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A new subgenus of *Heterotrigona* from New Guinea (Hymenoptera: Apidae)

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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.* (*Su.*) *moorei* (Schwarz). The stingless bees of Papuasia are briefly summarized, and a key is presented to the genera and subgenera of Paupasian 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

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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 press) 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 press). 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* because it lacked 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 press). The current diversity of *Heterotrigona* is summarized in Table 1.

MATERIAL AND METHODS

Material of representative *Heterotrigona* as well as other Papuasian meliponines was examined from the collections of the Division of Entomology, University of Kansas Natural History Museum, Lawrence (SEMC); the Division of Invertebrate Zoology, American Museum of Natural History, New York (AMNH); Naturalis Biodiversity Centre, Leiden, The Netherlands (RMNH); and the Claus Rasmussen Collection, Aarhus University, Denmark (CRCD). For the descriptive work, we have followed the format of Rasmussen *et al*. (in press), and the terminology of Engel (2001), Michener (2007), and, for venational elements and inner metatibial structures, Mason (1986) and Rasmussen *et al*. (in press). We have used the abbreviation P for preapical teeth of the mandible. 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 translingual symbols to indicate sexes and castes for eusocial insects: ♀ (Venus symbol), for reproductive female (in eusocial species this is the queen caste); ♂ (Mars symbol), for reproductive male (in eusocial species this is the drone caste); ☿ (neuter symbol), for sterile female (in eusocial species this is the worker caste); ♅ (Ura-

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

nus symbol), for the soldier caste (not applicable to the present species but occurring in at least some stingless bees of the genus *Tetragonisca* Moure: *vide* Grüter *et al*., 2012).

SYSTEMATICS

Genus *Heterotrigona* Schwarz

Sahulotrigona Engel & Rasmussen, new subgenus

ZooBank: urn:lsid:zoobank.org:act:502099C0-FE8A-440B-A30B-BDE0C1AE8C9B

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

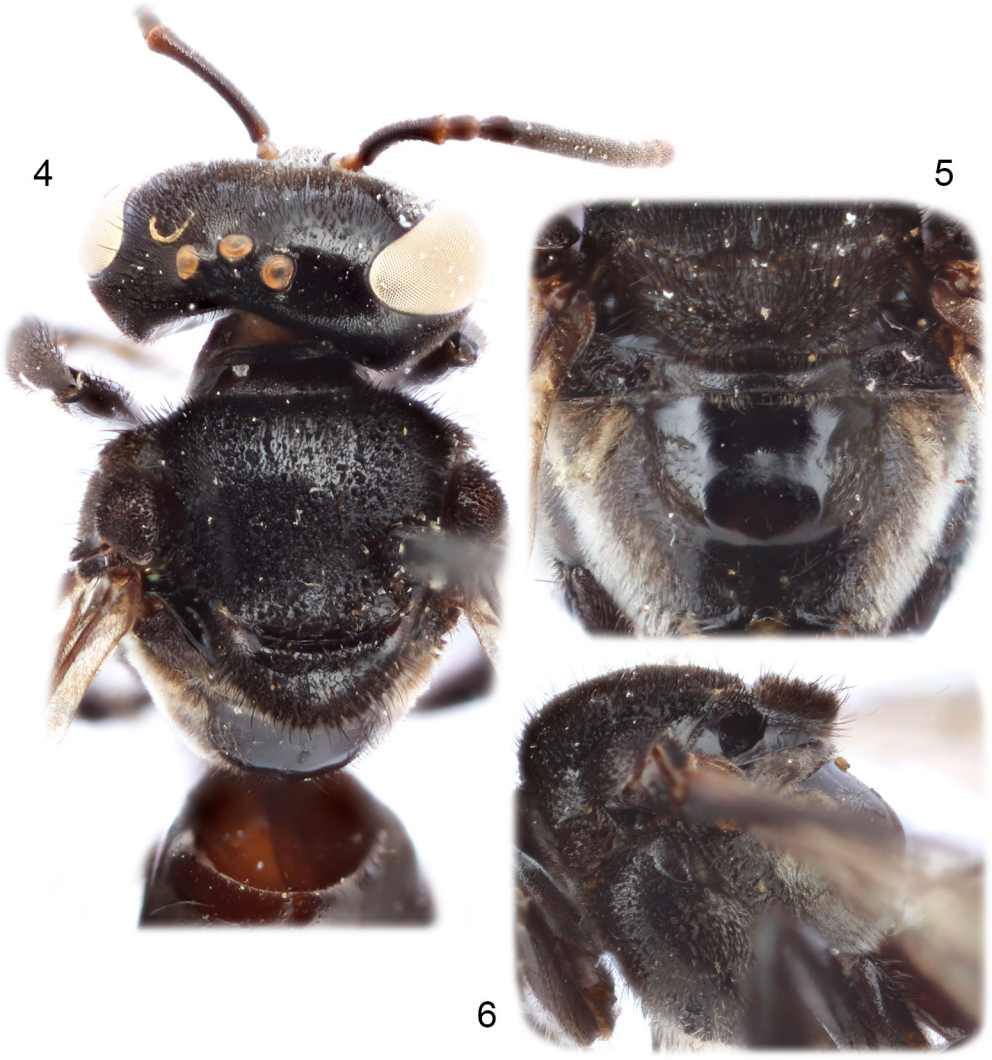
Type species: *Heterotrigona* (*Sahulotrigona*) *paradisaea* Engel & Rasmussen, new species.

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 (*i.e*., distad 1cu-a) (Fig. 7), and the posterior 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 to subglabrate zone on the posterior border of the inner surface of the metatibia. 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,

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 (P = preapical tooth).

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*).

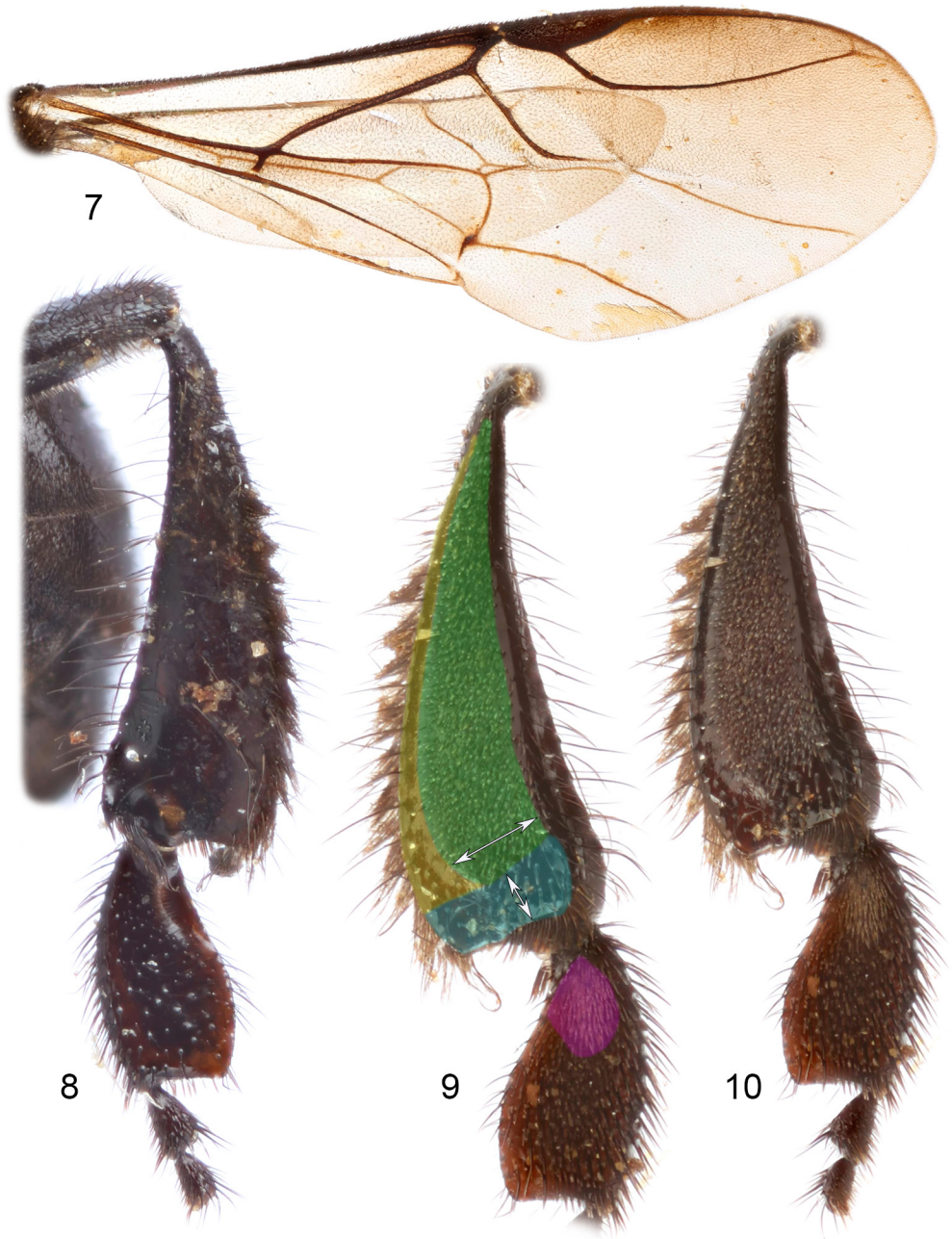
DESCRIPTION: Workers of small size, forewing length (including tegula) approximately 5.6–6.0 mm; integument shiny, smooth, with scattered microscopic punctures; integumental maculation absent (Figs. 1, 2, 4–6); fine, minute, white to off-white plumose pubescence on face and clypeus and fine, plumose pubescence on lateral surfaces



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.

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 but are more abundant ventrally on mesopleuron; 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 almost as long as torulocellar distance; first



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 posterior glabrate (yellow), apical glabrate (blue), keirotrichiate (green), and sericeous (pink) areas colored (arrows indicate width of posterior glabrate and length of apical glabrate zones). **10.** Unmodified view of inner surface of metatibia and metatarsus.

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 mid-length; 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, slightly shorter than ocellar diameter, and weakly impressed. Mesoscutellum short, ending at profile of metanotum and not overhanging propodeum (Fig. 6), rounded (Fig. 4), slightly swollen in profile, 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 4–4.5× as long as wide.

Forewing extending well 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 infuscate wing membrane (lightly infuscate 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+Cuβ 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 6–8 distal hamuli (6 in *H. atricornis*, 6–8 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 press); keirotrichiate area broader than posterior glabrate zone, width of keirotrichiate zone in the subapical region (wider portion) slightly greater than length of apical glabrate zone and narrower than its width (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 exceeding-

ly 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*, n. sp., 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, Indonesia (Papua)] .... *H.* (*Sahulotrigona*), n. subgen.
3(2). Posterior 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.*
—. Posterior 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
ZooBank: urn:lsid:zoobank.org:act:29B861B9-A7A4-4BD2-99E0-D2AC9F1C1890
(Figs. 1–10)

Trigona (*Pacificotrigona*) *okazawai* 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 frequently larger number of 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 5.8 mm (5.3–5.8 mm), forewing length (including tegula) 6.0 mm (5.6–6.3 mm). Head wider than long, width 2.08 mm (2.01–2.16 mm), length 1.56 mm (1.56–1.88 mm); compound eye length 1.28 mm (1.22–1.40) mm; upper interorbital distance 1.30 mm (1.25–1.40 mm), lower interorbital distance 1.25 mm (1.17–1.30 mm). Scape length 0.78 mm (0.76–0.80 mm), about as long as torulocellar distance, torulocellar distance 0.78 mm (0.76–0.86 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 0.52 mm (0.47–0.52 mm), width 0.94 mm (0.89–1.00 mm). Malar area short, length approximately sub-

equal to flagellar diameter or 0.6 times basal mandibular width (Fig. 2). Mandible with two, small preapical teeth (Fig. 3); P_1 with narrow incision separating apical edentate margin; incision separating P_1 and P_2 slightly less than orthogonal, with acutely rounded angular vertex (not to be confused with the vertex of the head; the angular vertex, *i.e.*, the geometric vertex or point where two edges of an angle meet; in this case is the point where the lower edge of P_2 meets the upper edge of P_1 and together form the angle between these two teeth, with the inner point of the incision between them representing the vertex for the angle, which in this case is acutely rounded: refer to figure 3).

Integument generally black to dark brown (Fig. 1), except labiomaxillary complex brown and reddish brown areas on inner surface of metatibia and metasomal terga I–IV; 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 setae; 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 subapically to 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).

Paratypes: **Papua New Guinea:** 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); 4♀♀, Gang Creek Camp, Mt. Rawlinson, 4500 ft, viii-3-1964 [3 August 1964], 7th Archbold Exped. to New Guinea, Huon Peninsula, Morobe District, H.M. Van Deusen collector (AMNH); 2♀♀, New Guinea, Papua, Mt. Dayman, Maneau Range, north slope, 1550 m, camp #5, July 5–8, 1953, G.M. Tate, 4th Archbold Expedition (AMNH); 5♀♀, Wau, Kaisinik, Morobe, xii 22 1973 [22 December 1973] // Papua New Guinea, xii 1973–I 1974 [December 1973–January 1974], T. Okazawa (RMNH).

COMMENTS: 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.

A series of specimens differ in their overall darker appearance. In particular, the minute white to silvery setae of the face, mesosomal dorsum, metanotum, and propodeum are dark fuscous to black. Longer, erect, simple setae of the mesosomal dorsum are black without any pale or light setae, unlike the type series of *H. paradisaea*. Sakagami considered these as a subspecies of what we have called *H. paradisaea*, but as we could not identify structural differences and have no biological or biogeographical information about the populations, we exclude them from the type series, listing them as *H.* (*S.*) *cf. paradisaea*. The label data are included below in a separate section for reference.

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 the unique biota cultivated by the indigenous peoples of New Guinea.

Heterotrigona (*Sahulotrigona*) *cf. paradisaea*

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

MATERIAL EXAMINED: **Papua New Guinea:** 2♀♀, Mt. Dayman, Maneu Range, 1550 m, N. slope, No. 5, June 30–July 13, 1953, Papua, New Guinea, Geoffrey M. Tate collector (AMNH); 1♀, No. 3, Gurakor, Wampit R. Valley, 45 mi from Lae, 670 m, May 9, 1959, Sixth Archbold Exped. to Papua New Guinea, Morobe District, L.J. Brass coll. (AMNH). **Indonesia (Papua Province):** 6♀♀, Neth. Ind.-American [literally, "Netherlands Indian-American Expedition"; *Nota bene*: "Nederlandsch-Indië" is Dutch for the Dutch East Indies], New Guinea Exped., Rattan Camp, 1100 m, 6.iii.1939 [6 March 1939], L.J. Toxopeus (RMNH); 1♀, Neth. Ind.-American, New Guinea Exped., Rattan Camp, 1100 m, 3.iii.1939 [3 March 1939], L.J. Toxopeus (RMNH); 1♀, Neth. Ind.-American, New Guinea Exped., Rattan Camp, 1200 m, ii.1939 [February 1939], L.J. Toxopeus (RMNH); 1♀, Neth. Ind.-American, New Guinea Exped., Rattan Camp, 1200 m, 4.iii.1939 [4 March 1939], L.J. Toxopeus (RMNH); 4♀♀, Neth. Ind.-Amer., New Guinea Exp., Iebele Camp 1938, 2250 m, 7 xi [7 November 1938], L.J. Toxopeus (RMNH); 2♀♀, Neth. Ind.-Amer., New Guinea Exp., Iebele Camp 1938, 2250 m, 15 xi [15 November 1938], L.J. Toxopeus (RMNH); 1♀, Neth. Ind.-Amer., New Guinea Exp., Iebele Riv. 1938, 2300 m, 28 x [28 October 1938], L.J. Toxopeus (RMNH); 5♀♀, Neth. Ind.-Amer., New Guinea Exp., Lower Mist camp, 14–1600 m, 31.I.1939 [31 January 1939], L.J. Toxopeus leg. (RMNH); 5♀♀, Neth. Ind.-Amer., New Guinea Exp., Lower Mist camp, 1550 m, 29.I.1939 [29 January 1939], L.J. Toxopeus leg. (RMNH); 1♀, Neth. Ind.-Amer.,

New Guinea Exp., Lower Mist camp, 1550 m, 1.II.1939 [1 February 1939], L.J. Toxopeus leg. (RMNH); 2♀♀, Neth. Ind.-Amer., New Guinea Exp., Lower Mist camp, 1450 m, 2.II.1939 [2 February 1939], L.J. Toxopeus leg. (RMNH); 1♀, Neth. Ind.-Amer., New Guinea Exp., Lower Mist camp, 1600 m, 14.I.1939 [14 January 1939], L.J. Toxopeus leg. (RMNH); 1♀, Neth. Ind.-Amer., New Guinea Exp., Lower Mist camp, 1600 m, 15.I.1939 [15 January 1939], L.J. Toxopeus leg. (RMNH); 1♀, Neth. Ind.-American, New Guinea Exped., Mist Camp, 1800 m, 3.I.1939 [3 January 1939], L.J. Toxopeus (RMNH); 2♀♀, Neth. Ind.-American, New Guinea Exped., Mist Camp, 1800 m, 5.I.1939 [5 January 1939], L.J. Toxopeus (RMNH); 3♀♀, Neth. Ind.-American, New Guinea Exped., Mist Camp, 1800 m, 9.I.1939 [9 January 1939], L.J. Toxopeus (RMNH); 2♀♀, Neth. Ind.-American, New Guinea Exped., Mist Camp, 1800 m, 10.I.1939 [10 January 1939], L.J. Toxopeus (RMNH); 1♀, Neth. Ind.-American, New Guinea Exped., Mist Camp, 1800 m, 11.I.1939 [11 January 1939], L.J. Toxopeus (RMNH); 2♀♀, Neth. Ind.-American, New Guinea Exped., Mist Camp, 1800 m, 12.I.1939 [12 January 1939], L.J. Toxopeus (RMNH); 1♀, Neth. Ind.-American, New Guinea Exped., Top Camp, 2100 m, 25.I.1939 [25 January 1939], L.J. Toxopeus (RMNH); 1♀, Neth. Ind.-American, New Guinea Exped., Top Camp, 2100 m, 17.I.1939 [17 January 1939], L.J. Toxopeus (RMNH: *Nota bene*: this specimen was labeled by Sakagami as the holotype of his unpublished "*Trigona okazawai irianensis*").

Comments: The above material could be conspecific with *H. paradisaea* but differs slightly in coloration and we have therefore hedged in our identification, pending further investigation. Toxopeus (1940) provides further details and a map for his various collecting camps. If the Toxopeus material proves to be truly conspecific with *H. paradisaea*, then the subspecific name "*irianensis*" would also be synonymous with the former.

Heterotrigona (*Sahulotrigona*) *atricornis* (Smith), **new combination**
(Figs. 11–14)

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). In addition to color, the dark morph appears to have denser and slightly longer pilosity, while the yellowish orange morph has setae denser and longer only in on the lower portion of the mesepisternum. 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. The holotype of *H. atricornis* belongs to the yellowish-orange morph and is deposited in Oxford (we have not had the opportunity to examine the type of this species).

Material examined: **Papua New Guinea:** 1♀, New Guinea (NE) [Papua New Guinea], Boana Mission [near Boana, Morobe Province, Nawae District], Huon Pen.

Figures 11–14. Workers of *Heterotrigona* (*Sahulotrigona*) *atricornis* (Smith), from eastern Papua New Guinea (non-type specimens). **11.** Lateral habitus of dark morph. **12.** Facial view of dark morph. **13.** Lateral habitus of yellowish orange morph. **14.** Facial view of yellowish orange morph.

[Peninsula], 900 m, ix-4–5-1956 [4–5 September 1956], E.J. Ford, Jr. (SEMC, dark morph); 1♀, PNG [Papua New Guinea]: Chimbu Province, Wara Sera Research Station, Crater Mtn. Conservation Area, October 6–10, 2000, A.S. & M.F. Whiting (AMNH, yellow morph). **Indonesia (Papua Province):** 3♀♀, tusschen bivak [between bivouac, or "camp"], ["Jasa am", handwriting is nearly illegible] Njao [Njao is situated along the border of northwestern Sandaun Province, Papua New Guinea and Muara Tami District, Kota Jayapura, Papua Province, Indonesia], 14.6.10 [14 June 1910], [illegible: possibly "v.k." which is likely an abbreviation for "van Kampen" as Pieter Nicolaas van Kampen (1878–1937), a Dutch zoologist mostly known for his work in herpetology, is known to have collected near Njao in mid-June 1910 (*e.g.*, Kampen, 1914; Blöte, 1936), and these specimens were identified as "*T. atricornis*" by Friese who subsequently sold them to the AMNH; in fact, these specimens could be some of those referenced by Friese (1915: p. 4) in his account of bees collected in northern New Guinea by van Kampen and K. Gjellerup in 1910] (AMNH, yellow morph).

Table 2. Checklist of stingless bees (Meliponini) from Papuasia (from West to East: Aru Islands, New Guinea, Bismarck Archipelago, and Solomon Islands except Santa Cruz Islands). Records based on observations of specimens in SEMC, AMNH, RMNH, and CRCD. NG = New Guinea; Solo = Solomon Islands.

	NG	Solo
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, **n. subgen.**		
Heterotrigona (*Sahulotrigona*) *atricornis* (Smith, 1865)	+	
Heterotrigona (*Sahulotrigona*) *paradisaea* Engel & Rasmussen, **n. sp.**	+	
Genus *Papuatrigona* Michener & Sakagami, 1990		
Papuatrigona genalis (Friese, 1908 [1909])	+	
Genus *Tetragonula* Moure, 1961		
Subgenus *Tetragonula* Moure, 1961		
Tetragonula (*Tetragonula*) *biroi* (Friese, 1898)‡	+	
Tetragonula (*Tetragonula*) *clypearis* (Friese, 1909)§	+	
Tetragonula (*Tetragonula*) *sapiens* (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).

DISCUSSION

Presently, the fauna of stingless bees in Papuasia includes 11 species recorded from New Guinea (West Papua and Papua Provinces in Indonesia and Papua New Guinea, proper) 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. At least initial observations tend to suggest that these could be separate species, but larger numbers of individuals are needed from more diverse localities. In addition, the material similar to *H. paradisaea* reported above (*vide supra*) needs further consideration. These could be variants of *H. paradisaea*, with darker overall coloration, or a cryptically similar species. Aside from these lingering challenges with New Guinean *Heterotrigona*, there are also new spe-

cies of *Tetragonula* needing further consideration (pers. obs. of material in SEMC and RMNH). 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 Papauasian 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 Papuasian 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 posterior 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 posterior 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 posterior glabrate zone ..... *Papuatrigona* 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 0.5–0.75× diameter of third flagellomere; vein M of forewing bent at trace of 1m-cu (genus *Heterotrigona* Schwarz) 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 0.5× 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 vein either confluent with or distad 1cu-a ..... *Heterotrigona* (*Platytrigona*) Moure

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