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Notes on Papuan and Malesian stingless bees, with the descriptions of new taxa (Hymenoptera: Apidae)

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Abstract. Two new species of the stingless bee genus *Heterotrigona* Schwarz (Apinae: Meliponini) are described and figured from Papua New Guinea: *Heterotrigona (Sahulotrigona) tricholoma* Engel, new species, lighter individuals of which superficially resemble the larger *H. (Platytrigona) lamingtonia* (Cockerell) and *H. (P.) keyensis* (Friese), and *H. (S.) taraxis* Engel, new species, a taxon generally misidentified as “*Trigona atricornis* Smith”. The western Malesian (Borneo) species *H. hobbyi* (Schwarz) is removed to *Borneotrigona* Engel, new subgenus, and distinguished from the otherwise eastern *Platytrigona* Moure, which occur in eastern Wallacea (east of Weber’s line) and Papuasias. The historically misidentified *T. atricornis* is a senior synonym of *T. genalis* Friese (**new synonymy**), the latter type species for the genus *Papuatrigona* Michener & Sakagami, resulting in the following nomenclatural change: *Papuatrigona atricornis* (Smith), **new combination**. *Flavotetragonula* Shanas is placed as a new synonym of *Tetragonula* Moure *s.str.* (**new synonymy**).

INTRODUCTION

The Malesian and Papuan (*sensu* Brummitt, 2001) faunas of stingless bees harbor the greatest number of species and genera for the Old World Meliponini, albeit still a mere shadow of the diversity that resides within the New World tropics (Michener, 2007, 2013; Kahono *et al.*, 2018). While this fauna is remarkably rich, there are vast gaps in our knowledge of the species, with inadequate information on their distributions, particularly across the various island groups of Wallacea (although Sulawesi is far better sampled than others), and throughout New Guinea and the Bismarck Archipelago. Most of the genera and subgenera are of manageable sizes, and aids to their iden-

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tification have greatly improved. Nonetheless, thorny problems persist among the genus *Tetragonula* Moure, the most species-rich of the genera and where distinctions among species can be notoriously subtle, sometimes better recognized by their diagnostically different nesting biologies than obvious morphological traits (e.g., Sakagami *et al.*, 1983; Sakagami & Inoue, 1985). A key to the Papuasian genera and subgenera of stingless bees was provided by Engel & Rasmussen (2017), while a general key to the Indomalayan-Australasian genera was provided by Rasmussen *et al.* (2017) and Engel *et al.* (2018).

Herein I provide various taxonomic notes on species of the genus *Heterotrigona* Schwarz, the second largest genus of Asiatic Meliponini. Two new species are described in the subgenus *Sahulotrigona* Engel & Rasmussen, one of which had been historically misidentified as *Trigona atricornis* Smith. Examination of the holotype of *T. atricornis* reveals that it is, in actuality, a senior synonym of *Papuatrigona genalis* (Friese). In addition, *Heterotrigona hobbyi* (Schwarz), traditionally placed in the subgenus *Platytrigona* Moure, is closer in many respects to the subgenus *Heterotrigona s.str.* and is here newly removed to its own subgenus. As circumscribed herein, the subgenera *Sahulotrigona* and *Platytrigona* are restricted to Papuaasia (Table 1) and Wallacea east of Weber's line, while *Heterotrigona s.str.*, *Sundatrigona* Inoue & Sakagami, and the new subgenus are restricted to Malesia, but west of Weber's line. A new key is provided to the subgenera of *Heterotrigona*, as are tentative keys to the species of *Sahulotrigona* and *Platytrigona*. Wallacea, representing an important critical area of biogeographic transition, and Papuaasia are in need of considerable further sampling to better refine our understanding of the diversity and potential role of the region's complex historical geography in the diversification of their resident bee faunas.

MATERIAL AND METHODS

Morphological terminology generally follows Engel (2001) and Michener (2007), while the format for the description follows that of Engel & Rasmussen (2017). Standard telegraphic symbols are used for sexes and castes (Rasmussen *et al.*, 2017); e.g., the symbol ♀ meaning the sterile worker caste. Measurements were made using an ocular micrometer on an Olympus SZX-12 stereomicroscope, and are provided for the holotype with the range from the entire type series in parentheses. Microphotographs were taken with a Canon 7D digital camera, and processed in Adobe Photoshop. Material discussed herein is largely in the Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas (SEMC), or the Division of Invertebrate Zoology, American Museum of Natural History, New York, New York (AMNH).

SYSTEMATICS

Genus *Heterotrigona* Schwarz

Subgenus *Sahulotrigona* Engel & Rasmussen

Sahulotrigona includes generally smaller bees relative to *Platytrigona* (forewing lengths 5.4–6.0 mm in the former, over 7.0 mm in the latter), as well as species with a largely glabrous basal area to the metasoma (versus entirely or largely pubescent in *Platytrigona*). Like *Platytrigona*, species of *Sahulotrigona* lack the stiff, thickened, erect, black bristles so prominent on the mesoscutum and mesoscutellum of *Heterotrigona s.str.* and the new subgenus described below (*vide infra*). Such bristles are shorter and

Table 1. Updated checklist of stingless bees (Meliponini) from Papuaasia (updated from Engel & Rasmussen, 2017).

Genus *Austroplebeia* Moure, 1961
Austroplebeia cincta (Mocsáry in Friese, 1898)

Genus *Heterotrigona* Schwarz, 1939
 Subgenus *Platytrigona* Moure, 1961
Heterotrigona (Platytrigona) flaviventris (Friese, 1908 [1909])
Heterotrigona (Platytrigona) keyensis (Friese, 1901)
Heterotrigona (Platytrigona) lamingtonia (Cockerell, 1929)
Heterotrigona (Platytrigona) planifrons (Smith, 1865)

Subgenus *Sahulotrigona* Engel & Rasmussen, 2017
Heterotrigona (Sahulotrigona) paradisaea Engel & Rasmussen, 2017
Heterotrigona (Sahulotrigona) taraxis, **n. sp.**
Heterotrigona (Sahulotrigona) tricholoma, **n. sp.**

Genus *Papuatrigona* Michener & Sakagami, 1990
Papuatrigona atricornis (Smith, 1865), **n. comb.**

Genus *Tetragonula* Moure, 1961
 Subgenus *Tetragonula* Moure, 1961*
Tetragonula (Tetragonula) biroi (Friese, 1898)
Tetragonula (Tetragonula) clypearis (Friese, 1909)
Tetragonula (Tetragonula) sapiens (Cockerell, 1911)

* Note that the recently and injudiciously proposed *Flavotetragonula* Shanas (Shanas & Faseeh, 2019) is a **new junior synonym** of *Tetragonula* Moure *s.str.*, and some of the purported new species established therein are likely synonyms.

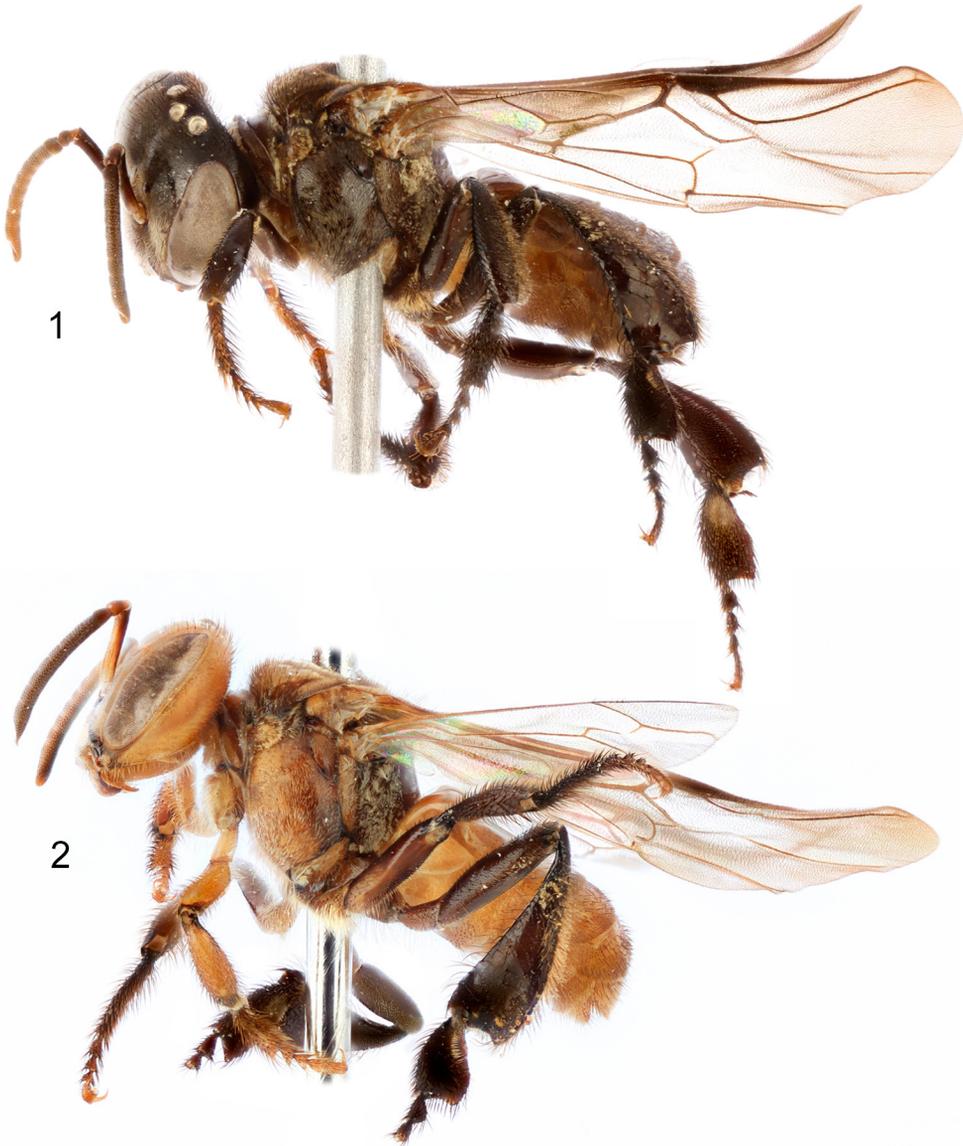
sparser but also present in *Sundatrigona*, particularly on the mesoscutellum. Three species are currently recognized in *Sahulotrigona*: *H. (S.) paradisaea* Engel & Rasmussen, *H. (S.) tricholoma* n. sp., and *H. (S.) taraxis* n. sp. (= "*Trigona atricornis*" *auctororum*). The subgenus is presently known only from New Guinea.

***Heterotrigona (Sahulotrigona) tricholoma* Engel, new species**

ZooBank: urn:lsid:zoobank.org:act:28942BD5-85F6-4EFA-9B80-4D959CA6E2FA
 (Figs. 1–7)

DIAGNOSIS: The new species can be distinguished from other *Sahulotrigona* by the presence of a distinctive fringe of minute, erect, plumose setae along the posterior border and extending along the lateral borders to the level of the tangent between the anterior margins of the tegulae (Fig. 7). In addition, the species is overall lighter in coloration, particularly the metasoma which is brown to almost yellowish brown, with more distinctive chestnut brown on the apical margins (giving the metasoma more of a banded appearance than in other *Sahulotrigona*) (*e.g.*, Figs. 3, 4). There is considerable variation in coloration, with individuals ranging from a dark morph to a lighter morph (Figs. 1–6), but aside from color all other aspects of their morphology and setation, particularly the presence of the mesoscutal fringe, are identical.

DESCRIPTION: ♀: Total body length approximately 5.13 mm (5.0–5.2 mm), forewing length (including tegula) 5.4 mm (5.3–5.5 mm). Head wider than long, width 1.88 mm (1.83–1.92 mm), length 1.60 mm (1.56–1.65 mm); compound eye length 1.28 mm (1.23–1.28) mm; upper interorbital distance 1.21 mm (1.10–1.21 mm), lower interorbital distance 1.15 mm (1.08–1.15 mm). Scape length 0.73 mm (0.69–0.73 mm), slightly shorter than torulocellar distance, torulocellar distance 0.76 mm (0.73–0.76 mm); flagellomeres about as long as wide except apical flagellomere longer than wide. Clypeus broader



Figures 1–2. Lateral habitus of workers of *Heterotrigona (Sahulotrigona) tricholoma*, new species, from Papua New Guinea. 1. Dark morph. 2. Light morph.

than long, approximately 2.1× as wide as long, length 0.46 mm (0.44–0.46 mm), width 0.96 mm (0.92–0.96 mm). Malar area short, length approximately subequal to flagellar diameter or 0.5× basal mandibular width. Intertegular distance 1.20 mm (1.20–1.33 mm). Hind wing with 7 distal hamuli (6–8 in *H. paradisaea*, 6 in *H. taraxis*, *vide infra*).

Integument generally dark brown to light chestnut brown or yellowish brown, except labiomaxillary complex yellow-brown, and darker reddish brown on mid and hind legs beyond trochanters; face with clypeus, supraclypeal area, and patches on lower face light brown to yellowish brown in darker individuals, face more extensively yellowish brown in lighter individuals with brown to back demarcating sulci and light chestnut brown patches on frons; mesosoma dark brown to light chestnut brown



Figures 3–6. Workers of *Heterotrigona* (*Sahulotrigona*) *tricholoma*, new species, from Papua New Guinea. 3. Dorsal habitus of dark morph. 4. Facial view of dark morph. 5. Dorsal habitus of light morph. 6. Facial view of light morph.

in lighter individuals, except with mesoscutellum (except axilla), metanotum, and propodeum dark brown; wing veins dark brown to brown, nebulous traces brown, membrane hyaline and clear except faint tinge apically; metasoma light brown to yellowish brown, with apical margins chestnut brown and giving banded appearance.

Integument largely smooth and shining, with exceedingly minute punctures at bases of setae but otherwise impunctate. Metasomal terga smooth, shining, and largely impunctate, faintly imbricate and more punctate in narrow apical zones owing to bases of minute, appressed, apically directed setae; sterna faintly imbricate, without impunctate apical margins.



Figure 7. Dorsal-posterior oblique view of mesosoma of worker of *Heterotrigona (Sahulotrigona) tricholoma*, new species, showing (arrow) distinctive plumose fimbria bordering the lateral and posterior margins of the mesoscutum.

Pubescence generally white to dark fuscous or black. Face with numerous fine, minute, appressed, silvery white, simple setae not obscuring integument; setae of upper frons gradually becoming more erect and in ocellar area intermingled with short, erect, simple setae, such erect, setae predominate on vertex; gena with setae as on face; postgena with long, erect, white, simple setae; scape with minute to short (shorter than diameter of scape), white, simple setae. Mesosomal dorsum with fine, minute, erect, light fuscous, simple setae intermixed with longer, erect, fuscous, simple setae, such longer setae sparser than minute setae, longer fuscous setae more numerous and elongate on mesoscutellum; mesoscutum with fringe of minute, erect, plumose setae along posterior border and lateral borders but not extending anterior of tangent between anterior margins of tegulae; metanotum with abundant, fine, minute, white setae; pleura with abundant, minute to short, subappressed, white, plumose setae, intermixed with longer, erect, simple, white setae, such setae becoming longer ventrally; basal area of propodeum glabrous except for sparse, apicolateral patches of fine, white setae, such setae with a few branches. Setae of legs white to dark fuscous. Metasoma with discs largely glabrous, with minute, suberect, simple, light fuscous setae laterally, such setae becoming progressively more present, albeit still sparse, over discs of fifth and sixth terga; apical margins with minute, simple, setae appressed vibrissae in narrow apical zones of second through fifth terga; longer, erect to suberect, simple, dark fuscous setae scattered laterally fifth and sixth tergum; fifth tergum with appressed to subappressed, minute, simple setae of apical zone extending more extensively posteriorly in apical portion of disc; sixth tergum with more extensive, suberect to subappressed,



Figures 8–9. Worker holotype of *Heterotrigona (Sahulotrigona) taraxis*, new species, from Papua New Guinea. 8. Lateral habitus. 9. Facial view.

white setae intermixed with other more erect setae. Sterna with long, erect, simple, white setae on discs and extending to apical margins.

♀: *Latet.*

♂: *Latet.*

HOLOTYPE: ♀, PNG [Papua New Guinea]: Chimbu Prov., Wara Sera Research Sta., Crater Mtn. Conserv. Area, 6–10 Oct 2000, A.S. & M.F. Whiting (AMNH).

Paratypes: 2♀♀, same data as holotype (AMNH).

ETYMOLOGY: The specific epithet is taken from the Greek words, *trichós* (τριχός), meaning “hair”, and *lôma* (λώμα), meaning, “border” or “fringe”, and is a reference to the fringe of setae bordering the mesoscutum posterolaterally.

COMMENTS: It is interesting to note that many stingless bees in New Guinea seem to include a range of coloration that at the lighter end of the spectrum encompasses a pattern of largely testaceous or aurantius individuals with darker middle and hind legs, and with similar facial patterning [aside from the current species, others include *H. lamingtonia* (Cockerell), *vide infra*; *H. keyensis* (Friese), and *P. atricornis* (Smith), *vide infra*]. Whether this is some kind of mimicry complex remains to be explored.

***Heterotrigona (Sahulotrigona) taraxis* Engel, new species**

ZooBank: urn:lsid:zoobank.org:act:14F27D4D-D8B9-4C39-AC58-D3B6B520DA40

(Figs. 8–9)

“*Trigona atricornis*” (Smith), *auctorum*.

DIAGNOSIS: This species is most similar to *H. paradisaea*, both of which lack the fringe of mesoscutal setae present in *H. tricholoma* (*vide supra*). *Heterotrigona taraxis* can be distinguished from *H. paradisaea* by the lighter integumental coloration which is dark chestnut brown (rather than black to dark brown in the latter species) (Figs. 8, 9), and the less abundant setation of the fifth metasomal tergum.

DESCRIPTION: ♀: Total body length approximately 5.1 mm, forewing length (including tegula) 5.5 mm. Head wider than long, width 1.96 mm, length 1.53 mm; compound eye length 1.23 mm; upper interorbital distance 1.26 mm, lower interorbital distance

1.16 mm. Scape length 0.70 mm, slightly shorter than torulocellar distance, torulocellar distance 0.73 mm; flagellomeres about as long as wide except apical flagellomere longer than wide. Clypeus broader than long, approximately 1.7× as wide as long, length 0.47 mm, width 0.80 mm. Malar area short, length approximately subequal to flagellar diameter. Intertegular distance 1.26 mm. Hind wing with 6 distal hamuli.

Integument generally dark chestnut brown (Figs. 8, 9), narrow apical marginal zones of terga lighter and semitranslucent; wing veins brown, lighter posteriorly, nebulous traces brown, membrane hyaline and clear albeit faintly around apex of marginal cell.

Integument mostly smooth and shining, with exceedingly minute punctures at bases of setae but otherwise impunctate. Metasomal terga smooth and largely impunctate except sparse punctures at bases of setae, minutely punctured in narrow apical zones owing to bases of minute, appressed, apically directed setae; sterna faintly imbricate, with weak nodulae at bases of setae on discs, narrow apical zones impunctate and glabrous.

Pubescence generally white to black and coppery. Face with numerous minute, silvery white setae, those on clypeus largely appressed to subappressed and simple, those on face more plumose and subappressed, but not obscuring integument; setae of upper frons gradually becoming finer, more erect, dark fuscous to nearly black and mostly simple, gradually intermingled with longer, erect, simple, black setae; such erect, black setae predominate on vertex; gena with fine, erect to appressed, minute, simple, white to coppery setae; postgena with erect, elongate, fine, simple setae; scape with minute to short (shorter than diameter of scape), fuscous, simple setae. Mesosomal dorsum with erect, dark fuscous to black setae (Fig. 8) and fine, minute, plumose, coppery setae, longer erect setae sparser on mesoscutum, particularly on centrally, more abundant and elongate on mesoscutellum; metanotum with abundant, fine, short, simple, white setae; basal area of propodeum glabrous except for diffuse, apicolateral patches of fine, white, largely simple setae. Pleura with abundant, minute, white, branched setae, intermingled anteriorly and ventrally with short to elongate, erect, simple, white setae; such plumose setae of metepisternum and propodeal lateral surface nearly obscuring integument. Setae of legs coppery to black. Metasoma with discs largely glabrous, with minute, suberect, simple, coppery to fuscous setae laterally, such setae becoming progressively more present, albeit still sparse, over discs of third through fifth terga; such setae forming appressed, diffuse vibrissae in narrow apical zones of second through fifth terga; longer, erect to suberect, simple, fuscous to black setae scattered laterally on fourth tergum, scattered over disc of fifth tergum, and abundant across sixth tergum; fifth tergum with appressed to subappressed, minute, simple setae of apical zone extending more extensively posteriorly in disc; sixth tergum with numerous, erect to suberect, short, branched, coppery setae. Sterna with long, erect, simple, coppery setae on discs, such setae paler on more basal sterna.

♀: *Latet.*

♂: *Latet.*

HOLOTYPE: ♀, New Guinea (NE) [Papua New Guinea, Northeast], Boana Mission [on the slope of Mt. Bangeta, a.k.a. Mt. Sarawaket], Huon Pen. [Huon Peninsula, Morobe Province], 900 m, ix-4-5-1959 [4-5 September 1959] // E.J. Ford, Jr., collector (SEMC).

ETYMOLOGY: The specific epithet is taken from the Greek, *taraxis* (τάραξις), meaning, "confusion", and is a reference to the historical confusion regarding the identity of this species.

COMMENTS: This species has been long confused as “*Trigona atricornis* Smith”, as most authors have relied on historical material identified as this species in collections (e.g., Michener & Sakagami, 1990; Engel & Rasmussen, 2017). A recent examination of the holotype of *T. atricornis* in the Oxford University Museum of Natural History reveals that Smith’s (1865) species in actuality belongs to the genus *Papuatrigona* Michener & Sakagami wherein it is a senior synonym of *T. genalis* Friese (*vide infra*). It appears as though Friese (1898, 1909, 1915) was the first to misidentify this species, and it seems that all subsequent authors have followed his concept based on material he identified.

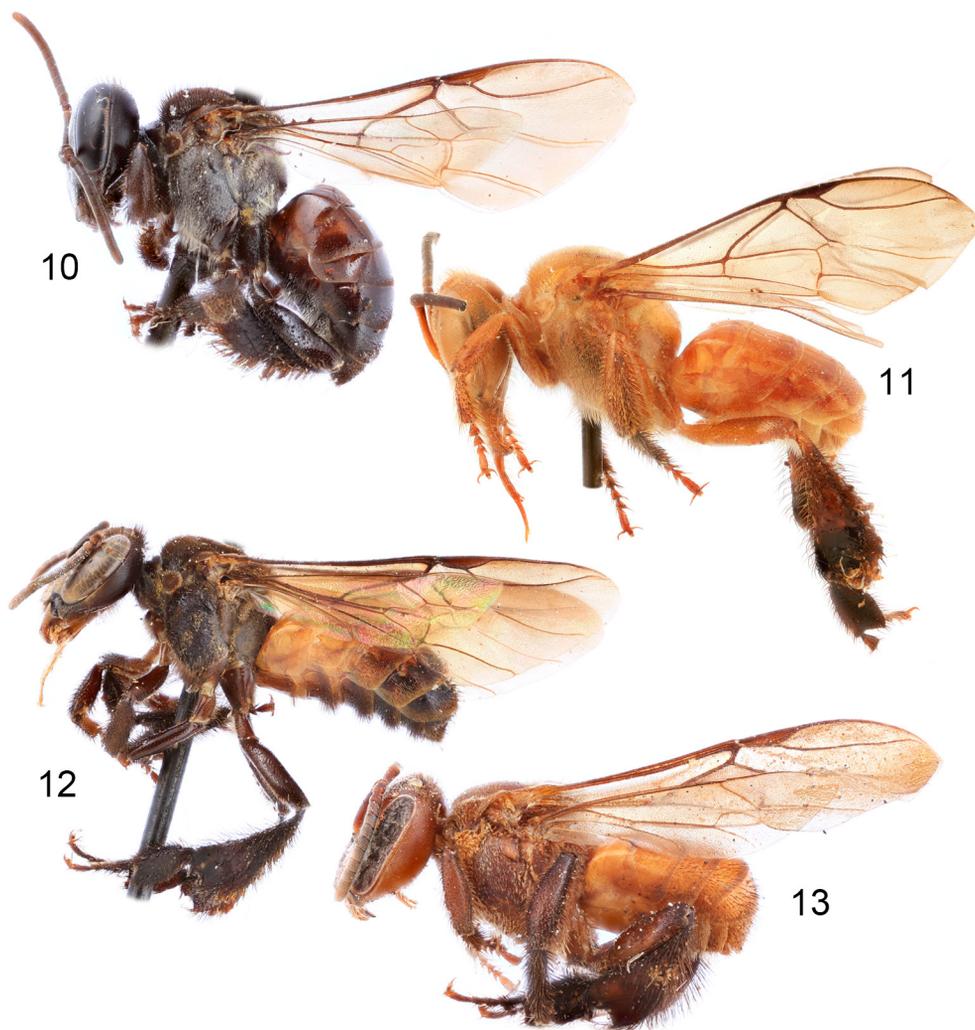
Tentative Key to Species of *Sahulotrigona*
(worker caste)

1. Mesoscutum without distinct fringe of short, erect, plumose setae along posterior and lateral borders to level of tangent between anterior margins of tegulae 2
- Mesoscutum with distinct fringe of short, erect, plumose setae along posterior and lateral borders to level of tangent between anterior margins of tegulae (Fig. 7) *H. (S.) tricholoma*, n. sp.
- 2(1). Integument black to dark brown; disc of tergum V with abundant erect to suberect setae *H. (S.) paradisaea* Engel & Rasmussen
- Integument chestnut brown; disc of tergum V with scattered erect to suberect setae *H. (S.) taraxis*, n. sp.

Subgenus *Platytrigona* Moure

The subgenus *Platytrigona* includes larger bees, with forewing lengths over 7 mm (Figs. 10–13), and therefore can be easily separated from the smaller bees of the subgenera *Sahulotrigona* and *Sundatrigona*. The species of the subgenus are also distinctive for the pubescence of the basal area of the propodeum (Figs. 22, 23, 32) (pubescent also in the new subgenus described herein), and absence of stout, thick, black bristles on the vertex, mesoscutum, and mesoscutellum (present in *Heterotrigona s.str.*, *Sundatrigona*, and the new subgenus described herein). Lastly, the posterior glabrate zone of the inner surface of the metatibia is narrower than the broad keirotrichiate zone, which differs from the condition of the new subgenus described below (*vide infra*), and the basal vein (1M) of the forewing is confluent or slightly distad 1cu-a (Figs. 18–21) (rather than basad in the new subgenus). *Platytrigona* as so narrowly circumscribed [*i.e.*, with *H. hobbyi* (Schwarz) removed to a separate subgenus], is likely related to *Sahulotrigona* as evidenced by the male genitalia (Michener, 1990: his “*T. atricornis*” actually being *H. taraxis*), while *Heterotrigona s.str.*, *Sundatrigona*, and the new subgenus (*vide infra*) likely form a reciprocal clade, each lineage diversifying on either side of Weber’s line. Clarification of this matter and the precise biogeographic boundaries of these lineages awaits surveys of the various archipelagos comprising the Moluccas, particularly from Seram to Buru, the Obi and Sulu Islands, and from Tanimbar across the Barat Daya Islands, Babar Islands, Sermata Islands, and Leti Islands toward Timor along with the eastern islands of the Lesser Sundas.

Platytrigona includes four species, with rather varied coloration (Figs. 10–17), all of which are found in New Guinea and Kei Archipelago of the southeastern Moluccas: *H. (P.) planifrons* (Smith), *H. (P.) lamingtonia*, *H. (P.) flaviventris* (Friese), and *H. (P.) keyensis*.



Figures 10–13. Lateral habitus of workers of species of subgenus *Platytrigona* Moure. **10.** *Heterotrigona* (*Platytrigona*) *planifrons* (Smith). **11.** *H. (P.) keyensis* (Friese). **12.** *H. (P.) flaviventris* (Friese). **13.** Paratype of *H. (P.) lamingtonia* (Cockerell).

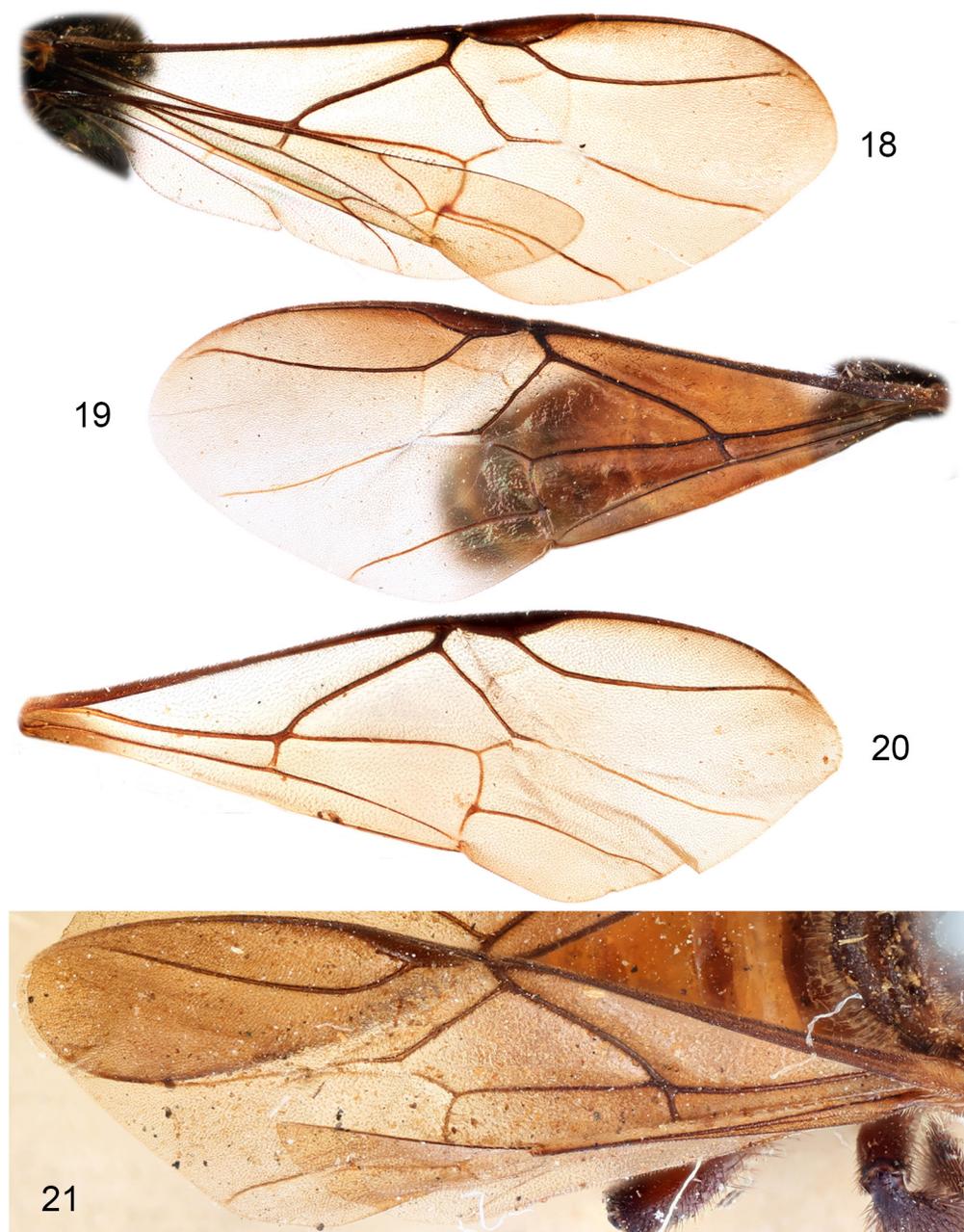
Heterotrigona (*Platytrigona*) *planifrons* (Smith)
(Figs. 10, 15, 18, 22)

RECORDS: INDONESIA: Papua Province: Central Mamberamo Regency: 1♀, West New Guinea [Indonesia: Papua Province], Central Mts., Archbold Lake [Central Mamberamo Regency, near 3°40'33''S 138°54'09''E], 760 m, 26.xi–3.xii.1961 [26 November–3 December 1961] // L.W. Quate, collector (SEMC). **PAPUA NEW GUINEA: Western Province:** 4♀♀, [Papua New Guinea], [Western Province] Palmer R. [River], at Black R. [River] [McGregor Junction where the Palmer River (= Wok Luap River) meets the Black River, near 5°45'23''S 141°42'34''E: *vide* Karius, 1929], Papua, June 7–14, 1936, Archbold Exped. [Archbold Expedition] (SEMC); **Morobe Province:** 1♀, New Guinea [Papua New Guinea], (NE), Bulolo [Morobe Province: Bulolo District], 1010 m, Aug.



Figures 14–17. Facial views of workers of species of subgenus *Platytrigona* Moure. **14.** Paratype of *Heterotrigona (Platytrigona) lamingtonia* (Cockerell). **15.** *H. (P.) planifrons* (Smith). **16.** *H. (P.) flaviventris* (Friese). **17.** *H. (P.) keyensis* (Friese).

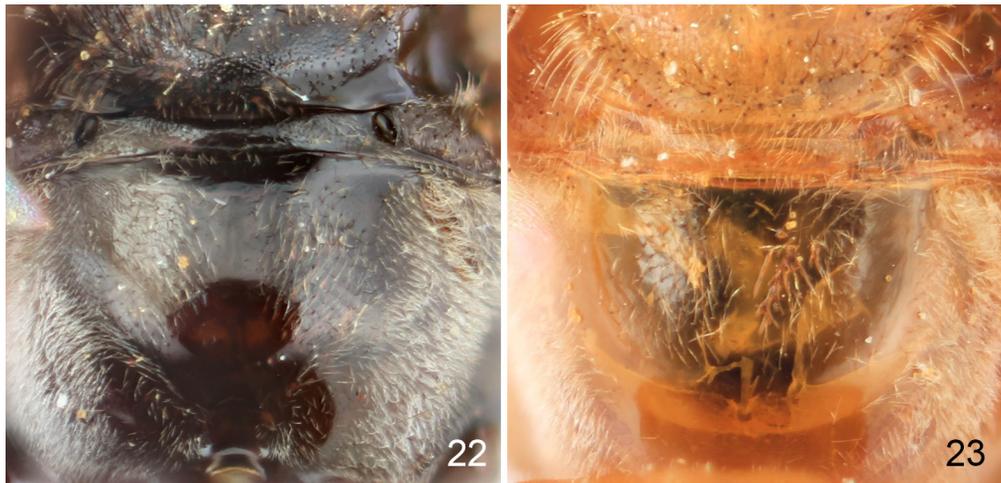
25, 1956 // R.J. Ford, Jr., collector (SEMC); 1♀, New Guinea [Papua New Guinea], (NE), Mosom [Morobe Province], Salawakot Range, 750 m, Sept. 20, 1956 // E.J. Ford, Jr., collector (SEMC); **Oro Province:** 1♀, Mt. Lamington, Northern Division [Oro Province], Papua, v.1927 [May 1927], C.T. McNamara (SEMC).



Figures 18–21. Forewings species of subgenus *Platytrigona* Moure. 18. *Heterotrigona* (*Platytrigona*) *planifrons* (Smith). 19. *H. (P.) flaviventris* (Friese). 20. *H. (P.) keyensis* (Friese). 21. Paratype of *H. (P.) lamingtonia* (Cockerell).

Heterotrigona (*Platytrigona*) *flaviventris* (Friese)
(Figs. 12, 16, 19)

RECORDS: **INDONESIA:** 2♀♀, Dasay, 150 m, Irian Jaya, 28.iii.1973 [28 March 1973] (SEMC). **Papua Province: Central Mamberamo Regency:** 1♀, West New Guinea [Pap-



Figures 22–23. Propodeal basal areas of representative species of *Platytrigona* Moure. **22.** *Heterotrigona* (*Platytrigona*) *planifrons* (Smith). **23.** *H.* (*P.*) *keyensis* (Friese).

ua New Guinea], Central Mts., Mulik R. [River], 10km E of Archbold Lake [Central Mamberamo Regency, near 3°39'41" S 138°59'47" E], 1050 m, 25.xi, 3–5.xii, '61 [25 November, 3–5 December 1961] // S. Quate & L. Quate, collectors (SEMC); **Paniai Regency:** 1♀, Euarotali [sic: Enarotali: Papua Province: Paniai Regency], 1760 m, Irian Jaya, 8.v.1973 [8 May 1973] (SEMC); 1♀, Madi, 1700 m, Euarotali [sic: Enaratoli: Papua Province: Paniai Regency], Irian Jaya, 8.v.1973 [8 May 1973] (SEMC).

Heterotrigona (*Platytrigona*) *keyensis* (Friese)
(Figs. 11, 17, 20, 23, 24–28)

NEW RECORDS: PAPUA NEW GUINEA: East Sepik Province: 2♀♀, Neuguinea [Papua New Guinea], Hunstein-Gebirge, Wagu [northern slopes of mountain range, East Sepik Province] / Black River, 3.10.1972 [3 October 1972], Hohmann (SEMC); 1♂, Neuguinea [Papua New Guinea], Hunstein-Gebirge, Wagu [northern slopes of mountain range, East Sepik Province] / Black River, 23.2.1973 [23 February 1973], Hohmann (SEMC).

COMMENTS: The Hunstein Mountains and a Wagu are within the April Salome Forest Management Area of East Sepik Province. The historically recognized “Black River” does not pass through East Sepik Province, but the name “black river” has been generally applied to many different sections of small offshoots of main rivers where the waters are particularly dark. Thus, it must be presumed that the “Black River” referred to in the above localities is some local reference and not to be confused with the historical usage of Black River for the tributary to the Wok Luap River (= Palmer River) that joins at McGregor Junction and is otherwise west of the Strickland River and south of the Kaban Range (e.g., Karius, 1929).

Since the male of *H. keyensis* has not been previously figured, pertinent images are included herein (Figs. 24–28). Unfortunately, the available male is not in good condition and had been dissected at some point in the past, with the terminalia glued to a card pinned beneath the specimen. A heavy dose of glue was used such that it overlays portions of structures and in the case of the eighth sternum has rendered it exceedingly difficult to interpret. One gonostylus is broken apically, and the apodemes and proximal border of the seventh sternum are distorted and partially damaged (Figs. 27, 28).

Heterotrigona (Platytrigona) lamingtonia (Cockerell)
(Figs. 13, 14, 21, 29–33)

NEW RECORDS: **PAPUA NEW GUINEA: Oro Province:** 2♀♀, Neuguinea [New Guinea], Lejo, 15 km WNW-Popondetta [Oro Province], 16.7.1973 [16 July 1973], Hohmann (SEMC).

COMMENTS: Included are images from a paratype of *H. lamingtonia* (Figs. 13, 14, 21), as well as of workers collected from a nearby locality to the north of Mount Lamington, perhaps no more than 25 km from where the type series was collected. These individuals are less faded and agree in all details with the type series except in more extensive lighter coloration on the head, pleura, and wing venation (cf. Figs. 13, 14, 21 vs. 29–33). Both of these color forms have identical structural details and both possess the erect to suberect black setae on the apical metasomal terga that help to distinguish this species from *H. keyensis*.

Tentative Key to Species of *Platytrigona*
(worker caste)

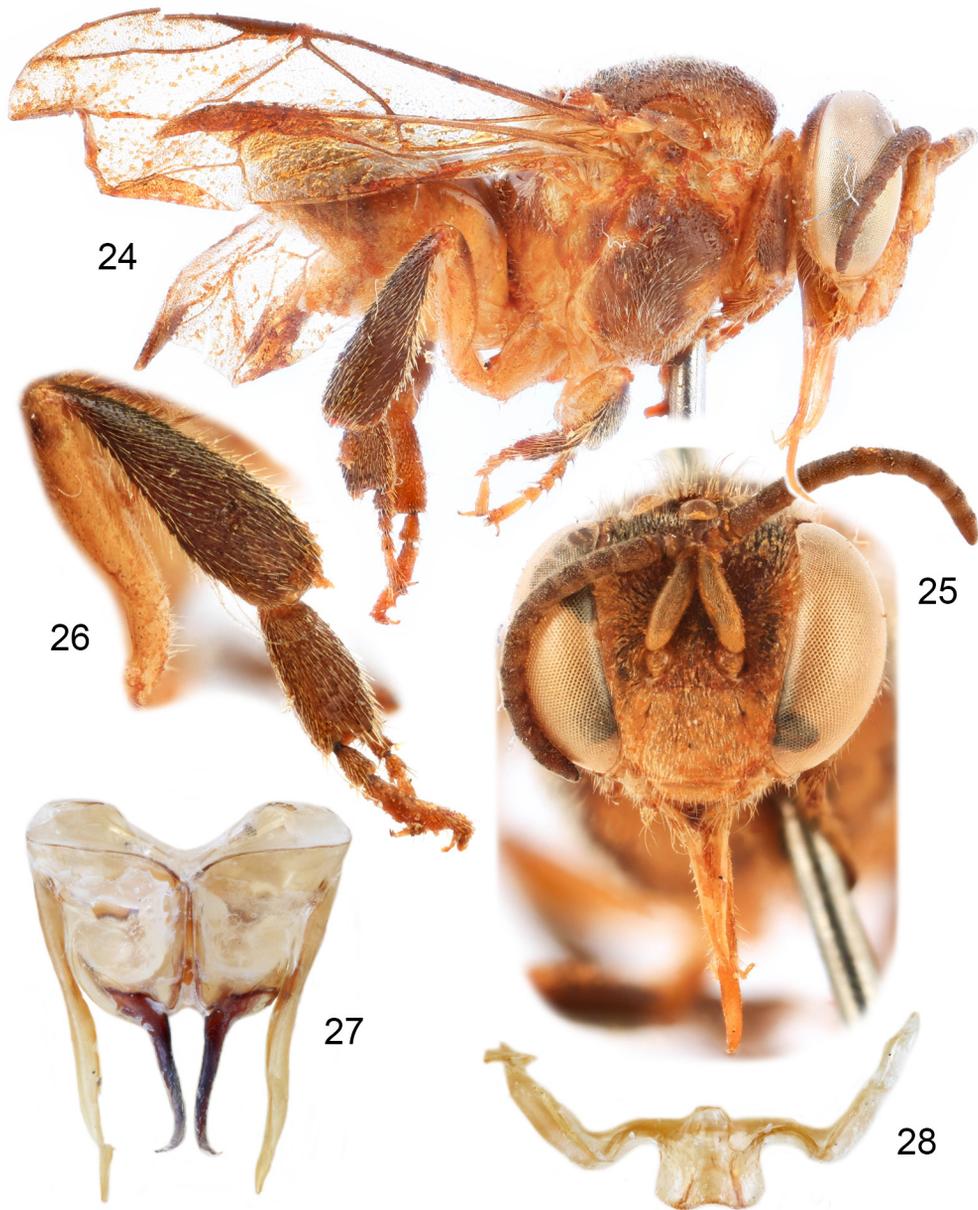
1. Integument of head and mesosoma variable, that of metasoma largely testaceous, aurantius, or light ferruginous (sometimes with apical terga and sterna darkened) (Figs. 11–13); intertorular distance about as wide as torular diameter 2
- Integument, including metasoma, wholly black (or dark brown in older, faded specimens) (Figs. 10, 15); intertorular distance narrower than torular diameter *H. (P.) planifrons* (Smith)
- 2(1). Metasoma entirely testaceous, aurantius, and/or light ferruginous (Figs. 11, 13, 29, 30); head and mesosoma largely testaceous, aurantius, and/or light ferruginous (Figs. 17, 31), sometimes with darker ferruginous areas or black around facial sulci and malar space (Fig. 31), legs variable but meso- and metatibiae and tarsi dark brown to black with noticeable ferruginous oval spot on inner surface of metatibia (difficult to see in older faded specimens) 3
- Basal metasomal terga and sterna testaceous, aurantius, or light ferruginous, contrasting with apical segments dark reddish brown to black (Fig. 12); mesosoma and legs black (without ferruginous spot on inner surface of metatibia), head largely black with some testaceous areas on face (Fig. 16) *H. (P.) flaviventris* (Friese)
- 3(2). Apical metasomal terga with scattered, erect to suberect, black setae (Figs. 29, 30); malar space as long as diameter of flagellomere
..... *H. (P.) lamingtonia* (Cockerell)
- Apical metasomal terga with scattered, erect to suberect, ferruginous setae (Fig. 11); malar space slightly shorter than diameter of flagellomere
..... *H. (P.) keyensis* (Friese)

Borneotrigona Engel, new subgenus

ZooBank: urn:lsid:zoobank.org:act:1278AC40-63E7-410A-A79E-B9B719375A1B

TYPE SPECIES: *Trigona hobbyi* Schwarz, 1937.

DIAGNOSIS: *Heterotrigona hobbyi* has long been recognized to be an outlier among *Platytrigona* and its combination of traits were used by some authors to highlight the lack of distinction between *Platytrigona* and other groups of Malesian and Papuanian



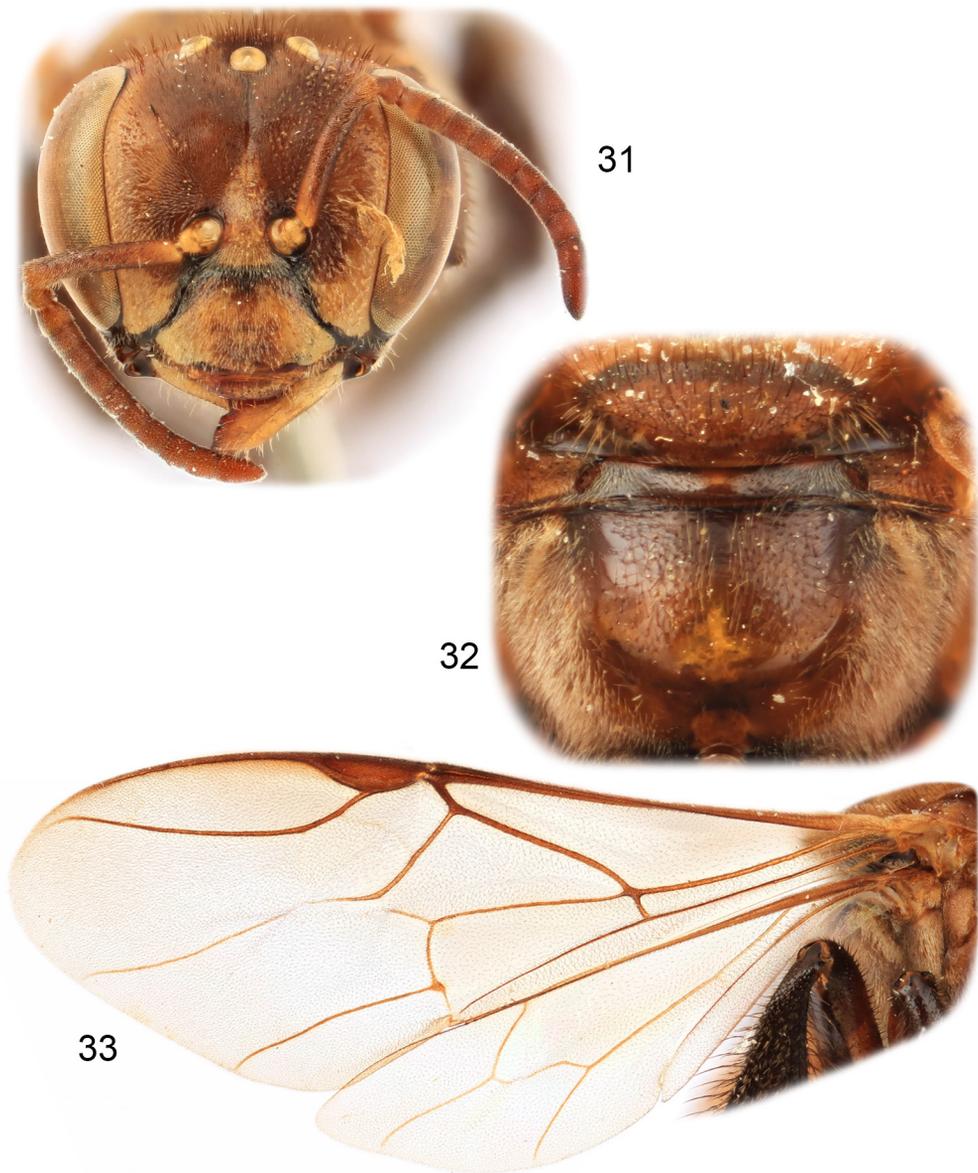
Figures 24–28. Male of *Heterotrigona (Platytrigona) keyensis* (Friese). 24. Lateral habitus. 25. Facial view. 26. Outer surface of metatibia and metatarsus. 27. Genital capsule. 28. Seventh sternum.

Meliponini (e.g., Michener, 1990). However, it seems clear that *H. hobbyi* has simply been misplaced. Like *Platytrigona*, these are larger bees relative to *Sahulotrigona* and *Sundatrigona*. The subgenus is similar to *Platytrigona* in the pubescent basal area of the propodeum, albeit with a slightly broader mediolongitudinal glabrous line (Fig. 37), but the similarity ends there (*Heterotrigona* and *Sundatrigona* lack such pubescence, while *Sahulotrigona* is largely glabrous except small apicolateral patches of wispy setae) (Sakagami & Inoue, 1987; Inoue & Sakagami, 1993; Engel & Rasmussen, 2017). Unlike *Platytrigona*, *Borneotrigona* has distinct erect, stiff, thickened, black, simple bris-



Figures 29–30. Worker of *Heterotrigona (Platytrigona) lamingtonia* (Cockerell). 29. Lateral habitus. 30. Dorsal habitus.

tles (Figs. 34–36) on the head, legs, and most abundantly on the mesosoma, particularly on the mesoscutum and mesoscutellum (Fig. 37). The presence of the thickened bristles in *Borneotrigona* is similar to those of *Heterotrigona s.str.* and *Sundatrigona* (albeit such bristles are sparser in the last subgenus), and it may be that these groups are related. In addition, the posterior glabrate zone of the inner surface of the metatibia is broader than the keitrichiate zone in *Borneotrigona* (Figs. 39, 40), while the situation is reversed in *Platytrigona*. In *Borneotrigona* the posterior distal angle is subangulate (Figs. 38–40), rather than more angulate in *Platytrigona*. In the forewing, the basal vein



Figures 31–33. Details of worker of *Heterotrigona* (*Platytrigona*) *lamingtonia* (Cockerell). 31. Facial view. 32. Basal area of propodeum. 33. Wing venation.

(1M) is distinctly basad 1cu-a and the wing strongly bicolorous in *Borneotrigona* (Fig. 41), while it is instead confluent or slightly postfurcal and more uniformly colored in *Platytrigona* (Figs. 18–21).

DESCRIPTION: Workers of moderate size, forewing length (including tegula) approximately 7.3–7.8 mm; integument black, shiny, smooth, with scattered microscopic punctures; integumental maculation absent (Figs. 34–36); setae largely black to dark fuscous except with fine, minute, dark coppery to dark greyish plumose pubescence intermingled on face and mesosoma; erect, stiff, thickened, black, simple bristles on uppermost face, vertex, mesosoma and legs.

Head slightly broader than mesosoma, with face distinctly broader than compound eye length (Fig. 36); vertex short, rounded; ocellocipital distance slightly greater than one ocellar diameter; interocellar distance approximately $2.0\times$ ocellar diameter; ocellular distance $2.0\times$ ocellar diameter; scape slightly longer than torulocellar distance; first flagellomere shorter than second flagellomere, second and third flagellomeres equal in length; second through tenth flagellomeres each slightly longer than wide; intertorular distance approximately $0.5\times$ torulorbital distance; upper torular tangent near facial midlength; frontal line weakly impressed, not carinate, extending from median ocellus to near midpoint of toruli; inner orbit of compound eye weakly concave in upper third; gena about as broad as compound eye in profile, posterior border rounded; malar area of moderate length, slightly longer than flagellar diameter, approximately $1.5\times$ flagellar diameter (Fig. 36); labrum weakly convex, short, much wider than long, apical margin medially blunt; mandible bidentate, teeth well defined and incised (as in most other *Heterotrígona s.l.*), incision between first and second preapical teeth slightly nearly orthogonal; first and second labial palpomeres with several elongate, apically wavy but simple setae (as in most other *Heterotrígona s.l.*).

Mesoscutum with median sulcus weakly impressed; notauli scarcely evident; parapsidal lines short, about as long as ocellar diameter, and weakly impressed. Mesoscutellum short, ending at profile of metanotum and not distinctly overhanging propodeum, rounded, slightly swollen in profile, with shining transverse depression along mesoscuto-mesoscutellar sulcus. Propodeum long and sloping (strongly declivitous), with distinct angle between basal area and posterior surface, dorsal-facing basal surface about as long as posterior surface; basal area smooth, shining, pubescent except mediolongitudinal glabrous area (Fig. 37), glabrous area slightly wider than medial length of metanotum and much narrower than pubescent areas (Fig. 37); propodeal spiracle elongate, approximately $4.5\times$ as long as wide.

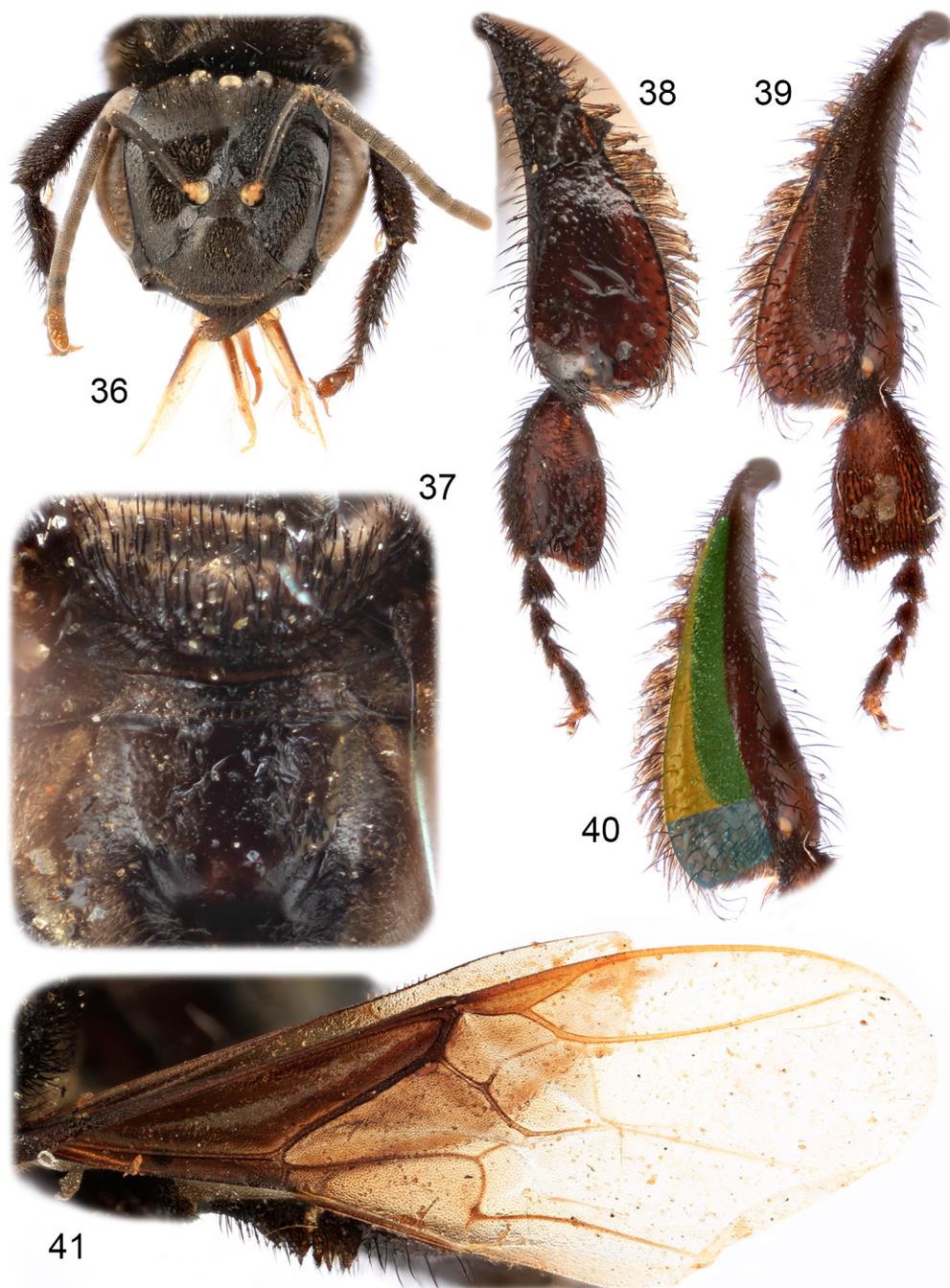
Forewing extending well beyond apex of metasoma, with 2Rs, 1rs-m, 1m-cu, apical half 3M, 4M, apical third 1Cu β , 2Cu, 3Cu, and 2cu-a indicated by brownish nebulous traces (Fig. 41); fenestrae demarcated by faint white spectral lines on infuscate-clear wing membrane; membrane in costal, radial, first cubital cells and anal area bordering cells darkly infumate, slightly less infumate beyond 1M and 1cu-a and blending to clear by tangent with pterostigmal apex, thus wing membrane strongly bicolorous (proximally dark, apically clear); prestigma exceptionally short, less than anterior width of 1Rs; pterostigma slender; marginal cell slightly more than four times as long as maximum breadth, separated from wing apex by slightly less than its maximum width, with apex broadly open, opening about one-third maximum marginal cell width, with nebulous, angled, appendiculate apex to 4Rs, without nebulous 2r-rs; 1M basad 1cu-a, thus short 2M+Cu present, shorter than 1cu-a; submarginal angle (*i.e.*, anterior angle between 1Rs and Rs+M) approximately 101° ; M obtusely angled at 1m-cu (*i.e.*, angle between 2M and 3M); 3M tubular in basal half, then nebulous; 2Rs with short basal nebulous stub, otherwise weakly nebulous, angulate; 1rs-m faintly nebulous, straight; r-rs distinctly longer than 3Rs. Hind wing with 8 distal hamuli; radial and cubital cells closed by nebulous veins.

Metatibia approximately $2.75\times$ as long as greatest width, elongate subtriangular (Fig. 38); posterior margin gently recurved with subangulate distal angle (Figs. 38–40) (angulate in *Platytrígona*), setae along posterior margin and upper outer surface mostly plumose; outer surface weakly concave apically, with corbicula occupying apical third; apical margin transverse; inner surface with narrow, elevated keirotrichiate zone and broad posterior subglabrous zone, with abrupt clivulus; keirotrichiate zone narrower



Figures 34–35. Worker of *Heterotrigona (Borneotrigona) hobbyi* (Schwarz). 34. Lateral habitus. 35. Dorsal habitus.

than posterior glabrate zone (Figs. 39, 40) (broader than in *Platytrigona*), width of keirotrichiate zone in the subapical region (wider portion) distinctly less than length of apical glabrate zone (Figs. 39, 40); penicillus and rastellar comb present, each composed of stiff setae. Metabasitarsus weakly trapezoidal, with posterior margin gently



Figures 36–41. Details of worker of *Heterotrigona* (*Borneotrigona*) *hobbyi* (Schwarz). 36. Facial view. 37. Mesoscutellum, metanotum, and basal area of propodeum. 38. Outer surface of metatibia and metatarsus. 39. Inner surface of metatibia and metatarsus. 40. Inner surface of metatibia and metatarsus with major zones colored (using color scheme of Engel & Rasmussen, 2017; Rasmussen *et al.*, 2017): yellow = posterior glabrate zone, green = keirotrichiate zone, blue = apical glabrate zone. 41. Forewing.

arched, distal angle not projecting (Figs. 38, 39); outer surface with fine basal posterior fimbriate line bordering depression (Fig. 38) (present in all *Heterotrigona* s.l. and several Asiatic genera, but lacking in nearly all New World lineages with some exceptions such as *Oxytrigona* Cockerell); inner surface with short basal sericeous area (Fig. 39).

Metasoma narrow, terga largely smooth and shining, with scattered appressed, minute, apically directed setae, intermingled with erect to suberect short black setae apically on tergum IV and more extensively on terga V and VI; postgradular surfaces of terga V and VI with short, erect to suberect, fuscous plumose setae.

ETYMOLOGY: The new subgeneric name is a combination of Borneo, the island from which the group is known, and *Trigona* Jurine. The gender of the name is feminine.

INCLUDED SPECIES: The subgenus presently includes only the type species, *H. (Borneotrigona) hobbyi* from northern Borneo [Brunei and Malaysia (Sarawak and Sabah)].

COMMENTS: One hypothesis, mentioned above under *Platytrigona*, is that *Borneotrigona*, *Heterotrigona* s.str., and *Sundatrigona* form a clade alongside another composed of *Platytrigona* and *Sahulotrigona*. Another possibility to be explored is that *Borneotrigona* is the sister group to a *Platytrigona* + *Sahulotrigona* clade as evidenced by the propodeal setation. Under such a scenario, the stout bristles of *Borneotrigona*, *Heterotrigona* s.str., and *Sundatrigona* would potentially be plesiomorphic for the genus, and subsequently lost in the Papuasian subgenera. To date, definitive species of *Platytrigona* and *Sahulotrigona* have not been included in phylogenetic estimates so these hypotheses await testing by either morphological, behavioral, molecular, or, ideally, combinations of these data.

Revised Key to Subgenera of *Heterotrigona*
(modified from Engel & Rasmussen, 2017)

1. Basal area of propodeum largely or entirely glabrous, at most with apico-lateral patches of setae (if patches present, then medial, broad glabrous area much wider than setal patches and occupying majority of propodeal basal surface) 2
- Basal area of propodeum entirely pubescent or with a narrow medial glabrous area (Figs. 22, 23, 32, 37) (glabrous area distinctly narrower than lateral setose areas, frequently width approximately equivalent to medial length of metanotum) 3
- 2(1). Basal vein (1M) basad 1cu-a (Fig. 41); wings strongly bicolorous, proximal portion (darkly infumate in costal, radial, and first cubital cells) contrasting with clear apical portion (Figs. 34, 35, 41); mesoscutum and mesoscutellum (Fig. 37) with abundant, erect, thick, stiff black bristles (similar to those of *Heterotrigona* s.str.); posterior glabrate zone of metatibial inner surface apically broader than keirotrichiate zone (Fig. 40) [Brunei, Malaysia (Sarawak, Sabah)] *Borneotrigona*, n. subgen.
- Basal vein (1M) confluent with or slightly distad 1cu-a (Figs. 18–21); wings not bicolorous, proximal half generally similar in color to apical half (Figs. 10–13, 18–21); mesoscutum and mesoscutellum without such erect, stiff, black bristles (some species may have fuscous setae but never the thickened, stiff bristles); posterior glabrate zone of metatibial inner surface apically narrower than keirotrichiate zone [Indonesia (West Papua, Moluccas), Papua New Guinea] *Platytrigona* Moure

- 3(1). Basal vein (1M) basad 1cu-a; basal area of propodeum glabrous, without small, wispy apicolateral patches of setae 4
 —. Basal vein (1M) distad 1cu-a; basal area of propodeum largely glabrous but with small, wispy, apicolateral patches of setae [Indonesia (Papua), Papua New Guinea] *Sahulotrigona* Engel & Rasmussen
- 4(3). Posterior glabrate zone of metatibial inner surface apically broader than keirotrichiate zone; larger bees, forewing length greater than 6 mm forewing length [Thailand, Singapore, Philippines, 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; smaller bees, forewing length less than 6 mm [Singapore, Malaysia (West Malaysia, Sarawak), Indonesia (Sumatra)] *Sundatrigona* Inoue & Sakagami

Genus *Papuatrigona* Michener & Sakagami

Trigona (*Papuatrigona*) Michener & Sakagami, 1990: 153. Type species: *Trigona genalis* Friese, 1908 [1909] (= *Trigona atricornis* Smith, 1865), by original designation and monotypy.

Papuatrigona atricornis (Smith), **new combination**
 (Figs. 42–44)

Trigona atricornis Smith, 1865: 94. Holotype ♀, Oxford: New Guinea (*visum*).

Trigona genalis Friese, 1908 [1909]: 354. Lectotype ♀, Berlin: Manikion (*visum*). **New synonymy.**

Trigona (*Tetragona*) *atricornis* Smith; Michener, 1965: 231.

Trigona (*Heterotrigona*) *atricornis* Smith; Michener, 1990: 127.

Trigona (*Papuatrigona*) *genalis* Friese; Michener & Sakagami, 1990: 154.

Papuatrigona genalis (Friese); Rasmussen, 2008: 24.

Platytrigona "*atricornis*" (Smith); Rasmussen, 2008: 26 [misidentification].

Heterotrigona (*Sahulotrigona*) "*atricornis*" (Smith); Engel & Rasmussen, 2017: 11 [misidentification].

COMMENTS: Quite unexpectedly, a recent examination of the holotype of *T. atricornis* (Fig. 42) preserved in the Oxford University Museum of Natural History reveals its identity as *Papuatrigona*. Of particular note, aside from the overall coloration (Figs. 42, 43), are the long malar space (Fig. 44); the exceptionally narrow posterior glabrate zone and low, sloping clivulus on the inner surface of the metatibia (Fig. 42); the largely simple setae along the posterior border of the metatibia (Fig. 42); and the lack of a basal sericeous area on the inner basal surface of the metabasitarsus (Fig. 42). These features are all indicative of *Papuatrigona* among the Indomalayan fauna, and the holotype is indistinguishable from that of *T. genalis*. Accordingly, the name "*atricornis*" is hereby transferred to *Papuatrigona* where it replaces that of *P. genalis* for the type species. The "*T. atricornis*" of authors is actually *H. taraxis*, described above (*vide supra*), and this confusion appears to have originated with the accounts of Friese (1898, 1909, 1915) who seems to have misidentified *T. atricornis* and thereby failed to recognize that this species and his *T. genalis* were one and the same.



Figures 42–44. Worker holotype of *Papuatrigona atricornis* (Smith), new combination (photographs provided by and reproduced with permission of James Hogan, Oxford University Museum of Natural History). 42. Lateral habitus. 43. Dorsal habitus. 44. Facial view.

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REFERENCES

- Brummitt, R.K. 2001. *World Geographical Scheme for Recording Plant Distributions* [2nd Edition]. Hunt Institute for Botanical Documentation; Pittsburgh, PA; xv+137 pp.
- 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. 1929. Bees in the Australian Museum collection. *Records of the Australian Museum* 17(5): 199–243.
- 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.
- Engel, M.S., & C. Rasmussen. 2017. A new subgenus of *Heterotrigona* from New Guinea (Hymenoptera: Apidae). *Journal of Melittology* 73: 1–16.
- Engel, M.S., S. Kahono, & D. Peggie. 2018. A key to the genera and subgenera of stingless bees in Indonesia (Hymenoptera: Apidae). *Treubia* 45: 65–84.
- Friese, H. 1898. Die *Trigona*-Arten Australiens. *Természetrájszi Füzetek* 21(3–4): 427–431.
- Friese, H. 1901. Neue Arten der Bienengattung *Trigona* Jur. (Hym.). *Zeitschrift für systematische Hymenopterologie und Dipterologie* 1(5): 265–271.
- Friese, H. 1908 [1909]. Hymenoptera II. Apidae. In: Wichmann, A. (Ed.), *Nova Guinea. Résultats de l'expédition scientifique Néerlandaise à la Nouvelle-Guinée en 1903. Vol. V. Zoologie* [Lieferung 3]: 353–359, +1 pl. [pl. xv]. Brill; Leiden, The Netherlands; v+651 pp., +28 pls.
- Friese, H. 1909. Die Bienenfauna von Neu-Guinea. *Annales Historico-Naturales Musei Nationalis Hungarici* 7: 179–288.
- Friese, H. 1915. Apiden aus Nord-Neu-Guinea gesammelt von Dr. P.N. van Kampen und K. Gjellerup, in den Jahren 1910 und 1911. *Tijdschrift voor Entomologie* 58(1–2): 1–4.
- Inoue, T., & S.F. Sakagami. 1993. A new name of *Trigona* (Hymenoptera, Apidae). *Japanese Journal of Entomology* 61(4): 769.
- Kahono, S., P. Chantawannakul, & M.S. Engel. 2018. Social bees and the current status of beekeeping in Indonesia. In: Chantawannakul, P., G. Williams, & P. Neumann (Eds.), *Asian Beekeeping in the 21st Century*: 287–306. Springer Singapore; Singapore; viii+325 pp.
- Karius, C.H. 1929. Exploration in the interior of Papua and North-East New Guinea: The sources of the Fly, Palmer, Strickland, and Sepik Rivers. *Geographical Journal* 74(4): 305–320, +4 pls., +1 map.
- Michener, C.D. 1965. A classification of the bees of the Australian and South Pacific regions. *Bulletin of the American Museum of Natural History* 130: 1–362, +15 pls.
- Michener, C.D. 1990. Classification of the Apidae (Hymenoptera). *University of Kansas Science Bulletin* 54(4): 75–163.
- Michener, C.D. 2007. *The Bees of the World* [2nd Edition]. Johns Hopkins University Press; Baltimore, MD; xvi+[i]+953 pp., +20 pls.
- Michener, C.D. 2013. The Meliponini. In: Vit, P., S.R.M. Pedro, & D.W. Roubik (Eds.), *Pot-Honey: A Legacy of Stingless Bees*: 3–17. Springer Verlag; Berlin, Germany; xxviii+654 pp.

- Michener, C.C. [sic: D.], & S.F. Sakagami. 1990. Appendix: *Trigona genalis* Friese, a hitherto unplaced New Guinea species. *University of Kansas Science Bulletin* 54(4): 153–157.
- Moure, J.S. 1961. A preliminary supra-specific classification of the Old World meliponine bees (Hymenoptera, Apoidea). *Studia Entomologica* 4(1–4): 181–242.
- Nagamitsu, T., & T. Inoue. 2005. Floral resource utilization by stingless bees (Apidae, Meliponini). In: Roubik, D.W., S. Sakai, & A.A. Hamid (Eds.), *Pollination Ecology and the Rain Forest: Sarawak Studies: 73–88*. Springer Science; New York, NY; xvii+307 pp.
- Rasmussen, C. 2008. Catalog of the Indo-Malayan/Australasian stingless bees (Hymenoptera: Apidae: Meliponini). *Zootaxa* 1935: 1–80.
- Rasmussen, C., J.C. Thomas, & M.S. Engel. 2017. A new genus of Eastern Hemisphere stingless bees (Hymenoptera: Apidae), with a key to the supraspecific groups of Indomalayan and Australasian Meliponini. *American Museum Novitates* 3888: 1–33.
- Roubik, D.W. 1996. Wild bees of Brunei Darussalam. In: Edwards, D.S., W.E. Booth, & S.C. Choy (Eds.), *Tropical Rainforest Research – Current Issues: Proceedings of the Conference held in Bandar Seri Begawan, April 1993: 59–66*. Kluwer Academic Publishers; Dordrecht, The Netherlands; x+566 pp.
- Sakagami, S.F., & T. Inoue. 1985. Taxonomic notes on three bicolorous *Tetragonula* stingless bees in Southeast Asia. *Kontyû* 53(1): 174–189.
- Sakagami, S.F., & T. Inoue. 1987. Stingless bees of the genus *Trigona* (subgenus *Trigonella*) with notes on the reduction of spatha in male genitalia of the subgenus *Tetragonula* (Hymenoptera, Apidae). *Kontyû* 55(4): 610–627.
- Sakagami, S.F., S. Yamane, & G.G. Hambali. 1983. Nests of some Southeast Asian stingless bees. *Bulletin of the Faculty of Education, Ibaraki University (Natural Sciences)* 1983(32): 1–21.
- Sakagami, S.F., T. Inoue, & S. Salmah. 1985. Key to the stingless bee species found or expected from Sumatra. In: Ohgushi, R. (Ed.), *Evolutionary Ecology of Insects in Humid Tropics, especially in Central Sumatra: 37–43*. Kanazawa University; Kanazawa, Japan; [iii]+65 pp., +2 pls.
- Sakagami, S.F., T. Inoue, & S. Salmah. 1990. Stingless bees of central Sumatra. In: Sakagami, S.F., R. Ohgushi, & D.W. Roubik (Eds.), *Natural History of Social Wasps and Bees in Equatorial Sumatra: 125–137*. Hokkaido University Press; Sapporo, Japan; xi+274 pp., +8 pls.
- 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.
- Shanas, S., & P. Faseeh. 2019. A new subgenus and three new species of stingless bees (Hymenoptera: Apidae: Apinae: Meliponini) from India. *Entomon* 44(1): 33–48.
- Smith, F. 1865. Descriptions of new species of hymenopterous insects from the islands of Sumatra, Sula, Gilolo, Salwatty, and New Guinea, collected by Mr. A.R. Wallace. *Journal of the Proceedings of the Linnean Society, Zoology* 8(30): 61–94, +1 pl. [pl. iv].



Journal of Melittology

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

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