous (fig. 1A). Size similar to that of *T. testaceitarsis* (Cameron, 1901) (likely senior synonym of *T. valdezi* [Cockerell, 1918]), larger than *T. laeviceps* (as restricted by Rasmussen and Michener, 2010), *T. pagdeni*, and *T. pagdeniformis* (see Discussion, below). Mesoscutum with pale pubescence not or weakly banded (fig. 1B), sublateral bare bands not or scarcely recognizable. Setae of body largely pale, but those of vertex, especially behind ocelli, blackish or sometimes dusky. Mean metatibial length 1.81 mm, mean forewing length including tegula 4.58 mm, mean head width 1.90 mm. Male generally colored as in worker (fig. 2), with S5 lacking gradulus (fig. 3C), apical process of S6 long and parallel sided (fig. 3D), S7 and T7 sharply pointed apically (figs. 3B, 3E); genitalia with penis valves and gonostyli directed posteriorly (figs. 3F, 3H), sclerotization probably representing gonobase across base (figs. 3F, 3H).

Description: **Worker.** Body length 3.92 mm (3.50–4.70 mm); forewing length, including tegula, 4.58 mm (4.40–4.70 mm); head length from anterior margin of clypeus to summit of vertex, in facial view 1.42 mm (1.40–1.50 mm); head width 1.91 mm (1.75–2.00 mm); metatibia length 1.82 mm (1.63–1.88 mm); forewing diagonal from base of vein M to base of crossvein r-rs at margin of pterostigma 1.31 mm (1.23–1.38 mm). Scape (excluding basal bulb) more than half as long as compound eye; flagellomere IV slightly broader than long. Ocelloccipital distance over half OD, ocellocular distance less than interocellar distance. Genal area widest at about upper third of compound eye, and narrower than compound eye in profile. Metatibia and metabasitarsus shaped as usual in this group (see Sakagami, 1978: fig. 2); basal sericeous area at base of inner surface of metabasitarsus well defined, reaching to middle of metabasitarsus [variable, not attaining middle or extending beyond middle]. Metasoma short, about as wide as head, widest at T2 and T3, remaining terga progressively much narrower and largely telescoped into preceding segments. Cuticular surface polished and shining with few minute punctures or setal bases.

Head black, the following parts yellow testaceous [to reddish testaceous or pale yellowish brown]: clypeus except dusky upper and upper lateral margins [entire clypeus commonly yellowish], supraclypeal area [sometimes dusky or blackish], mandible except blackish apex and extreme base, and labrum. [Lower genal area and hypostomal area behind mandibular base sometimes weakly brownish, grading into black background]. Antenna yellowish [to reddish] testaceous, flagellum blackish [or dusky] on upper surface, on lower surface part of each flagel-

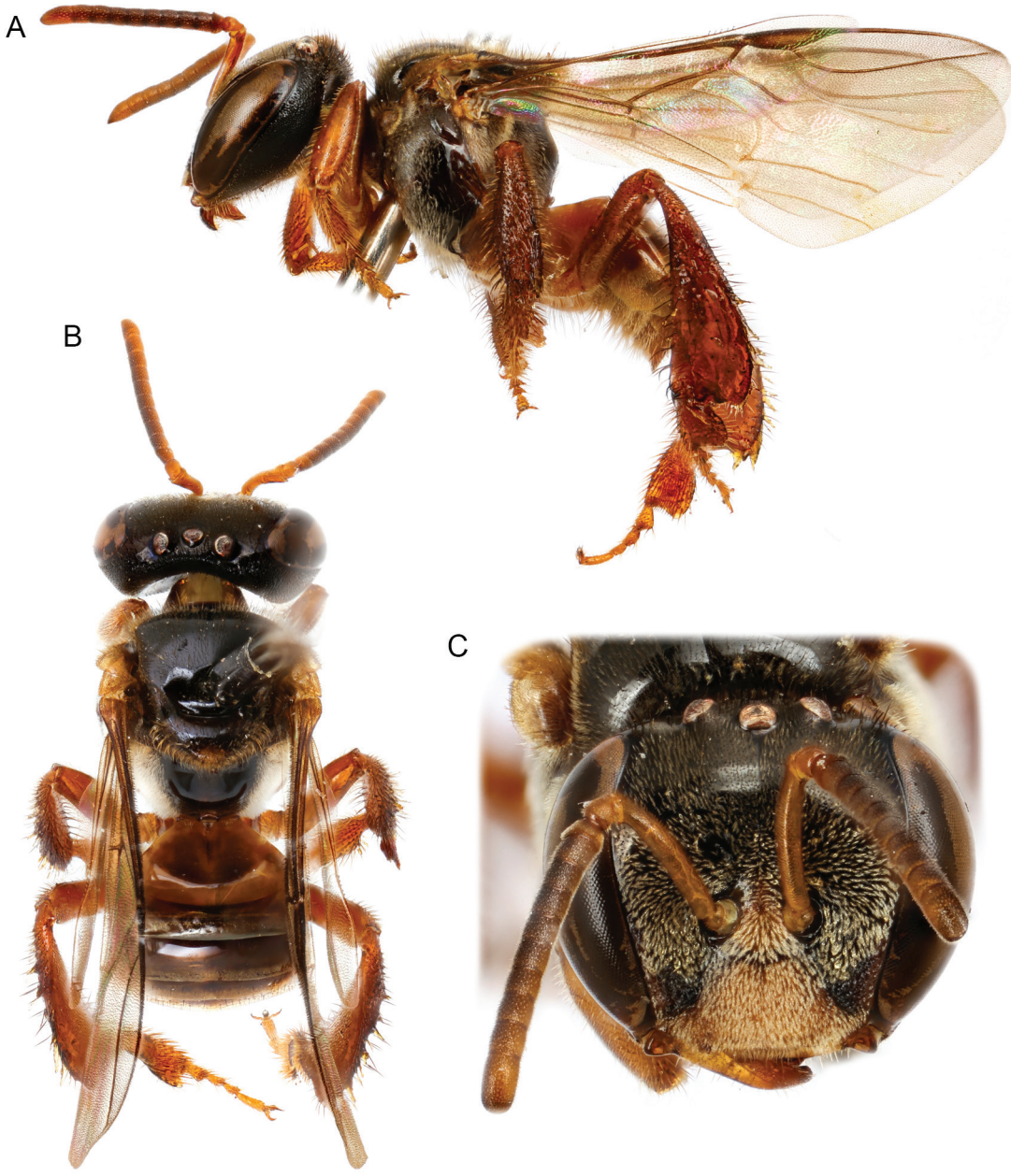

FIGURE 1. Worker of *Tetragonula malaipanae*, new species. **A.** Lateral habitus. **B.** Dorsal habitus. **C.** Facial view.

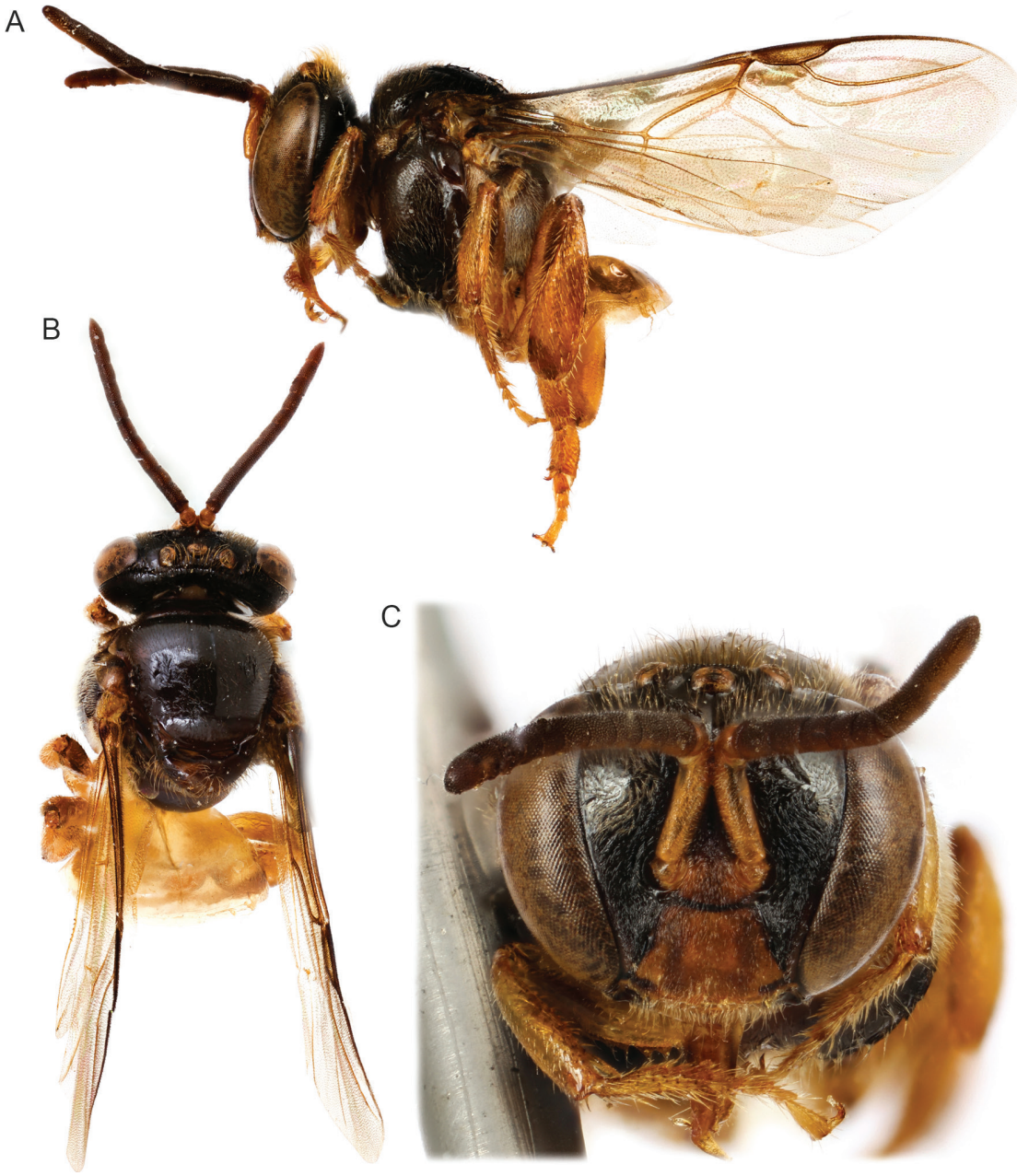

FIGURE 2. Male of *Tetragonula malaipanae*, new species (specimen with metasoma dissected). **A.** Lateral habitus. **B.** Dorsal habitus. **C.** Facial view.

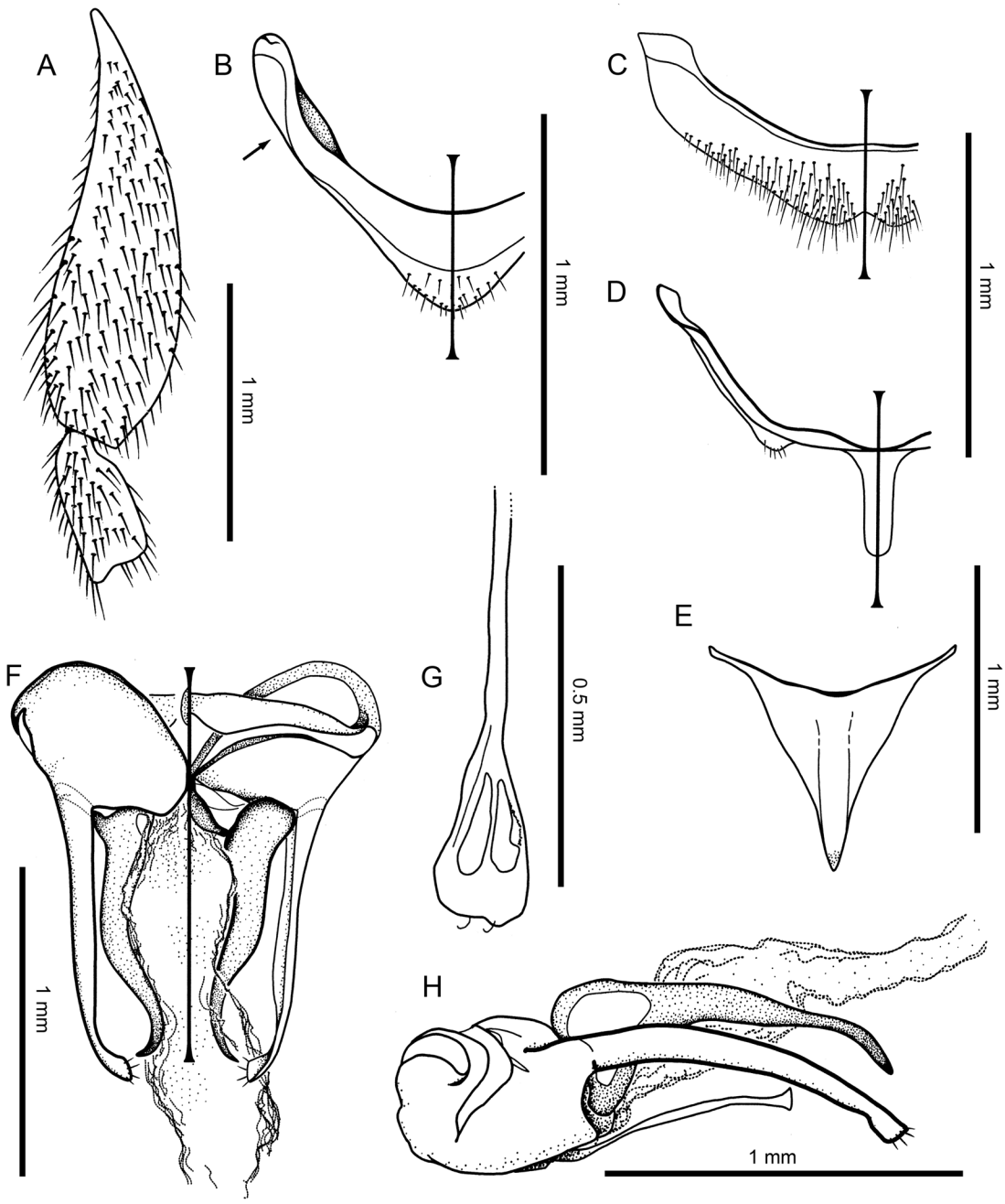

FIGURE 3. Male of *Tetragonula malaipanae*, new species. **A.** Outer view of metatibia and metabasitarsis. **B.** Dorsal view of T7 (arrow indicates the position of the spiracle on the side of the sclerite). **C.** Ventral view of S5. **D.** Ventral view of S6. **E.** Ventral view of S7. **F.** Male genitalia (dorsal view at left, ventral view at right), distal part of membranous aedeagus omitted. **G.** Midventral membranous process. **H.** Male genitalia in right lateral view.

lomere dusky [or not]. Thorax black except pronotum dark brown [to blackish], pronotal lobe dusky testaceous [to black], mesoscutellum brownish [or black], [mesepisternum sometimes brownish black], anterolateral part of mesepisternum brown [to black]. Legs (including coxae and trochanters) reddish brown, meso- and metatibiae and tarsi dark reddish brown [or rarely legs testaceous or legs blackish brown, sometimes only mid and hind legs dark, inner surface of metatibia and metatarsus and often basal part of metafemur reddish brown]. Tegula dusky testaceous. Wings clear, faintly dusky, veins and pterostigma blackish. Metasoma with T1 dusky brown [brown], anterior surface largely testaceous; T5 and T6 [sometimes on T6] testaceous [brown or dusky]; T2 and T4 [sometimes also T5] brownish black, posterior margins paler translucent [posterior part of T1 sometimes similarly dark]. [Sometimes, especially specimens from nests 6 and 9, with all terga testaceous, posterior ones darker than anterior ones]. Metasomal sterna testaceous [brown, sometimes slightly dusky].

Pubescence decumbent and pallid except as otherwise noted, mostly ochraceous; clypeus without erect simple setae, even lower margin without such setae. Setae of face short (0.5 OD), plumose, rather dense but not hiding surface, particularly sparse and thin on lower paraocular area, whitish, those of frons [or upper half of frons] brownish to yellowish and hence inconspicuous in certain views; erect setae of scape absent except for exceedingly short ones; longer setae (1 OD) of vertex, especially behind ocelli, blackish or dusky; short pale setae of mesoscutum weakly [or not recognizably] banded. When recognizable, median asetose band ("G1" of Sakagami, 1978) narrow, extending full length of mesoscutum except anterior extremity, G2 similarly narrow anteriorly but broadening and diverging posteriorly, G3 (lateral asetose band) poorly defined, especially on anterior half of mesoscutum [not recognizable except in some fresh, clean specimens]; longer, erect setae of mesoscutum (2 OD) pale or in certain illuminations dusky; fringe of long setae (up to 3 OD) on posterior margin of mesoscutellum ochraceous, with longest setae (3–4 OD) sometimes appearing dusky; metepisternum, side of propodeum, and anterior half of mesepisternum covered with dense white setae hiding surface [those of mesepisternum sometimes ochraceous]; some setae of outer surfaces of meso- and metatibiae and basitarsi dusky [commonly most setae of these parts, including large simple discal setae of corbicula, black or blackish]; anterior fringe of corbicula with a few [nearly all] setae dusky or blackish. T1 smooth and asetose; T2 to T5 smooth and asetose except for preapical very sparse bands, that of T2 consisting of only a few minute ochraceous setae, those of following terga with progressively more and longer setae, a few of those of T4 reaching beyond apical margin of tergum, those of T5 and T6 still longer, but all small and not conspicuous; setae of sterna denser and longer, almost white.

Male. Agrees with description of worker except for variation noted above in brackets, in measurements provided, and as follows (except for measurements, description based on male collected from nest 4 on 17 September 2007): body length 4.50 mm; forewing length, including tegula, 4.45 mm (4.40–4.50 mm); head length (measured as for worker) 1.40 mm; head width 1.78 mm; metatibia length 1.46 mm (1.43–1.48 mm); forewing diagonal (measured as for worker) 1.26 mm (1.25–1.27 mm).

Scape (excluding basal bulb) slightly less than half as long as compound eye. Flagellomere 4 (also 2–10) longer than broad. Ocelloccipital distance less than half OD; ocellocular distance about half of interocellar distance. Metatibia widest at about apical third, narrowed at apex, without plumose setae (fig. 3A). Metasomal T7 without Y-shaped ridge, apex broadly rounded (fig. 3B); S5 short, without noticeable gradulus, with shallow, broad, midapical emargination (fig. 3C); apical process of S6 slender, parallel sided (fig. 3D); terminalia as illustrated in figures 3D–3H; unbroken, weakly sclerotized band in position of gonobase (fig. 3F); long membranous midventral genital process present (figs. 3G, 3H), presumably fragmentum from base of penis; penis valves and gonostyli directed posteriorly (figs. 3F, 3H); gonostylus arising near outer distal margin of gonocoxite (figs. 3F, 3H), flattened, so that in lateral view it is rather broad and subapically constricted (fig. 3H), in dorsal view very slender apically.

Pale areas of head yellowish brown, upper median part of supraclypeal area black. Genal and hypostomal areas black. Flagellum black. Pronotum including pronotal lobe, mesoscutellum, and mesepisternum black. Legs yellowish brown, distal parts of femora, basal parts of tibiae, and distal parts of meso- and metatibia infuscated. Metasoma with T1 testaceous, with broad preapical dusky band; remaining terga cleared for study but apparently dusky testaceous (note that when dissected the metasoma appears pale testaceous).

Pubescence generally thinner and sparser than in female, particularly on clypeus, mesoscutellum, and mesepisternum; pubescence of head, mesosoma, and legs largely ochraceous. Mesoscutum almost without banding of setae; setae of mesepisternum and sides of propodeum white, somewhat less dense than in worker; dense setae of anterior part of mesepisternum dusky.

Holotype: ♀, Thailand, Kanchanaburi [Province], Thong Pha Phum [District], 17.ix.2007 [17 September 2007], Y. Boontop, nest 2 (SEMC). The holotype is from nest number 2 in Boontop's records, a site 549 m above sea level at coordinates 14.42° N, 98.28° E.

Paratypes (2♂♂, 340♀♀): 1♂, same data as holotype except nest 4 (SEMC); 1♂, same data as holotype except 12.iii.2008 [12 March 2008] and nest 11 (SEMC); 24♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 1 (16 SEMC, 2 CSCA, 2 DZUP, 2 EMBT, 2 ICNC); 11♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 1 (SEMC); 18♀♀, same data as holotype (16 SEMC, 2 EMBT); 17♀♀, same data as holotype except 12.iii.2008 [12 March 2008] (9 SEMC, 4 AMNH, 2 BBSL, 2 CNIN); 24♀♀, same data as holotype except 27.vii.2009 [27 July 2009] (16 SEMC, 2 NHML, 2 SANC, 2 USNM, 2 EMBT); 8♀♀, same data as holotype except nest 3 (SEMC); 13♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 3 (SEMC); 14♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 3 (10 SEMC, 2 ZMHB, 2 ZISP); 2♀♀, same data as holotype except nest 4 (SEMC); 12♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 4 (10 SEMC, 2 KSMA); 11♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 4 (SEMC); 2♀♀, same data as holotype except nest 5 (SEMC); 14♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 5 (11 SEMC, 3 EMBT); 15♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 5 (11 SEMC, 2 KUEC, 2 EMBT); 5♀♀, same data as holotype except 31.vii.2006 [31 July 2006] and nest 6 (SEMC); 9♀♀, same data as holotype except

nest 6 (SEMC); 15♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 6 (13 SEMC, 1 FSCA, 1 LIPI); 21♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 6 (19 SEMC, 1 FSCA, 1 LIPI); 5♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 7 (SEMC); 12♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 7 (SEMC); 5♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 8 (SEMC); 9♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 9 (SEMC); 5♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 10 (SEMC); 4♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 10 (SEMC); 14♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 11 (SEMC); 3♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 11 (SEMC); 6♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 12 (SEMC); 3♀♀, same data as holotype except 27.vii.2009 [27 July 2009] and nest 12 (SEMC); 8♀♀, same data as holotype except 12.iii.2008 [12 March 2008] and nest 13 (SEMC); 2♀♀, same data as holotype except 31.vii.2006 [31 July 2006] and nest 19 (SEMC); 2♀♀, same data as holotype except 17.ix.2007 [17 September 2007] (SEMC).

Additional material: A further six workers are remarkably similar to *T. malaipanae* and we tentatively include them here, pending further work on these more southern populations, particularly utilizing morphometrics, males, and DNA data: 4♀♀, Thailand, Nakhonsithammarat, Khao Laung, 3.v.2007 [3 May 2007], Y. Boontop, nest 11 [a site 359 m above sea level at coordinates 8.49° N, 99.78° E] (SEMC); 2♀♀, Thailand, Suratthani, Khao sok, 3.v.2007 [3 May 2007], Y. Boontop, nest 15 [a site 421 m above sea level at coordinates 8.91° N, 98.52° E] (SEMC).

Comments: Probably variation in coloration of males is more or less comparable to that of workers. The male taken 12 March 2008 at nest number 11 differs from the male described above as follows: integument of head and mesosoma (including clypeus and tegula) black; scape and pedicel reddish brown; legs dusky pale brown; meso- and metatarsi and distal parts of tibiae blackish, palest areas on outer and posterior surfaces of protibia and basal parts of meso- and metatibiae; metasoma reddish brown with vague transverse dusky areas, apical terga darker; membranous midventral genital process not evident (likely a result of damage during dissection).

Etymology: The specific epithet honors Savitree Malaipan of the Department of Agriculture, Kasetsart University, Bangkok, beloved mentor of Y.B. and a prominent Thai melittologist.

Tetragonula (*Tetragonula*) *sarawakensis* (Schwarz, 1937)

Trigona sarawakensis Schwarz, 1937: 313. Cotype workers (AMNH, examined by M.S.E. and C.D.M.).
Trigona (Tetragona) sarawakensis var. *sarawakensis* Schwarz; Schwarz, 1939: 106.
Tetragonula sarawakensis (Schwarz); Moure, 1961: 210.
Trigona (*Tetragonula*) *sarawakensis* (Schwarz); Sakagami, 1978: 210.

Since this is not a well-known species, we include below notes based on a series of workers in the AMNH, two labeled as cotypes, and include comparative information on *T. malaipanae* in brackets.

Descriptive notes: Setae of clypeus and lower face minute, minutely if at all plumose, not at all hiding smooth surface [broadly plumose, partially hiding surface which shows some punctation]; tegula ferruginous [dark testaceous, sometimes grading to dusky especially near inner margin]; mesoscutellum with posterior extremity (overhanging propodeum) with transverse yellow mark (sometimes ferruginous, perhaps artificially darkened in such instances owing to method of collection or changes resulting from long-term preservation) [no such mark or if mark recognizable, testaceous or dusky]; legs ferruginous [usually dull ferruginous or brown with dusky areas at least on meso- and metatibiae]; setae of legs whitish or yellowish, sometimes a few dusky setae on tibiae and basitarsi [some setae on tibiae and basitarsi dusky or blackish, large simple setae arising from corbicular surface black or dusky although marginal setae largely or partly yellowish]; metasoma entirely ferruginous [dusky brown to testaceous].

Material examined (7♀♀): 1♀ [cotype], Sarawak, Mt. Dulit, 4000 ft, moss forest, 18.x.1932 [18 October 1932], Oxford Univ. Exp. B.M. Hobby & A.W. Moore (AMNH); 1♀ [cotype], same data as preceding specimen except 19.x.1932 [19 October 1932] (AMNH); 5♀♀, Mt. Tibang [Mount Tibang, Sarawak, near border with Kalimantan], 1300 m, Borneo, Nov. 1925, Eric Mjöberg (AMNH).

DISCUSSION

In Sakagami's (1978) key based on workers, *T. malaipanae* runs best to *T. laeviceps* or *T. sarawakensis*. The latter is rather different as indicated in the section above on that species. *Tetragonula laeviceps* in the sense of Sakagami (1978) is probably at least two species, as Sakagami himself suggested. Rasmussen and Michener (2010) indicated probable separation of a smaller form (*T. laeviceps* proper) and a larger form (here called *T. testaceitarsis* [Cameron] of which *T. valdezi* [Cockerell] is a probable junior synonym). *Tetragonula malaipanae* is the size of *T. testaceitarsis*. It differs from that species (as well as from *T. laeviceps*) by the entirely or almost entirely yellowish testaceous clypeus and the extensively reddish brown or sometimes testaceous legs. *Trigona malaipanae* is, however, more similar to the bicolorous species dealt with by Sakagami and Inoue (1985). Of the species listed above, only *T. sarawakensis* is bicolorous and distinguished by the features referenced. *Tetragonula malaipanae* is most similar to *T. drescheri* (Schwarz, 1939), a species characterized by a sharply defined black stripe on the underside of each femur, the largely chestnut brown outer surface of the metatibia, and the black inner surface of the metatibia except for a well-defined, large oval yellow spot on the inner metatibial ridge. These features are not found in *T. malaipanae*. Some of the individuals that Sakagami and Inoue (1985: figs. 16, 17) considered as pale forms of *T. laeviceps* may have been *T. malaipanae*.

If, following Sakagami's (1978) key based on workers, one incorrectly goes to couplet 6 (pale setae of mesoscutum strongly banded), *T. malaipanae* does not lead clearly to any species. The possibilities are *T. hirashimai* (Sakagami, 1978), *T. minor* (Sakagami, 1978), *T. pagdeniformis* (Sakagami), *T. pagdeni* (Schwarz), and *T. iridipennis* (Smith, 1854). The last is restricted to Sri Lanka and India. Workers of the four remaining species, all of which occur in Southeast Asia including Thailand, differ in size, such that they can often be recognized superficially. Of

FIGURE 4. A large *Ficus* L. (Moraceae) containing a nest of *Tetragonula malaipanae*, new species. **A.** Photo of the tree. **B.** Detail of nest entrance showing guard bees (from nest 2 in 2007 at the type locality in Thong Pha Phum District, Kanchanaburi Province).

these species, *T. minor* is the smallest (forewing length including tegula less than 3.8 mm) and *T. hirashimai* is the largest (forewing more than 4.9 mm). The other two species are intermediate, with forewing lengths from 3.9 to 4.5 mm. *Tetragonula malaipanae* falls with this latter group, with forewing lengths from 4.4 to 4.7 mm. Head width is similarly different, ranging for *T. pagdenformis* and *T. pagdeni* from 1.6 to 1.8 mm, and for *T. malaipanae* from 1.8 to 1.9 mm. In size, the new species agrees best with *T. testaceitarsis*.

Most workers of *T. malaipanae* differ from those of *T. pagdeniformis* and *T. pagdeni*, as well as *T. hirashimai* and *T. minor*, in paler coloration. In specimens of *T. malaipanae* the clypeus, labrum, and usually the supraclypeal area are largely or entirely yellowish to reddish testaceous and the legs are entirely or partly reddish brown. Rarely the legs are blackish with only the inner surface of the metatibia reddish brown. In the other species listed above these parts are largely black or brownish black.

The male (only two specimens) has large areas on the legs yellowish brown to dusky testaceous. The clypeus is yellowish testaceous to black. The terminalia differ from those of *T. laeviceps* and *T. testaceitarsis* in characters listed in the description above, summarized as follows: shape and lack of gradulus of S5 (fig. 3C), the apical process of S6 (fig. 3D), and the acute apices of S7 (fig. 3E) and T7 (fig. 3B). In both males of *T. malaipanae* the penis valves are subparallel, convergent posteriorly, while in all males seen of *T. laeviceps* and *T. testaceitarsis* they are directed laterally, in opposite directions. In Sakagami's (1978) key to the known males, *T. malaipanae* runs to *T. laeviceps* (probably including *T. testaceitarsis*) and *T. pagdeniformis*. In *T. malaipanae* the gonostylus is very slightly swollen apically and slightly constricted preapically in certain views (figs. 3F, 3H), as in *T. pagdeniformis* shown by Sakagami (1978: his figures 87, 98).

At sites specified above, at least 15 nests of *T. malaipanae* were found, with most specimens obtained from nest entrances as they attempted to depart. The nests were in trunks of large living trees of *Ficus* L. (Moraceae) within forests of mostly smaller trees. The *Ficus* trees inhabited by *T. malaipanae* were 20–30 m in height and 155–211 cm in trunk diameter at breast height. Nest entrances varied in height from near the ground to 5.4 m above the ground surface. The trees appear to have developed as stranglers with many parts forming the trunks (fig. 4A); presumably the bee nests are in cavities among these parts or within the old, interior trunk. We have not, however, felled trees or opened nests for study. The nest entrances are variable, rather irregular, of gray to black resinous material, almost circular to much elongate (e.g., fig. 4B). The following are diameters of some entrance openings, two diameters at right angles per nest: 1.5 × 2.5 cm; 1.7 × 2.9 cm; 2.5 × 2.8 cm; 3.0 × 3.5 cm; 1.3 × 3.9 cm. The entrances are consistently large in diameter compared to the bees, so that several bees take positions, looking outward, on the inner surfaces of the openings. Entrances sometimes project little above the surface of the trunk, but also often extend as tubes up to 5 cm in length adhering to the surface of the trunk. The outer surfaces of such tubes are irregularly nodulose while the inner surfaces are smoother, and while the openings are sometimes irregular, the lower portion often extends as a broad lip serving as a point of departure and landing for the bees. Irregular openings may be the result of earlier damage to entrances. The entrances commonly are within or arise from areas of batumen (Wille and Michener, 1973; Wille, 1983) that close originally larger openings into the cavities occupied by the nests.

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REFERENCES

Bänziger, H., and S. Bänziger. 2010. Mammals, birds and reptiles as hosts of *Lisotrigona* bees, the tear drinkers with the broadest host range (Hymenoptera, Apidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 83 (3–4): 271–282.

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

Bingham, C.T. 1897. The fauna of British India, including Ceylon and Burma. Hymenoptera, vol. 1: Wasps and bees. London: Taylor and Francis, xxix + 579 pp., +4 pls.

Cameron, P. 1897. Hymenoptera Orientalia, or contributions to a knowledge of the Hymenoptera of the Oriental zoological realm. Part 5. Memoirs and Proceedings of the Manchester Literary and Philosophical Society 41 (4): 1–144, +2 pls.

Cameron, P. 1901. On the Hymenoptera collected during the "Skeat Expedition" to the Malay Peninsula, 1899–1900. Proceedings of the Zoological Society of London 2 (1): 16–44.

Cameron, P. 1908. On some Bornean species of *Trigona* (Apidae). Entomologist 41 (543): 192–195.

Cockerell, T.D.A. 1911. The bees of the Solomon Islands. Proceedings of the Linnean Society of New South Wales 36 (1): 160–178.

Cockerell, T.D.A. 1912. Descriptions and records of bees – XLII. Annals and Magazine of Natural History (8) 9 (50): 220–229.

Cockerell, T.D.A. 1918. Descriptions and records of bees – LXXX. Annals and Magazine of Natural History (9) 2 (10): 384–390.

Cockerell, T.D.A. 1919a. Descriptions and records of bees – LXXXV. Annals and Magazine of Natural History (9) 3 (15): 240–250.

Cockerell, T.D.A. 1919b. The social bees of the Philippine Islands. Philippine Journal of Science 14 (1): 77–81.

Cockerell, T.D.A. 1920. Descriptions and records of bees – LXXXVIII. Annals and Magazine of Natural History (9) 5 (25): 113–119.

Cockerell, T.D.A. 1925. Descriptions and records of bees – CIV. Annals and Magazine of Natural History (9) 15 (88): 489–496.

Cockerell, T.D.A. 1926. Descriptions and records of bees – CXII. Annals and Magazine of Natural History (9) 18 (104): 216–227.

Cockerell, T.D.A. 1929a. Bees in the Queensland Museum. Memoirs of the Queensland Museum 9 (111): 298–323.

Cockerell, T.D.A. 1929b. Bees from the Australian region. American Museum Novitates 346: 1–18.

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

Franck, P., E. Cameron, G. Good, J.-Y. Rasplus, and 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. 1898. Die *Trigona*-Arten Australiens. Természetrajzi Füzetek 21 (3–4): 427–431.

Friese, H. 1908 [1909]. Hymenoptera II. Apidae. *In* A. Wichmann (editor), Nova Guinea. Résultats de l'expédition scientifique Néerlandaise à la Nouvelle-Guinée en 1903, vol. 5: Zoologie [Lieferung 3]: 353–359, +1 pl. [pl. xv]. Leiden: Brill, v + 651 pp., +28 pls.

Friese, H. 1918. Wissenschaftliche Ergebnisse einer Forschungsreise nach Ostindien, ausgeführt im Auftrage der Kgl. Preuß Akademie der Wissenschaften zu Berlin von H. v. Buttel-Reepen. VII. Bienen aus Sumatra, Java, Malakka und Ceylon. Gesammelt von Herrn Prof. Dr. v. Buttel-Reepen

in den Jahren 1911–1912. Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere 41 (5): 489–520.

Friese, H. 1925. Neue neotropischen Bienenarten, zugleich II. Nachtrag zur Bienenfauna von Costa Rica (Hym.). Stettiner Entomologische Zeitung 86 (2): 1–41.

Friese, H. 1933. Eine neue *Trigona* von Sumatra (Hymenoptera, Apidae). Natuurhistorisch Maandblad 22 (12): 147.

Gribodo, G. 1893. Note imenotterologische. Nota II. Nuovi generi e nuove specie di imenotteri antofili ed osservazioni sopra alcune specie già conosciute. Bollettino della Societ*à* Entomologica Italiana 25: 248–287.

Horne, C., and F. Smith. 1870. Notes on the habits of some hymenopterous insects from the north-west provinces of India, with an appendix containing descriptions of some new species of Apidae and Vespidae collected by Mr. Horne. Transactions of the Zoological Society of London 7 (3): 161–196, +2 pls. [pls. xix–xxii].

Karunaratne, W.A.I.P., J.P. Edirisinghe, and M.S. Engel. 2017. First record of a tear-drinking stingless bee *Lisotrigona cacciae* (Nurse) (Hymenoptera: Apidae: Meliponini), from the central hills of Sri Lanka. Journal of the National Science Foundation of Sri Lanka 45 (1): 79–81.

Michener, C.D. 1990. Classification of the Apidae (Hymenoptera). University of Kansas Science Bulletin 54 (4): 75–163.

Michener, C.D. 2000. The bees of the world. Baltimore: Johns Hopkins University Press, xiv + [i] + 913 pp., +16 pls.

Michener, C.D. 2007. The bees of the world, 2nd ed. Baltimore: Johns Hopkins University Press, xvi + [i] + 953 pp., +20 pls.

Michener, C.D. 2013. The Meliponini. *In* P. Vit, S.R.M. Pedro, and D.W. Roubik (editors), Pot-honey: a legacy of stingless bees: 3–17. Berlin: Springer Verlag, xxviii + 654 pp.

Michener, C.D., and S. Boongird. 2004. A new species of *Trigona* from peninsular Thailand (Hymenoptera: Apidae: Meliponini). Journal of the Kansas Entomological Society 77 (2): 143–146.

Moure, J.S. 1951. Notas sôbre Meliponinae (Hymenopt. – Apoidea). Dusenia 2 (1): 25–70, +1 pl. [pl. ii].

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

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

Rasmussen, C., and S.A. Cameron. 2007. A molecular phylogeny of the Old World stingless bees (Hymenoptera: Apidae: Meliponini) and the non-monophyly of the large genus *Trigona*. Systematic Entomology 32 (1): 26–39.

Rasmussen, C., and 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., and C.D. Michener. 2010. The identity and neotype of *Trigona laeviceps* Smith (Hymenoptera: Apidae). Journal of the Kansas Entomological Society 83 (2): 129–133.

Sakagami, S.F. 1975. Stingless bees (excl. *Tetragonula*) from the continental Southeast Asia in the collection of Berince [sic] P. Bishop Museum, Honolulu (Hymenoptera, Apidae). Journal of the Faculty of Science, Hokkaido University, Series 6, Zoology 20 (1): 49–76.

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 6, Zoology 21 (2): 165–247, +1 pl. [pl. v].

Sakagami, S.F., and T. Inoue. 1985. Taxonomic notes on three bicolorous *Tetragonula* stingless bees in Southeast Asia. Kontyû 53 (1): 174–189.

Schwarz, H.F. 1937. Results of the Oxford University Sarawak (Borneo) expedition: Bornean stingless bees of the genus *Trigona*. Bulletin of the American Museum of Natural History 73 (3): 281–328, +6 pls. [pls. ii–vii].

Schwarz, H.F. 1939. The Indo-Malayan species of *Trigona*. Bulletin of the American Museum of Natural History 76 (3): 83–141.

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.

Smith, F. 1854. Catalogue of hymenopterous insects in the collection of the British Museum. Part II. Apidae. London: British Museum, 199–465 pp., +6 pls. [pls. vii–xii].

Smith, F. 1857. Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A.R. Wallace. Journal of the Proceedings of the Linnean Society, Zoology 2 (6): 42–88, +2 pls.

Walker, F. 1860. Characters of some apparently undescribed Ceylon insects. Annals and Magazine of Natural History (3) 5 (28): 304–311.

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

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

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