

A new subgenus of *Heterotrigona* from New Guinea (Hymenoptera: Apidae)Michael S. Engel<sup>1,2</sup> & Claus Rasmussen<sup>3</sup>

<sup>1</sup> Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045, USA (msengel@ku.edu).

<sup>2</sup> Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79<sup>th</sup> Street, New York, New York 10024-5192, USA.

<sup>3</sup> Department of Bioscience, Aarhus University, Ole Worms Allé 1, DK-8000 Aarhus, Denmark (alrunen@yahoo.com).

**Abstract.** A new subgenus is established within the Indomalayan stingless bee genus *Heterotrigona* Schwarz (Meliponini). *Sahulotrigona* Engel & Rasmussen, new subgenus, is distinguished from amongst other *Heterotrigona*, particularly the subgenus *Platytrigona* Moure, within which one of the two included species was previously placed. The subgenus presently includes two species from New Guinea: *Heterotrigona (Sahulotrigona) paradisaea* Engel & Rasmussen, new species, and *H. (S.) atricornis* (Smith), **new combination**. A key to the subgenera of *Heterotrigona* is provided and the species are tabulated, resulting in the following **new combinations**: *Heterotrigona (Platytrigona) flaviventris* (Friese), *H. (P.) hobbyi* (Schwarz), *H. (P.) keyensis* (Friese), *H. (P.) lamingtonia* (Cockerell), *H. (P.) planifrons* (Smith), *H. (Sundatrigona) lieftincki* (Sakagami & Inoue), and *H. (S.) moorei* (Schwarz). The stingless bees of Papuasias are briefly summarized, and a key is presented to the genera and subgenera of Paupasias Meliponini.

## INTRODUCTION

Although depauperate compared to the New World fauna, the diversity of stingless bees (Apinae: Meliponini) occurring in the Old World are quite varied morphologically and biologically, particularly across the Indomalayan and Australasian region where most Eastern Hemisphere species reside (Michener, 2007). Historically, this diversity was classified within the genus *Trigona* Jurine, a group of otherwise exclusively Neotropical species, albeit at times within subgenera unique to the African and Asian continents (*e.g.*, Schwarz, 1939). It was not until the early 1960s that the late Padre Moure provided the initial framework for a radically reconceived classification of the Old World Meliponini, segregating at that time most of the species into genera separate from those found within the New World fauna (Moure, 1961). His system was adopted by Sakagami (1975, 1978), albeit with modifications that, for example, returned many of the Old World genera to subgeneric status under the otherwise Neotropical *Trigona*. Michener (1990, 2007) similarly advocated for a more retrograde classificatory arrangement in which these lineages were subordinate within *Trigona* and further reduced the subgenera by lumping many of Moure's genera into a few, broadly circumscribed units. During the course of phylogenetic studies on the tribe, Rasmussen & Cameron (2007, 2010) demonstrated considerable non-monophyly of *Trigona* in this broad sense and advocated for a return to the system proposed by Moure (1961), particularly in relation to the Old World diversity (*e.g.*, Rasmussen, 2008). Most recently, Rasmussen *et al.* (in rev.) have provided an update to this system, combining several of Moure's genera into more workable generic and subgeneric units, and have given a revised key to the Indomalayan and Australasian fauna. In their system, the genus *Heterotrigona* Schwarz, a group initially recognized as a subgenus of *Trigona* (Schwarz, 1939), was unified with *Platytrigona* Moure, and *Sundatrigona* Inoue & Sakagami, retaining the latter as subgenera (Rasmussen *et al.*, in rev.). However, it has been known for some time that at least two species are uneasily placed within any of the systems proposed, particularly challenging the circumscription of *Platytrigona*. The species originally described as *Trigona atricornis* Smith from eastern New Guinea was noted by the late Prof. Sakagami (in Michener, 2007) as particularly distinct among *Platytrigona* and lacking some of the defining features of this subgenus. In addition, an undescribed species (Fig. 1), also from eastern New Guinea, possessed a unique combination of traits and Sakagami had intended to establish a new subgenus, within *Trigona s.l.*, for this species (Tadauchi *et al.*, 1998: listed under the *nomen nudum Pacificotrigona*). It is unknown whether Sakagami also believed *T. atricornis* to belong within the same group as the new species, but our examination reveals both to share the same suite of traits. We provide a description of the new subgenus here, placing it within *Heterotrigona* (*contra* Sakagami), and so that the name will be available for use in the key to Indomalayan and Australasian meliponines of Rasmussen *et al.* (in rev.). The current diversity of *Heterotrigona* is summarized in Table 1.

## MATERIAL AND METHODS

Material of representative *Heterotrigona* as well as other Papuan meliponines was examined from the collections of the Division of Entomology, University of Kansas Natural History Museum, Lawrence (SEMC) and the Claus Rasmussen Collection, Aarhus University, Denmark (CRCD). For the descriptive work, we have followed the format of Rasmussen *et al.*

(in rev.), and the terminology of Engel (2001), Michener (2007), and, for venational elements and inner metatibial structures, Rasmussen *et al.* (in rev.). Microphotographs were prepared using a Canon EOS-7D digital camera with a K-2 long-distance microscope lens. In reporting material examined, we have used standard symbols to indicate sexes and castes for eusocial insects: ♀, for reproductive female (in eusocial species this is the queen caste); ♂, for reproductive male (in eusocial species this is the drone caste); ♀, for sterile female (in eusocial species this is the worker caste); ♂, for the soldier caste (not applicable to the present species but occurring in at least some *Tetragonisca* Moure: *vide* Grüter *et al.*, 2012).

## SYSTEMATICS

### Genus *Heterotrigona* Schwarz

#### *Sahulotrigona* Engel & Rasmussen, new subgenus

*Trigona* (*Pacificotrigona*) Tadauchi *et al.*, 1998: 245, *nomen nudum*.

TYPE SPECIES: *Heterotrigona* (*Sahulotrigona*) *paradisaea* Engel & Rasmussen, new species.

DIAGNOSIS: The subgenus *Sahulotrigona* is distinctive among species of *Heterotrigona* for the combination of a basal propodeal area that is largely glabrous (Fig. 5), the basal vein (1M) postfurcal (Fig. 7), and the upper glabrate zone of the metatibial inner surface narrower than the raised keirotrichiate zone (Figs. 9, 10). The subgenus includes the most easterly of the known species of *Heterotrigona* and is most similar to the subgenera *Platytrigona* and *Sundatrigona*, all three subgenera possessing a narrow glabrate zone. From the former, *Sahulotrigona* can be readily distinguished by the largely glabrous basal area of the propodeum, while both subgenera share a postfurcal basal vein (albeit in some *Platytrigona* the basal vein is confluent with 1cu-a). Species of *Platytrigona* are also larger than those of *Sahulotrigona*, the latter more closely approximate the smaller proportions of *Sundatrigona*. From the latter subgenus, *Sahulotrigona* can be distinguished by the postfurcal basal vein (antefurcal in *Sundatrigona*), longer scape which is about as long as the torulocellar distance (scape distinctly shorter than torulocellar distance in *Sundatrigona*), and the gena about as wide as compound eye in profile (gena narrower than compound eye in profile in *Sundatrigona*).

DESCRIPTION: Workers of small size, forewing length (including tegula) approximately 5.6–6.0 mm; integument shiny, smooth, with scattered microscopic punctures; integumental maculation absent (Figs. 1, 2, 4–6); fine, minute, white to off-white plumose pubescence on face and clypeus and fine, plumose pubescence on lateral surfaces of mesosoma and somewhat obscuring integument; mesoscutum and mesoscutellum with evenly distributed, abundant, minute, erect, branched, fuscous to black setae (except pale in yellow morph of *H. atricornis*), intermingled with more scattered, longer, erect, simple setae, neither of which obscure integument; metasomal terga with sparse, minute, simple setae except apical tergum with numerous, fuscous, erect, short, apically plumose setae; sterna with long, erect, simple setae.

Head as broad as mesosoma, with face slightly broader than compound eye length; vertex short, rounded; ocelloccipital distance slightly greater than one ocellar diameter; interocellar distance approximately 2.0 times ocellar diameter; ocellocular distance 2.0 times ocellar diameter; scape about as long as torulocellar distance; first flagellomere longer than second,

second and third flagellomeres equal in length; second through tenth flagellomeres each about as long as wide; intertorular distance a little more than one-half torulorbital distance; upper torular tangent near facial midlength; frontal line weakly impressed, not carinate, extending from median ocellus to near upper torular tangent; 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, about as long as flagellar diameter (Fig. 2); labrum weakly convex, short, much wider than long, apical margin medially blunt to weakly convex; mandible bidentate, teeth well defined and incised (as in other *Heterotrigona*), incision between first and second preapical teeth slightly less than orthogonal (Fig. 3); first and second labial palpomeres with several elongate, apically wavy but simple setae.

Mesoscutum with median sulcus weakly impressed, notauli scarcely evident, parapsidal lines short and weakly impressed. Mesoscutellum short, rounded (Fig. 4), slightly swollen in profile, ending at profile of metanotum and not overhanging propodeum (Fig. 6), with shining transverse depression along mesoscuto-mesoscutellar sulcus. Propodeum long and sloping, with distinct angle between basal area and posterior surface (Fig. 6), dorsal-facing surface about as long as posterior surface; basal area smooth, shining, largely glabrous except apicolateral patches of setae (but never largely pubescent as in *Platytrigona* Moure) (Fig. 5); propodeal spiracle elongate, approximately 4–4.5x as long as wide.

Forewing extending beyond apex of metasoma (Fig. 1), with 2Rs, 1rs-m, 1m-cu, apical half 3M, 4M, apical third 1Cu, 2Cu, 3Cu, and 2cu-a indicated by brownish nebulous traces (Fig. 7); fenestrae demarcated by faint white spectral lines on otherwise infusate wing membrane (lightly infusate over most of membrane, darker in apical portion of radial cell and in and around marginal cell); membrane with dark brown microtrichia; prestigma short, about twice as long as anterior width of 1Rs; pterostigma slender; marginal cell approximately four times as long as maximum breadth, separated from wing apex by slightly more than its maximum width, with apex narrowly open, opening about one-fifth maximum marginal cell width, with nebulous, angled, appendiculate apex to 4Rs and nebulous 2r-rs (absent in *H. atricornis*); 1M distad 1cu-a, thus minute M+Cu $\beta$  present, shorter than 1cu-a; submarginal angle (*i.e.*, anterior angle between 1Rs and Rs+M), nearly orthogonal; M obtusely angled at 1m-cu (*i.e.*, angle between 2M and 3M); 3M tubular in basal half, then nebulous; 2Rs weakly nebulous, angulate; 1rs-m faintly nebulous, almost spectral, straight; r-rs slightly longer than 3Rs. Hind wing with 6–7 distal hamuli (6 in *H. atricornis*, 7 in *H. paradisaea*); radial and cubital cells closed by nebulous veins.

Metatibia slightly less than three times as long as greatest width, elongate subtriangular; posterior margin gently recurved with subangulate distal angle (Figs. 8–10), setae along posterior margin and upper outer surface mostly plumose (Figs. 8–10); outer surface weakly concave apically, with corbicula occupying apical third (Fig. 8); apical margin transverse; inner surface with broad, elevated keirotrichiate zone and narrow subglabrous zone (Figs. 9, 10), with abrupt clivulus (*sensu* Rasmussen *et al.*, in rev.); keirotrichiate broader than upper glabrate zone, width of keirotrichiate zone slightly greater than length of apical glabrate zone (Fig. 9); penicillus and rastellar comb present, each composed of stiff setae. Metabasitarsus weakly trapezoidal, with posterior margin gently arched, distal angle not projecting (Figs. 8–10); outer surface with fine basal posterior fimbriate field bordering depression; inner surface with short basal sericeous area (Figs. 9, 10).

Metasoma narrow, with first metasomal tergum smooth and shining, second through fourth terga largely smooth and shining to faintly imbricate except exceedingly narrow apical

marginal zones imbricate with appressed, minute, apically directed setae; postgradular surface of sixth tergum with short, erect, fuscous plumose setae.

ETYMOLOGY: The subgeneric name is a combination of Sahul, a reference to the occurrence of the known species within a distinct zoogeographic region relative to those *Heterotrigona* occurring in Sundaland, and the generic name *Trigona* Jurine. The gender of the name is feminine.

INCLUDED SPECIES: The subgenus as currently constituted contains only two species, both from New Guinea: *Heterotrigona (Sahulotrigona) paradisaea*, new species, and *H. (S.) atricornis* (Smith).

#### Key to Subgenera of *Heterotrigona*

1. Basal area of propodeum largely or entirely glabrous, at most with apicolateral patches of setae ..... 2
- Basal area of propodeum entirely pubescent or with a small medial glabrous area [in *H. hobbyi* (Schwarz)] [Indonesia (West Papua, Moluccas), Papua New Guinea] ..... *H. (Platytrigona)* Moure
- 2(1). Basal vein (1M) basad 1cu-a ..... 3
- Basal vein (1M) distad 1cu-a [Papua New Guinea] ..... *H. (Sahulotrigona)*, n. subgen.
- 3(2). Upper glabrate zone of metatibial inner surface apically broader than keirotrichiate zone [Thailand, Singapore, Malaysia (West Malaysia, Sarawak, Sabah), Brunei, Indonesia (Java, Sumatra, Kalimantan)] ..... *H. (Heterotrigona)* Schwarz, *s.str.*
- Upper glabrate zone of metatibial inner surface apically narrower than or at most as broad as keirotrichiate zone [Singapore, Malaysia (West Malaysia, Sarawak), Indonesia (Sumatra)] ..... *H. (Sundatrigona)* Inoue & Sakagami

*Heterotrigona (Sahulotrigona) paradisaea* Engel & Rasmussen, new species  
(Figs. 1–10)

*Trigona (Pacifcotrigona) okazawai* Tadauchi *et al.*, 1998: 245, *nomen nudum*.

*Trigona (Pacifcotrigona) okazawai irianensis* Tadauchi *et al.*, 1998: 245, *nomen nudum*.

DIAGNOSIS: The new species is distinguished from its closest relative, *H. atricornis*, by its darker coloration (*cf.* Figs. 1 and 11), more pronounced pubescence on the apical terga, and seven distal hamuli on the hind wing. There are likely morphometric differences between the two species, but given the small sample sizes available we have not made an attempt to establish diagnostic differences which likely would require significant revision once series of workers become available.

DESCRIPTION: ♀: Total body length approximately 5.6–5.8 mm, forewing length (including tegula) 5.6–6.0 mm. Head wider than long, width 2.01–2.08 mm, length 1.56 mm; compound eye length 1.22–1.28 mm; upper interorbital distance 1.25–1.30 mm, lower interorbital distance 1.17–1.25 mm. Scape length 0.76–0.78 mm, about as long as torulocellar distance, torulocellar distance 0.76–0.78 mm; flagellomeres about as long as wide except apical flagellomere longer than wide. Clypeus broader than long, approximately 1.8–1.9 times as wide as long, length 0.47–0.52 mm, width 0.89–0.94 mm. Malar area short, length approximately subequal to flagellar diameter or 0.6 times basal mandibular width (Fig. 2). Mandible with two,

small preapical teeth (Fig. 3); P<sub>1</sub> with narrow incision separating apical edentate margin; incision separating P<sub>1</sub> and P<sub>2</sub> slightly less than orthogonal, with acutely rounded angular vertex.

Integument generally black to dark brown (Fig. 1), except labiomaxillary complex brown; wing veins dark brown, nebulous traces dark brown to brown, membrane infuscate more so apically in radial cell and in and around marginal cell (Fig. 7).

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

Pubescence generally white or dark fuscous to black (Figs. 1, 2, 4–6). Face with numerous minute, silvery white setae (Fig. 2), those on clypeus largely appressed to subappressed and simple except apically plumose, those on face more plumose and subappressed, but not obscuring integument; setae of upper frons gradually becoming dark fuscous to nearly black and mostly simple, gradually intermingled with longer, erect, simple, black setae; such erect, black setae predominate on vertex, particularly posterior to ocelli; gena with scattered erect to suberect, black setae; scape with minute to short (always much less than scape diameter), dark fuscous, simple setae. Mesosomal dorsum with dark fuscous to black setae (Fig. 4), except fine, minute setae of metanotum silvery white; mesoscutum and mesoscutellum with abundant, erect, minute setae with some branches, such setae not obscuring integument and intermingled with more scattered, longer, erect, simple, black setae, such longer setae more abundant on mesoscutellum than mesoscutum; basal area of propodeum glabrous except for sparse, apicolateral patches of fine, white setae, such setae with a few branches. Pleura with abundant, minute, white, branched setae, intermingled anteriorly with some erect, simple, fuscous setae; shorter setae of propodeal lateral surfaces becoming somewhat fuscous posteriorly. Setae of legs dark fuscous to black. Metasoma with discs largely glabrous, with minute, suberect, simple, fuscous setae laterally, such setae becoming progressively more present, albeit still sparse, over discs of third through fifth terga; such setae forming appressed vibrissae in narrow apical zones of second through fifth terga; longer, erect to suberect, simple, black setae scattered laterally on fourth tergum and progressively more abundant across 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 numerous, erect to suberect, short, branched, dark fuscous setae. Sterna with long, erect, simple, fuscous setae on discs.

♀: *Latet.*

♂: *Latet.*

HOLOTYPE: ♀, Neu Guinea [Papua New Guinea], Straße Wau-Mt. Kaindi, 7 km S Wau [southern Morobe Province, Momase Region, Bulolo District], 12.9.1972 [12 September 1972], Hohmann (SEMC).

PARATYPE: 1♀, Neu Guinea [Papua New Guinea], Straße Wau-Mt. Kaindi, 7 km S Wau [southern Morobe Province, Momase Region, Bulolo District], 12.9.1972 [12 September 1972], Hohmann (SEMC). It is interesting to note that Hohmann (2003) does not mention this locality in his summary of his studies on the biology of New Guinean stingless bees. This is perhaps because while he collected at the locality, he did not manage to sample nests or amass communication data from species while there.

ETYMOLOGY: The specific epithet is based on the generic name *Paradisaea* Linnaeus (Aves: Passeriformes: Paradisaeidae), the genus of the Emperor bird-of-paradise (*Paradisaea*

*guilielmi* Cabanis) which is the national emblem of Papua New Guinea. The name is meant to honor to the unique biota cultivated by the indigenous peoples of New Guinea.

*Heterotrigona (Sahulotrigona) atricornis* (Smith), **new combination**  
(Figs. 11–13)

*Trigona atricornis* Smith, 1865: 94.

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

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

*Platytrigona atricornis* (Smith); Rasmussen, 2008: 26.

DIAGNOSIS: As currently circumscribed, *H. atricornis* encompasses two color morphs (*vide* Michener & Sakagami, 1990). Some individuals, including the holotype, are of the yellowish-orange morph (Fig. 13), a color pattern generally similar to *Papuatrigona genalis* (Friese), while others are more chestnut brown in coloration (Figs. 11, 12). It remains to be tested whether or not these color morphs are truly conspecific. For now, the species can be distinguished from *H. paradisaea* by the lighter color (the above species is largely black), whether chestnut brown or yellowish orange. In addition, *H. atricornis* has the fifth and sixth terga more sparsely pubescent, the preapical teeth of the mandible less developed, and six distal hamuli on the hind wing.

MATERIAL EXAMINED: 1♀, New Guinea (NE) [Papua New Guinea], Boana Mission [near Boana, Morobe Province, Nawae District], Huon Pen. [Peninsula], 900 m, ix-4-5-1956 [4-5 September 1956], E.J. Ford, Jr. (SEMC).

## DISCUSSION

Presently, the fauna of stingless bees in Papuasias includes 11 species recorded from New Guinea (West Papua and Papua New Guinea) and the Solomon Islands (excluding the Santa Cruz Islands) (Table 2). Unfortunately, the available records are comparatively few and large swaths of the region remain to be sampled (*e.g.*, Aru Islands, Bismarck Archipelago, many individual islands across the Solomon Islands). The fauna is comparatively rich, with representatives of four distinctive genera (Table 2), but aside from further surveys the species are in need of considerable investigation. For example, males remain unknown for the species of *Sahulotrigona* and several other species and the nesting, behavioral, and floral habits of most of the Papuasian species are yet to be discovered. There are also interesting taxonomic challenges. As alluded to above, there are two rather dramatically different color morphs within *H. atricornis* as described by Michener & Sakagami (1990). It remains to be determined whether *H. atricornis* is truly a polychromatic species or if these are perhaps biologically distinct. In addition, we have seen smaller specimens superficially similar to *H. paradisaea*, likely representing additional undescribed diversity from New Guinea. With greater sampling, the phylogeny and historical biogeography of these species can be further elaborated and the connection between the Australian fauna and that of continental Southeast Asia be better understood.

In order to aid future work on the Papuasian fauna of stingless bees, we present here a brief key to the genera and subgenera of the region as it is understood to us. This key will undoubtedly require augmentation as more is known of the fauna, and the diversity becomes documented.

## Key to Genera and Subgenera of Papuan Meliponini

1. Head and mesosoma without distinct maculation; inner surface of metatibia with strong longitudinal keirotrichiate ridge above which is a broad, depressed shining marginal area ..... 2
- Mesoscutellum and usually face and mesoscutum with well-developed yellow maculation; inner surface of metatibia with keirotrichiate area broad, nearly reaching upper margin of metatibia ..... *Austroplebeia* Moure
- 2(1). Setae along upper margin of worker metatibia and some males partly plumose; clivulus bordering elevated keirotrichiate median zone of inner surface of metatibia forming abrupt slope ..... 3
- Setae along upper margin of worker metatibia and males at most plumose on apical one-fifth or one-sixth of margin; clivulus bordering keirotrichiate median zone of inner surface of metatibia forming gentle slope to shining upper glabrate zone ..... *Papuatriгона* Michener & Sakagami
- 3(2). Mesoscutellum short, not or only slightly projecting over metanotum; malar area variable, typically as long as diameter of diameter of third flagellomere or greater but sometimes approximately 0.5–0.75x diameter of third flagellomere; vein M of forewing bent at trace of 1m-cu ..... 4
- Mesoscutellum well projected posteriorly, extending over propodeum as far as posterior propodeal angle (change in slope between basal area and posterior surface); malar area linear or at least narrower than 0.5x diameter of third flagellomere; vein M of forewing straight and ending at or shortly after 1m-cu ..... *Tetragonula* Moure
- 4(3). Basal area of propodeum glabrous, at most with apicolateral patches of setae; basal vein distad 1cu-a ..... *Heterotrigona* (*Sahulotrigona*), n. subgen.
- Basal area of propodeum pubescent; basal veins either confluent with or distad 1cu-a ..... *Heterotrigona* (*Platytrigona*) Moure

## ACKNOWLEDGEMENTS

We are grateful to Jennifer C. Thomas and Kellie K. Magill Engel for assistance during the course of this work. We dedicate this small contribution to the memory of Shôichi F. Sakagami (1927–1996), who initially recognized the distinctiveness of the taxon and whose many contributions to the stingless bees of the Indomalayan and Australasian realms have served as a strong foundation for our fundamental understanding of this rich diversity. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

## REFERENCES

- 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. 1918. Descriptions and records of bees – LXXX. *Annals and Magazine of Natural History, Ninth Series* 2(10): 384–390.
- Cockerell, T.D.A. 1919a. The social bees of the Philippine Islands. *Philippine Journal of Science* 14(1): 77–81.



- Cockerell, T.D.A. 1919b. Descriptions and records of bees – LXXXV. *Annals and Magazine of Natural History, Ninth Series* 3(15): 240–250.
- Cockerell, T.D.A. 1929. Bees in the Australian Museum collection. *Records of the Australian Museum* 17(5): 199–243.
- Dollin, A.E., L.J. Dollin, & S.F. Sakagami. 1997. Australian stingless bees of the genus *Trigona* (Hymenoptera: Apidae). *Invertebrate Taxonomy* 11(6): 861–896.
- Friese, H. 1898. Die *Trigona*-Arten Australiens. *Természetráji 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.
- Grüter, C., C. Menezes, V.L. Imperatriz-Fonseca, & F.L.W. Ratnieks. 2012. A morphologically specialized soldier caste improves colony defense in a neotropical eusocial bee. *Proceedings of the National Academy of Sciences, U.S.A.* 109(4): 1182–1186.
- Hohmann, H. 2003. Zur Kommunikation stachelloser Bienen in Neuguinea. *Trigona s.l., Meliponini, Apinae, Apidae, Hymenoptera, Insecta. Tendenzen, Jahrbuch des Übersee-Museums, Bremen* 11: 9–26.
- Inoue, T., & S.F. Sakagami. 1993. A new name of *Trigona* (Hymenoptera, Apidae). *Japanese Journal of Entomology* 61(4): 769.
- 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.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.
- Rasmussen, C. 2008. Catalog of the Indo-Malayan/Australasian stingless bees (Hymenoptera: Apidae: Meliponini). *Zootaxa* 1935: 1–80.
- Rasmussen, C., & 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., & 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., J.C. Thomas, & M.S. Engel. In review. 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*
- Sakagami, S.F. 1959. Stingless bees collected by Prof. S. Matsumura from Singapore (Hymenoptera, Apidae). *Insecta Matsumurana* 22(3–4): 119–121.

- 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 VI, 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 VI, Zoology* 21(2): 165–247.
- 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.
- 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.
- 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].
- Tadauchi, O., M. Ito, J.-I. Kojima, & M.J. Toda. 1998. Species and subspecies described by the late professor Dr. Sh.F. Sakagami (Insecta: Hymenoptera). *Natural History Bulletin of Ibaraki University* 2: 229–246.

**Table 1.** Hierarchical classification of *Heterotrigona* Schwarz, *sensu* Rasmussen *et al.* (in rev.) (Meliponini).

---

Genus *Heterotrigona* Schwarz, 1939

Subgenus *Heterotrigona* Schwarz, 1939

*H. (Heterotrigona) bakeri* (Cockerell, 1919a)

*H. (Heterotrigona) erythrogastra* (Cameron, 1902)

=*Trigona luteiventris* Friese, 1908 [1909]

=*Trigona sandacana* Cockerell, 1919b

*H. (Heterotrigona) itama* (Cockerell, 1918)\*

=*Trigona breviceps* Cockerell, 1919b

Subgenus *Platytrigona* Moure, 1961

*H. (Platytrigona) flaviventris* (Friese, 1908 [1909]), n. comb.

*H. (Platytrigona) hobbyi* (Schwarz, 1937), n. comb.

*H. (Platytrigona) keyensis* (Friese, 1901), n. comb.

*H. (Platytrigona) lamingtonia* (Cockerell, 1929), n. comb.

*H. (Platytrigona) planifrons* (Smith, 1865), n. comb.

Subgenus *Sahulotrigona* Engel & Rasmussen, n. subgen.

*H. (Sahulotrigona) atricornis* (Smith, 1865)

*H. (Sahulotrigona) paradisiaea* Engel & Rasmussen, n. sp.

Subgenus *Sundatrigona* Inoue & Sakagami, 1993

*H. (Sundatrigona) lieftincki* (Sakagami & Inoue, 1987), n. comb.

*H. (Sundatrigona) moorei* (Schwarz, 1937), n. comb.

=*Trigona (Tetragona) matsumurai* Sakagami, 1959

---

**Table 2.** Checklist of stingless bees (Meliponini) from Papuaasia (from West to East: Aru Islands, New Guinea, Bismarck Archipelago, and Solomon Islands except Santa Cruz Islands).

	NG	Solo
Genus <i>Austroplebeia</i> Moure		
<i>Austroplebeia cincta</i> (Mocsáry in Friese, 1898)	+	
Genus <i>Heterotrigona</i> Schwarz		
Subgenus <i>Platytrigona</i> Moure		
<i>Heterotrigona (Platytrigona) flaviventris</i> (Friese, 1908 [1909])	+	
<i>Heterotrigona (Platytrigona) keyensis</i> (Friese, 1901)	+*	
<i>Heterotrigona (Platytrigona) lamingtonia</i> (Cockerell, 1929)	+	
<i>Heterotrigona (Platytrigona) planifrons</i> (Smith, 1865)	+	
Subgenus <i>Sahulotrigona</i> Engel & Rasmussen		
<i>Heterotrigona (Sahulotrigona) atricornis</i> (Smith, 1865)	+	
<i>Heterotrigona (Sahulotrigona) paradisaea</i> Engel & Rasmussen, n. sp.	+	
Genus <i>Papuatrigona</i> Michener & Sakagami		
<i>Papuatrigona genalis</i> (Friese, 1908 [1909])	+	
Genus <i>Tetragonula</i> Moure		
Subgenus <i>Tetragonula</i> Moure		
<i>Tetragonula (Tetragonula) biroi</i> (Friese, 1898)‡	+	
<i>Tetragonula (Tetragonula) clypearis</i> (Friese, 1909)§	+	
<i>Tetragonula (Tetragonula) sapiens</i> (Cockerell, 1911)#	+	+

\* Reported by Hohmann (2003) and confirmed by C.R.

‡ *carbonaria* species group (*vide* Dollin *et al.*, 1997).

§ *iridipennis* species group. Likely the '*Tetragonula iridipennis*' reported in the literature (*e.g.*, Hohmann, 2003).

# *laeviceps* species group. Likely the '*Tetragonula laeviceps*' reported in the literature (*e.g.*, Hohmann, 2003).

## FIGURE CAPTIONS

**Figures 1–3.** Worker of *Heterotrigona (Sahulotrigona) paradisaea*, new subgenus and species, from eastern Papua New Guinea. **1.** Lateral habitus. **2.** Facial view. **3.** Outer view of mandible.

**Figures 4–6.** Worker of *Heterotrigona (Sahulotrigona) paradisaea*, new subgenus and species, from eastern Papua New Guinea. **4.** Dorsal view of head and mesosoma. **5.** Detail of propodeum in oblique dorso-posterior view. **6.** Lateral view of mesosoma, detailing mesoscutellar profile.

**Figures 7–10.** Worker of *Heterotrigona (Sahulotrigona) paradisaea*, new subgenus and species, from eastern Papua New Guinea. **7.** Forewing. **8.** Outer view of metatibia and metatarsus. **9.** Inner view of metatibia and metatarsus with upper glabrate (yellow), apical glabrate (blue), keirotrichiate (green), and sericeous (pink) areas colored. **10.** Unmodified view of inner surface of metatibia and metatarsus.

**Figures 11–12.** Workers of *Heterotrigona (Sahulotrigona) atricornis* (Smith), from eastern Papua New Guinea. **11.** Lateral habitus of dark morph. **12.** Facial view of dark morph. **13.** Lateral habitus of yellow morph (photograph by C.R.).

1



2



3



4



5



6







