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Stingless bees from meliponiculture in South Kalimantan, Indonesia

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Abstract. *Purwanto H, Soesilohadi RCH, Trianto M. 2022. Stingless bees from meliponiculture in South Kalimantan, Indonesia. Biodiversitas 23: 1254-1266.* Kalimantan Island has many species of stingless bees that are widespread throughout the province. However, their morphology, morphometry, and nest structure characteristics have not been documented comprehensively. This paper described the morphological characters, morphometric measurements, nest entrance, and brood cell characteristics of stingless bees from meliponiculture in South Kalimantan, Indonesia. Ten stingless bee species were identified based on their morphological features: *Tetragonula laeviceps* (Smith, 1857), *T. fuscobalteata* (Cameron, 1908), *T. drescheri* (Schwarz, 1939), *T. melanocephala* (Gribodo, 1893), *T. biroi* (Friese, 1898), *Homotrigona apicalis* (Smith, 1857), *H. canifrons* (Smith, 1857), *Heterotrigona itama* (Cockerell, 1918), *Geniotrigona thoracica* (Smith, 1857), and *Lepidotrigona terminata* (Smith, 1878). Principal component analysis was performed to identify the grouping characters and thus determine their diagnostic characters. Furthermore, the shape, diameter, length, ornamentation, and color of the nest entrance and the arrangement, cells, and color of brood cells were observed. This study is the first to report high variations in the type of entrance opening and arrangement of brood cells for stingless bee species, which are abundant in South Kalimantan.

Keywords: Klanceng, meliponiculture, meliponini, South Kalimantan

INTRODUCTION

The tropics and subtropics are home to thousands of different types of bees, including stingless bees (Ávila et al. 2018). Stingless bees account for about half of the bees pollinating flowers in Indo-Malayan and Australasia. Similar to honey bees (Apini), stingless bees live in colonies and produce honey. They are potential pollinators of thousands of plant species and play important roles in human cultures (Chuttong et al. 2020). Stingless bees are corbiculates (Hymenoptera, Apidae), as are bumble bees (Bombini), orchid bees (Euglossini), and honey bees (Apini) (Michener 2007). With approximately 550 described species belonging to dozens of genera, stingless bees contain more species than the three other groups combined (Rasmussen et al. 2017). Hence, stingless bees are widely cultured worldwide.

Stingless bee beekeeping is called meliponiculture. Humans have kept stingless bees and used their products since Millennia. The Mayans, in particular, incorporated meliponiculture in their social, economic, and religious activities (Rosales 2013; Quezada-Euán 2018; Źrałka et al. 2018; Quezada-Euán and Alves 2020). Honey and cerumen, for example, were used for trading with the Aztecs (Quezada-Euán 2018) and for paying taxes to Spanish conquistadores in the 16th century (Jones et al. 2012; Quezada-Euán 2018; Giannini et al. 2020). Stingless bees continue to be important in the traditions and cultures of many native communities, such as the Kayapó in Brazil (Quezada-Euán et al. 2018), the Aché in Paraguay (sometimes called "civilization of honey"), the Abayanda pygmies in Uganda, rural communities in Madagascar (Randrianandrasana and Berenbaum 2015), indigenous communities in the Himalayas, and the Yolngu Aboriginal communities in Australia (Fijn and Baynes-Rock 2018). Meliponiculture provides income to people in many communities in the tropics (Alves 2013; Tornyie and Kwapong 2015; Giannini et al. 2017; Quezada-Euán et al. 2018). Dozens of different species are kept for honey or cerumen production. Recently, stingless bees have improved crop pollination (Giannini et al. 2015).

The main products of meliponiculture are honey, cerumen or resin, and bee pollen (Couvillon 2012; Jaffé et al. 2015; Hrncir et al. 2016; Jacob et al. 2019), but many people keep stingless bees simply for pleasure and relaxation (Carvalho et al. 2018). In the last decades, different hives have been developed, most notably in Indonesia. Colonies are collected from the wild and transferred to wooden boxes, logs, or clay pots. Experienced beekeepers can establish new colonies by dividing existing ones (Choudhari et al. 2012), a strategy already used by the ancient Mayans (Źrałka et al. 2018).

In Indonesia, the managed beekeeping of stingless bees is the ideal choice because it can be performed in all-natural environments. Moreover, ordinary people can conduct it safely, cheaply, easily, and with less maintenance (Kahono 2015). Recently, beekeeping of stingless bees has grown significantly in every region across their distribution, progressively increasing the national production of honey, raw propolis, and derivative products. However, to the best of our knowledge, no studies have examined the stingless bee species from meliponiculture in Indonesia, especially in South Kalimantan. Therefore, this study described the morphological characters, morphometric measurements, nest entrance, and brood cell characteristics of stingless bees from meliponiculture in South Kalimantan, Indonesia.

MATERIALS AND METHODS

Study area

The study areas are situated in Banjar District, Hulu Sungai Selatan District, Tabalong District, Tanah Bumbu District, and Tanah Laut District in South Kalimantan Province, Indonesia (Figure 1, Table 1). All sites were meliponiculture run by local beekeepers. Stingless bee specimens were caught directly from the colony and preserved dry for morphological and morphometric identification.

Morphological identification

Stingless bee specimens were identified based on their morphological characters and morphometric measurements as described by Smith (2012), Syafrizal et al. (2020), Trianto and Purwanto (2020), Purwanto and Trianto (2021) and Sayusti et al. (2021). Overall, we used the following 10 morphological features to distinguish the nine species: body color, pilosity of mesonotum, shape of scutellum, pilosity of propodeum, forewing color, number of hamuli, type of posterior fringe on the hind tibia, and the presence of elliptical disk on the inner basitarsus. Morphological identification was performed under a USB digital microscope Supereyes^{tm} A005/A005^{+}.

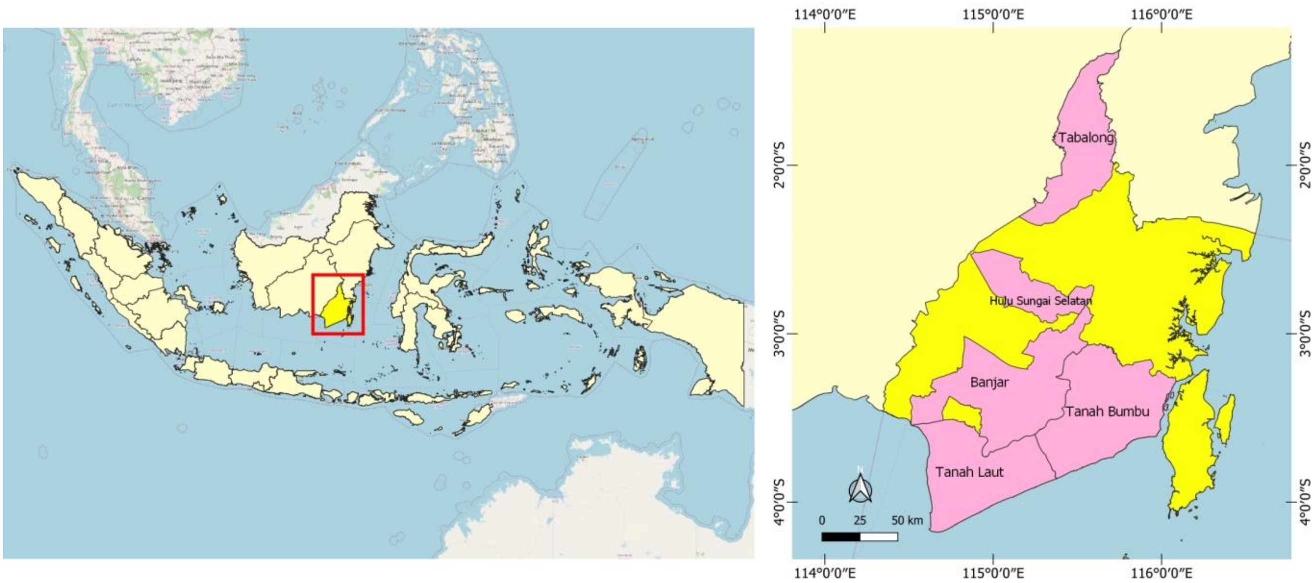

Figure 1. Study sites employed for the sampling of stingless bees from meliponiculture in South Kalimantan, Indonesia

Table 1. Sites of collection and species of stingless bees from meliponiculture in South Kalimantan, Indonesia

Sites	Coordinates	Species
Banjar District	3°19′00.01″ S 115°40′59.99″ E	*Tetragonula laeviceps* (Smith, 1857)
		Tetragonula fuscobalteata (Cameron, 1908)
		Tetragonula drescheri (Schwarz, 1939)
Hulu Sungai Selatan District	2°46′00.48″ S 115°16′00.12″ E	*Tetragonula laeviceps* (Smith, 1857)
		Tetragonula fuscobalteata (Cameron, 1908)
		Homotrigona apicalis (Smith, 1857)
		Heterotrigona itama (Cockerell, 1918)
		Homotrigona canifrons (Smith, 1857)
Tabalong District	1°51′54.01″ S 115°33′14.78″ E	*Tetragonula laeviceps* (Smith, 1857)
Tanah Bumbu District	3°27′42.15″ S 115°34′55.11″ E	*Heterotrigona itama* (Cockerell, 1918)
		Tetragonula laeviceps (Smith, 1857)
		Tetragonula drescheri (Schwarz, 1939)
Tanah Laut District	3°52′12.36″ S 114°38′32.43″ E	*Tetragonula fuscobalteata* (Cameron, 1908)
		Tetragonula laeviceps (Smith, 1857)
		Tetragonula melanocephala (Gribodo, 1893)
	3°19′00.01″ S 115°40′59.99″ E	*Tetragonula biroi* (Friese, 1898)
		Tetragonula drescheri (Schwarz, 1939)
		Heterotrigona itama (Cockerell, 1918)
		Geniotrigona thoracica (Smith, 1857)
		Lepidotrigona terminata (Smith, 1878)

Principal component analysis (PCA) based on morphometric measurements

PCA was conducted using PAST version 3.22 with seven morphological features based on Smith (2012): body length, width of the second flagellomere, width of the eye, width of the gena, width of the hind tibia, width of the hind basitarsus, and malar space (Figures 2-11; Table 2). The sum of the first and second Eigen values (>70%) was examined in the interpretation of the PCA output. Character loadings were generated for the first two principal components to determine the characters influenced in each component. Then, the first two principal component scores were plotted to visualize the result.

Nest entrance and brood cell characteristics

Nest entrances were characterized based on the shape, diameter or width, and height of their openings; the shape and length of their external entrance; and their ornamentation and color (Tables 3-4). All measurements were conducted using ImageJ (imagej.nih.gov). Brood cells of stingless bee species were collected from five districts in South Kalimantan (Table 1). Then, they were characterized based on four parameters: whether they were arranged in clusters, semicombs, or combs; the shape, diameter, and height of the cells; their color; and whether they had columnar or lamellate pillars or connective types (Table 5, Figure 13).

RESULTS AND DISCUSSION

Morphological characters for species

Morphological analysis of the 10 stingless bee species in South Kalimantan indicated that the species from the genus *Tetragonula* have a small body size (<6 mm), i.e., *Tetragonula laeviceps* (Smith, 1857), *T. fuscobalteata* (Cameron, 1908), *T. drescheri* (Schwarz, 1939), *T. melanocephala* (Gribodo, 1893), and *T. biroi* (Friese, 1898), and the species from the other five genera have a large body size (>6 mm), i.e., *Tetrigona apicalis* (Smith, 1857), *Heterotrigona itama* (Cockerell, 1918), *Homotrigona canifrons* (Smith, 1857), *Geniotrigona thoracica* (Smith, 1857), and *Lepidotrigona terminata* (Smith, 1878). Generally, the five *Tetragonula* species from Kalimantan are characterized by a short malar space, usually five hamuli on the hind wing, a backward projecting scutellum, and an elliptical disk on a backward projecting scutellum the inner hind basitarsus, which agrees with the *Tetragonula* characters. *Tetragonula melanocephala* can be distinguished from the four other *Tetragonula* species by its predominantly yellowish-brown body color (Rasmussen and Cameron 2010; Smith 2012; Vijayakumar and Jeyaraaj 2014; Efin et al. 2019; Trianto and Purwanto 2020; Purwanto and Trianto 2021). However, these two species can be distinguished by their size (Table 2).

Homotrigona apicalis (Smith, 1857) is characterized by several evident morphological features compared with *Tetragonula* bees (Salim et al. 2012; Kelly et al. 2014; Samsudin et al. 2018). In *H. itama*, the gastral tergite and sternite are completely blackish brown; the frons and clypeus are also completely black but fully covered with thick white hairs. The wing venation is dark brown, and the total number of hamuli on the anterior hindwing is usually seven (Samsudin et al. 2018; Trianto and Purwanto 2020; Purwanto and Trianto 2021). Furthermore, *H. canifrons* can be recognized by the presence of white moss-like hairs that cover black frons. This species often has a black clypeus and slightly brown at the posterior edge, covered with brownish hairs. This stingless bee species can be distinguished from other species by the coloration of antennae; it has a completely black flagellum and black scape but is slightly brownish at the apical and basal (Rasmussen et al. 2017; Samsudin et al. 2018). *Geniotrigona thoracica* is the largest among the other stingless bee species in Asia. The scutellum and propodeum are usually short and possess a very long forewing (Table 2). The abdomen of *G. thoracica* is often triangular without broadened as certain groups of stingless bees. It is recognized by the presence of two vertical black stripes at the middle of the completely brown mesoscutum (Rasmussen et al. 2017; Samsudin et al. 2018).

Ten species of stingless bees belong to five genera found in South Kalimantan, namely, *Tetragonula* (five species), *Homotrigona* (two species), *Heterotrigona* (one species), *Geniotrigona* (one species), and *Lepidotrigona* (one species) (Figures 2-11).

Tetragonula laeviceps

The body color of the worker bee *T. laeviceps* is predominantly black. Thorax is black. Mesonotum is streaked by six longitudinal hair bands, including the lateral fringes. Scutellum is extended over the propodeum. Abdomen is uniformly brown from tergites 1-6. Forewing color is uniform and semi-transparent. The number of hamuli is five per hindwing. Posterior fringe of the hind tibia is plumose (branched). Elliptical disk is present on the inner basitarsus (Figure 2.A-F).

Tetragonula fuscobalteata

The body color of the worker bee *T. fuscobalteata* is bicolorous. Thorax is black. Mesonotum is streaked by six longitudinal hair bands, including the lateral fringes. Scutellum is extended over the propodeum. Abdomen is tergites 1-2 yellowish, 3-6 chestnut brown. Forewing color is uniform and semi-transparent. The number of hamuli is five per hindwing. Posterior fringe of the hind tibia is plumose (branched). Elliptical disk is present on the inner basitarsus (Figure 3.A-F).

Tetragonula drescheri

The body color of the worker bee *T. drescheri* is predominantly black. Thorax is black. Mesonotum is streaked by six longitudinal hair bands, including the lateral fringes. Scutellum is extended over the propodeum. Abdomen is uniformly brown from tergites 1-6. Forewing color is uniform and semi-transparent. The number of hamuli is five per hindwing. Posterior fringe of the hind tibia is plumose (branched). Elliptical disk is present on the inner basitarsus (Figure 4.A-F).

Tetragonula melanocephala

The body color of the worker bee *T. melanocephala* is bicolorous. Thorax is yellowish brown. Mesonotum is streaked by six longitudinal hair bands, including the lateral fringes. Scutellum is extended over the propodeum. Abdomen is uniformly yellowish brown from tergites 1-6. Forewing color is uniform and semi-transparent. The number of hamuli is five per hindwing. Posterior fringe of the hind tibia is plumose (branched). Elliptical disk is present on the inner basitarsus (Figure 5.A-F).

Tetragonula biroi

The body color of the worker bee *T. biroi* is predominantly black. Thorax is black. Mesonotum is streaked by six longitudinal hair bands, including the lateral fringes. Scutellum is extended over the propodeum. Abdomen is uniformly brown from tergites 1-6. Forewing color is uniform and semi-transparent. The number of hamuli is five per hindwing. Posterior fringe of the hind tibia is plumose (branched). Elliptical disk is present on the inner basitarsus (Figure 6.A-F).

Homotrigona apicalis

The body color of the worker bee *H. apicalis* is predominantly black. Thorax is black. Mesonotum is black, fully covered with black setae at the anterior edge. Scutellum is short, reaching back only to metanotum. Abdomen is tergites 1-5 blackish brown, six brown. Forewing color is uneven, 1/2 blackish brown on basal and 1/2 semi-transparent on apical. The number of hamuli is seven per hindwing. Posterior fringe of the hind tibia is simple (unbranched). Elliptical disk is present on the inner basitarsus (Figure 7.A-F).

Homotrigona canifrons

The body color of the worker bee *H. canifrons* is predominantly black. Thorax is black. Mesonotum is black, coarser, covered with long setae at anterior. Scutellum is short, reaching back only to metanotum. Abdomen is uniformly black from tergites 1-6. Forewing color is uniform and semi-transparent, and wing venation of forewings is dark brown. The number of hamuli is seven per hindwing. Posterior fringe of the hind tibia is simple (unbranched). Elliptical disk is absent on the inner basitarsus (Figure 8.A-F).

Heterotrigona itama

The body color of the worker bee *H. itama* is predominantly black. Thorax is black. Mesonotum is wholly black, coarser, covered with long setae at anterior. Scutellum is short, reaching back only to metanotum. Abdomen is uniformly black from tergites 1-6. Forewing color is uniform, and wing venation is dark brown and semi-transparent. The number of hamuli is seven per hindwing. Posterior fringe of the hind tibia is simple (unbranched). Elliptical disk on the inner basitarsus is absent (Figure 9.A-F).

Geniotrigona thoracica

The body color of the worker bee *G. thoracica* is predominantly black. Thorax is brown. Mesonotum is streaked by five longitudinal hair bands, including the lateral fringes. Scutellum is short, reaching back only to metanotum. Abdomen is tergites 1-4 blackish brown, 5-6 brown. Forewing color is uneven; wing venation is dark brown but slightly brown at the apical and semi-transparent. The number of hamuli is nine per hindwing. Posterior fringe of the hind tibia is simple (unbranched). Elliptical disk is present on the inner basitarsus (Figure 10.A-F).

Lepidotrigona terminata

The body color of the worker bee *L. terminata* is fulvous, basal tergite ivory. Thorax is black. Mesonotum is enclosed by a border of yellowish short thick scale-like. Scutellum is short, reaching back only to metanotum. Abdomen is fulvous, basal tergite ivory. Forewing color is uniform and semi-transparent. The number of hamuli is eight per hindwing. Posterior fringe of the hind tibia is simple (unbranched). Elliptical disk is absent on the inner basitarsus (Figure 11.A-F).

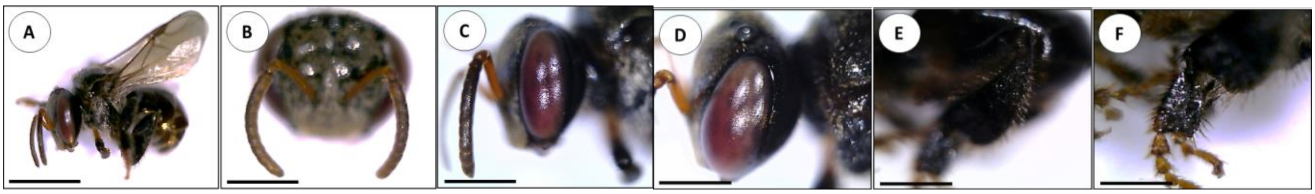

Figure 2. *Tetragonula laeviceps*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

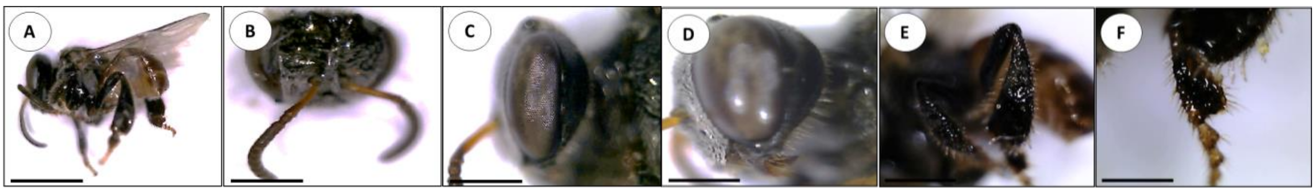

Figure 3. *Tetragonula fuscobalteata*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

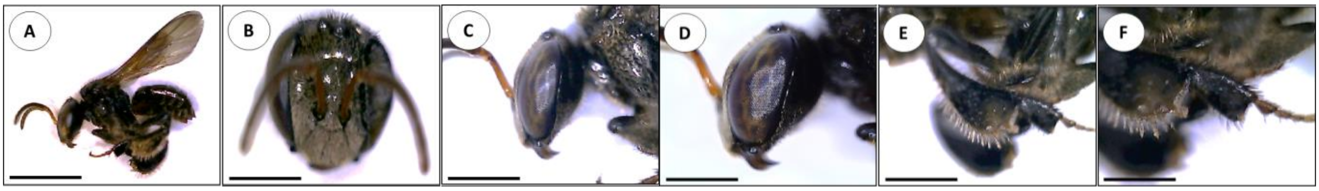

Figure 4. *Tetragonula drescheri*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

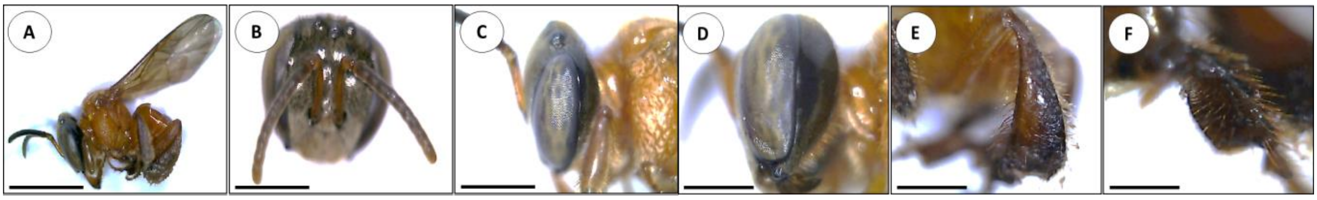

Figure 5. *Tetragonula melanocephala*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

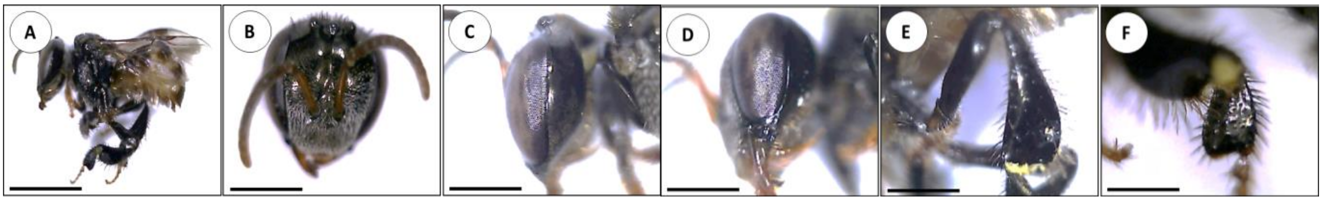

Figure 6. *Tetragonula biroi*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

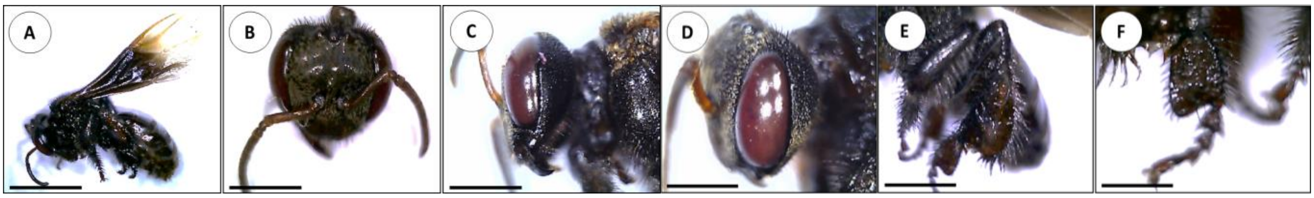

Figure 7. *Homotrigona apicalis*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

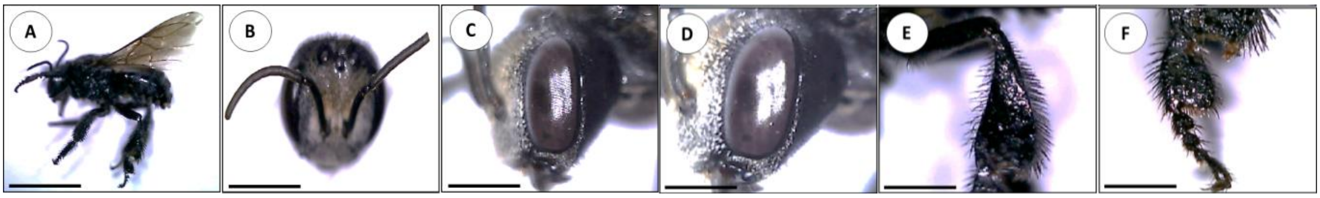

Figure 8. *Homotrigona canifrons*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

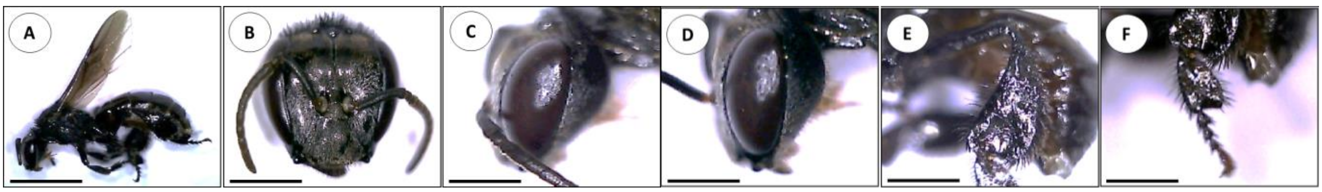

Figure 9. *Heterotrigona itama*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

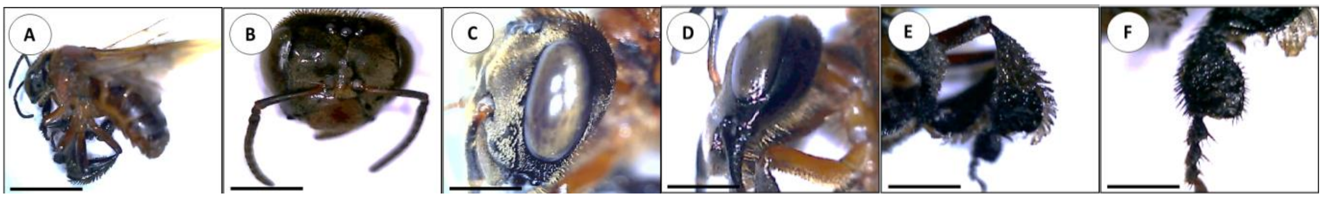

Figure 10. *Geniotrigona thoracica*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

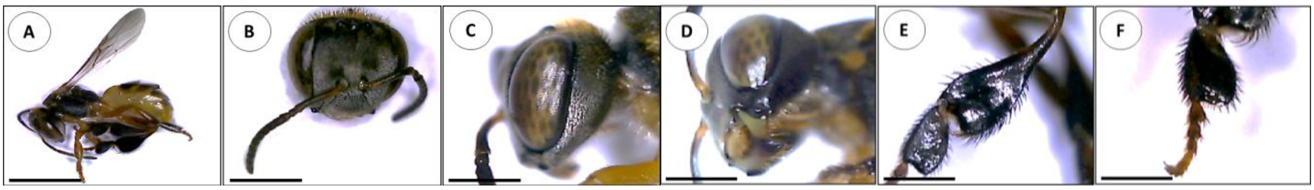

Figure 11. *Lepidotrigona terminata*; A. Body length; B. Width of the second flagellomere; C. Width of the gena; D. Width of the eye and malar space; E. Width of the hind tibia; and F. Width of the hind basitarsus. Black bar = 1 mm

Table 2. Seven morphological feature measurements of stingless bees for morphological identification and principal component analysis (PCA) (n: 50 individuals) (mm)

Species	Mean/SD	BL	WSF	WG	WE	MS	WHt	WHb
T. laeviceps	Mean	4.0	0.321	0.456	0.257	0.240	0.670	0.457
	SD	0.3	0.004	0.035	0.003	0.004	0.040	0.012
T. fuscobalteata	Mean	3.3	0.220	0.347	0.148	0.131	0.569	0.358
	SD	0.4	0.006	0.030	0.011	0.003	0.013	0.016
T. drescheri	Mean	4.6	0.332	0.467	0.268	0.251	0.681	0.468
	SD	0.2	0.011	0.003	0.013	0.016	0.004	0.035
T. melanocephala	Mean	5.0	0.346	0.470	0.272	0.265	0.696	0.472
	SD	0.2	0.004	0.030	0.011	0.003	0.004	0.035
T. biroi	Mean	4.1	0.322	0.457	0.258	0.241	0.671	0.458
	SD	0.3	0.005	0.020	0.012	0.004	0.012	0.015
H. apicalis	Mean	7.5	0.371	0.518	0.702	0.366	0.960	0.747
	SD	0.3	0.003	0.004	0.040	0.012	0.005	0.020
H. itama	Mean	6.1	0.258	0.405	0.689	0.253	0.857	0.634
	SD	0.2	0.001	0.002	0.001	0.002	0.002	0.001
H. canifrons	Mean	8.0	0.460	0.607	0.891	0.455	0.989	0.836
	SD	0.1	0.012	0.004	0.004	0.030	0.011	0.003
G. thoracica	Mean	8.2	0.462	0.609	0.893	0.457	0.991	0.838
	SD	0.1	0.004	0.035	0.012	0.004	0.012	0.016
L. terminata	Mean	6.5	0.260	0.407	0.691	0.255	0.859	0.636
	SD	0.3	0.003	0.044	0.017	0.016	0.050	0.023

Note: BL: Body length; WSF: Width of the second flagellomere; WG: Width of the gena; WE: Width of the eye; MS: Malar space; WHt: Width of the hind tibia; WHb: Width of the hind basitarsus

Table 3. Influence of environmental factors on the nest entrance structure of stingless bees from meliponiculture in South Kalimantan, Indonesia

Environmental influence	Nest entrance structure	Species	Function
Rain	Well-developed	*H. itama, T. drescheri, H. apicalis, H. canifrons*	To be rain tight entrance tube (Sakagami et al. 1984)
Predation	Funnel entrance which deposited by a spray of sticky propolis droplets	*L. terminata T. melanocephala, T. biroi, H. itama,*	To prevent invading ants (Alves et al. 2018)
	Slit entrance with thick and hard structure of the propolis enlargement	*T. laeviceps, T. fuscobalteata, T. drescheri, H. apicalis, H. itama, G. thoracica, H. canifrons*	To prevent against vertebrate predators that probably exist in the habitat (Sayusti et al. 2021)

Table 4. Entrance characteristics of stingless bee species from meliponiculture in South Kalimantan, Indonesia

Species	Characters of entrance									
	Diameter (cm)			Length (cm)			Shape	Ornamentation	Color	Rigidity
	Mean	Range	St.dev	Mean	Range	St.dev				
T. laeviceps	1.11	0.61-1.41	0.13	1.39	0.86-1.66	0.18	F, Ct, S	Sp, Dp, Ir, Emp	Bl, Br	S, H
T. fuscobalteata	1.39	1.25-2.28	0.12	1.76	1.50-2.43	0.17	F	Sp	Db, Lb	H
T. drescheri	0.90	0.30-1.34	0.19	1.24	0.55-1.59	0.24	Ct	Sp, Ir	Db	H
T. melanocephala	0.96	0.36-1.20	0.15	1.17	0.51-1.45	0.19	S	Sp	Br	S
T. biroi	1.85	1.43-2.85	0.29	2.65	1.68-3.10	0.34	Ct, F	Dp	Br, Lb, Db	S
H. apicalis	1.17	0.89-1.45	0.12	1.35	1.04-1.70	0.17	Ct	Emp	Bl	H
H. itama	1.38	1.59-2.25	0.13	1.85	1.74-2.50	0.18	Ct, F	Dp, Sp, Ir	Br, Lb, Db	S, H
H. canifrons	1.98	1.61-2.75	0.16	2.35	1.86-2.98	0.21	S	Sp	Bl	H
G. thoracica	2.57	3.38-4.39	0.16	3.99	3.62-4.74	0.21	Ct	Emp	Br, Lb, Db	H
L. terminata	1.31	1.13-2.35	0.18	1.68	1.38-2.60	0.23	Ct	Dp	Lb	S

Note: St.dev: Standart deviation; Shape (F: Funnel, Ct: Cylindrical tube, S: Slit); Ornamentation (Sp: Spread of propolis, Dp: Droplet of propolis, Emp: Enlargement mount of propolis, Ir: Irregular ridges); Color (Bl: Black, Br: Brown, Lb: Lightbrown, Db: Dark brown); and Rigidity (S: Soft, H: Hard)

Table 5. Brood cells characteristics of stingless bee species from meliponiculture in South Kalimantan, Indonesia

Species	Characters of entrance									
	Diameter (cm)			Height (cm)			Arrangement	Shape	Color	Pillars
	Mean	Range	St.dev	Mean	Range	St.dev				
T. laeviceps	0.28	0.27-0.28	0.01	0.31	0.30-0.32	0.02	C, Scl	Ssp	Lb, Db	C
T. fuscobalteata	0.26	0.25-0.26	0.01	0.40	0.39-0.40	0.01	C	Ssp	Lb, Db	C
T. drescheri	0.27	0.26-0.27	0.01	0.33	0.32-0.33	0.01	C	Ssp	Lb	C
T. melanocephala	0.26	0.25-0.26	0.01	0.32	0.31-0.32	0.01	C	Ssp	Lb, Db	C
T. biroi	0.29	0.28-0.29	0.01	0.37	0.36-0.38	0.02	S	Ssp	Lb	L
H. apicalis	0.49	0.48-0.49	0.01	0.61	0.60-0.61	0.01	C	Ssp	Db	C
H. itama	0.51	0.50-0.51	0.01	0.63	0.62-0.63	0.01	Hlc	E	Db	L
H. canifrons	0.50	0.49-0.50	0.01	0.66	0.65-0.66	0.01	Scl	Ssp	Db	C
G. thoracica	0.57	0.56-0.57	0.01	0.65	0.64-0.65	0.01	Sco	Ssp	Db	L
L. terminata	0.33	0.32-0.33	0.01	0.57	0.56-0.57	0.01	Hlc	E	Lb, Db	L

Note: St.dev: Standart deviation; Arrangement (C: Cluster, S: Spiral, Hlc: Horizontal layered comb, Scl: Semi-cluster, Sco: Semi-comb); Shape (Ssp: Sub-spherical, E: Elongate); Color (Bl: Black, Br: Brown, Lb: Lightbrown, Db: Dark brown); and Pillars (C: Columnar, L: Lamellate)

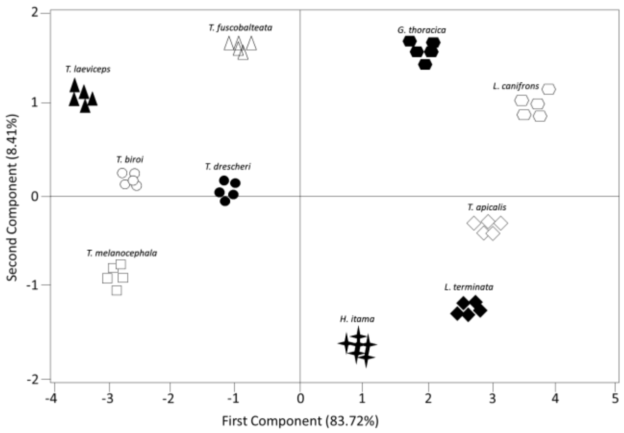

Figure 12. Principal Component Analysis (PCA) of seven morphological characters of the five stingless bee species from meliponiculture in South Kalimantan, Indonesia.

PCA based on morphometric measurement

PCA results showed that the total of the first two principal components was 92.13%, to which PC1 and PC2 contributed 83.72% and 8.41%, respectively. Based on the PCA results, body length (0.993) and eye width (0.698) contributed the highest values in PC1 and PC2, respectively, in the differentiation of the species (Table 2). The 10 stingless bee species were distinguished based on morphological characters (Figures 2-11). *G. thoracica* and *H. canifrons* were all in quadrant 2 of the PCA; *T. sapiens* was in quadrant 1; *T. laeviceps, T. biroi, T. fuscobalteata*, and *T. drescheri* were in quadrant 2; *T. melanocephala* was in quadrant 3; and *H. apicalis, H. itama*, and *L. terminata* were in quadrant 4 of the PCA (Figure 12).

Nest entrance and brood cell characterization

Characteristics of the nest entrance can be used to identify species of stingless bees. The entrance opening type, diameter, length, shape, ornamentation, and color of the 10 stingless bee species from meliponiculture in South Kalimantan, Indonesia show substantial variation. We found three types of shapes, i.e., funnel (F), cylindrical tube (Ct), and slit (S); three propolis ornamentation types, i.e., spread of propolis (Sp), droplet of propolis (Dp), and enlargement mount of propolis (Emp); four types of color entrance, i.e., black (Bl), brown (Br), lightbrown (Lb), and dark brown (Db); and two types of rigidity, i.e., soft (S) and hard (H) (Table 4). Furthermore, we found a variation in the nest entrance structures of stingless bee species from meliponiculture in South Kalimantan, Indonesia (Table 3). Sayusti et al. (2021) reported that the nest entrance structures of Sulawesi stingless bees are influenced by environmental factors, such as rain and predation. These environmental factors possibly affect the variation observed in South Kalimantan.

Brood cells without eggs are darker in color, whereas those containing eggs are transparent (Figure 14). Oldroyd and Pratt (2015) stated the new cells of the stingless bees are yellow-brownish in color but become transparent after the wax erodes. Cells are connected with another cell by pillars. Leonhardt et al. (2010) showed brood cells associated with one pillar with a small ball shape. This structure is built in rotted cavities to protect the colony from predators and parasites. Alves et al. (2018) reported that these bees build the architecture inside the hive to protect against natural enemies. In addition, the colonies used a lot of wax to avoid predators and parasites.

Among the five *Tetragonula* species, *T. laeviceps* shows the highest variation in entrances with diameters of 0.61-1.41 cm and lengths of 0.86-1.66 cm, four entrance shapes, three ornamentation types, two color variations, and two rigidity types (Table 4). Irregular ridges were found in Hulu Sungai Selatan District and Tanah Laut District, South Kalimantan, and consisted of three entrance types: a short grayish brown funnel entrance with irregular ridges (Figure 13.A), an extended blackish-brown funnel (Figure 13.B), and an extended flare funnel (Figure 13.C). A type of oval entrance opening was found in Tanah Laut, South Kalimantan, and it consists of two entrance types: a short brown entrance with propolis droplets around the funnel (Figure 13.D) and a cylindrical tube entrance varying in color from light to dark brown (Figure 13.E). An ellipse entrance opening was found in Tanah Bumbu District, South Kalimantan (Figure 13.F). We found three types of entrance openings for other *Tetragonula* species with variations in their size diameter (0.90-1.39 cm), length (1.17-1.76 cm), color, ornamentation, and rigidity (Table 4). An ellipse entrance opening was found in Banjar District, South Kalimantan (Figure 13.G-H), and oval entrance openings consisting of two entrance types were found: an extended funnel entrance with brown propolis placed under the funnel in Tabalong District, South Kalimantan (Figure 13.I-J) and a slit entrance opening in Tanah Laut District, South Kalimantan (Figure 13.K). The fourth entrance type was an irregular entrance opening that was found in a natural colony nested in the trunk of a mango tree from meliponiculture in Banjar District, South Kalimantan (Figure 13.L).

We found different types of entrance openings for *H. apicalis* with variations in their size diameter (0.89-1.45 cm), length (1.04-1.70 cm), color, ornamentation, and rigidity (Table 4). A cylindrical tube opening was found in Hulu Sungai Selatan District, South Kalimantan, which consists of one ornamentation type, an enlargement mount of propolis with black color (Figure 13.M). Furthermore, the entrance of *H. itama* is large with a diameter of 1.59-2.25 cm and a length of 1.74-2.50 cm, and it is surrounded by soft and hard propolis (Table 4). The propolis, which enlarges the nest mounds, was observed in brown, light brown in Hulu Sungai Selatan District and Tanah Laut District, and dark brown in Tanah Bumbu District, South Kalimantan (Figure 13.N-P).

The entrance of *H. canifrons* has a narrow slit with a diameter of 1.61-2.75 cm and a length of 1.86-2.98 cm, and it shows the spread of propolis with hard rigidity (Table 4). The propolis is black in Hulu Sungai Selatan District, South Kalimantan (Figure 13.Q). The other large stingless bee species in Tanah Laut District, South Kalimantan, *G. thoracica*, have nests with light and dark brown cylindrical tube openings with a diameter of 3.38-4.39 cm and a length of 3.62-4.74 cm with an enlargement mount of propolis (Figure 13.R-S and Table 4). We found large entrance openings for *L. terminata* with a diameter of 1.13-2.35 cm and a length of 1.38-2.60 cm, ornamented with droplets of propolis on the upper surface of the entrance (Figure 13.T).

Observations of the five *Tetragonula* species revealed five brood cell arrangements: cluster, spiral, horizontally layered comb, semi-cluster, and semi-comb. Cluster brood cells were found in *T. laeviceps, T. fuscobalteata, T. melanocephala, T. drescheri,* and *H. apicalis* (Figure 14.A-D, J). Several brood cells are waxed irregularly and joined with a columnar pillar structure that connects the brood cells to the hive substrate (Table 5). The spiral brood cell arrangement was only found in *T. biroi* (Figure 14.G). The brood cell shape of the five *Tetragonula* species vary from sub-spherical to elongate with a diameter and height of 0.26-0.29 cm and 0.31-0.40 cm, respectively (Table 5).

The brood cells of *H. itama* and *L. terminata* are arranged in clusters with long columnar pillars (0.50-0.51 cm and 0.32-0.33 cm) connecting the brood cells and hive substrate (Figure 14.E, H). Furthermore, the brood cells of *G. thoracica* are semi-comb with long columnar pillars (0.56-0.57 mm). The brood cell nests are light to dark brown and elongate, respectively. The light brown brood cells are located under the dark brown brood cells and contain mature brood. Young brood cells are found in the dark brown cells (Table 5).

Figure 13. Entrance types of stingless bee species from meliponiculture in South Kalimantan, Indonesia. A–F. Funnel, cylindrical tube, and slit entrance of *T. laeviceps*, G. Funnel entrance of *T. fuscobalteata*, H. Slit entrance of *T. melanocephala*, I–J. Funnel and cylindrical tube entrance of *T. biroi*, K. Cylindrical tube entrance of *T. drescheri*, L. Slit entrance of *T. biroi*, M. Cylindrical tube entrance of *H. apicalis*, N–P. Funnel and cylindrical tube of *H. itama*, Q. Slit entrance of *H. canifrons*, R-S. Cylindrical tube entrance of *G. thoracica*, and T. Cylindrical tube entrance of *L. terminata*. Bar = 1 cm.

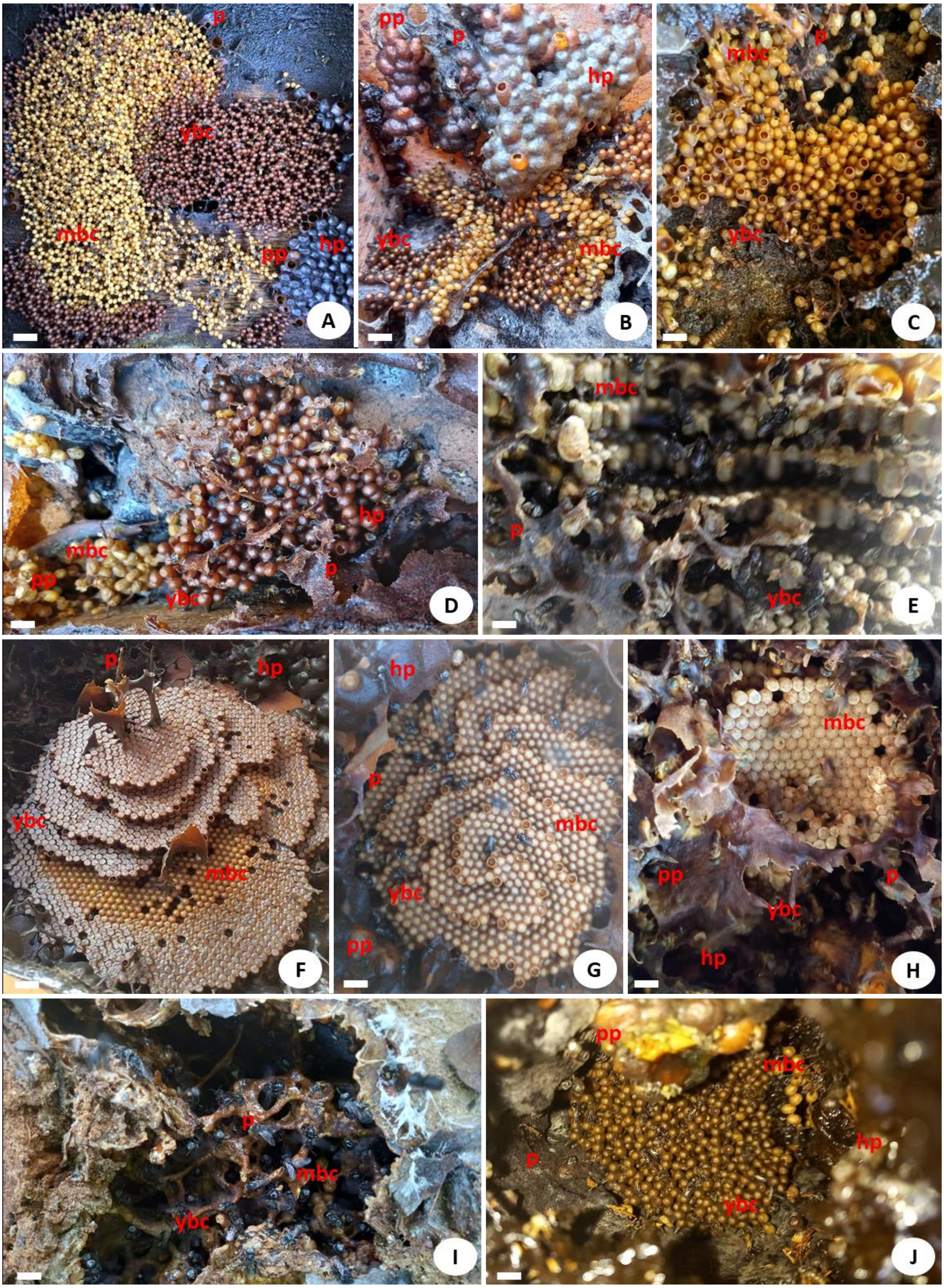

Figure 14. Brood cell arrangement of stingless bee species from meliponiculture in South Kalimantan, Indonesia: A. Cluster brood cells of *T. laeviceps*, B. Cluster brood cells of *T. fuscobalteata*, C. Cluster brood cells of *T. drescheri*, D. Cluster brood cells of *T. melanocephala*, E. Horizontal layered comb brood cells of *H. itama*, F. Semi-comb brood cells of *G. thoracica*, G. Spiral brood cells of *T. biroi*, H. Horizontal layered comb brood cells of *L. terminata*, I. Semi-cluster brood cells of *H. canifrons*, J. Cluster brood cells of *H. apicalis.* Bar = 1 cm. ybc = young brood cells, mbc = mature brood cells, hp = honey pot, pp = pollen pot, and p = pillars.

Discussion

This study aimed to explore the stingless bee species from meliponiculture in South Kalimantan, Indonesia by analyzing their morphology, morphometric measurement, and nest structures. In addition, we provide the first report of stingless bee species from meliponiculture in South Kalimantan, Indonesia. We found 10 species of Kalimantan stingless bees, namely, *T. laeviceps*, *T. fuscobalteata*, *T. drescheri*, *T. melanocephala*, *T. biroi*, *H. apicalis*, *H. itama*, *H. canifrons*, *G. thoracica*, and *L. terminata* were exploited in meliponiculture in the region. We had information from beekeepers in South Kalimantan that *T. biroi* was obtained from their fellow beekeeper from Balikpapan. Therefore, we suspect that the *T. biroi* collected during this study is an introduced species from Sulawesi through Balikpapan. The species of the stingless bees from meliponiculture in Kalimantan Island, especially from East Kalimantan and North Kalimantan, have previously been summarized by Syafrizal et al. (2020), i.e., *G. thoracica, H. itama, L. terminata, H. fimbriata, T. biroi, T. fuscobalteata, T. iridipennis, T. laeviceps, T. reepeni, T. sarawakensis,* and *T. testaceitarsis.* Syafrizal et al. (2014) previously identified stingless bees from East Kalimantan, i.e., *T. incisa, H. apicalis, T. melina, T. itama, T. fuscibasis, T. fuscobalteata, T. laeviceps, T. drescheri*, and *T. terminata*. Sadam et al. (2016) listed stingless bees from East Kalimantan, such as *T. melanocephala*, *T. geissleri, T. fuscobalteata,* and *T. laeviceps*. Meanwhile, Syaifudin and Normagiat (2020) reported collecting two species of stingless bees, *T. laeviceps* and *H. itama*, from West Kalimantan.

The dominant stingless bees in this study are from the genus *Tetragonula*. The genus comprises small stingless bees (Smith 2012) distributed from Continental Asia to Oceania. Genus *Tetragonula* has been reported in the Sri Lanka and continental Asia, Indian subcontinent (Rasmussen 2013), Southeast Asia, Vietnam, Philippines, Thailand (Boongird 2011), Peninsular Malaysia (Rasmussen and Michener 2010; Salim et al. 2012), and Indonesia (Erniwati 2013). In Indonesia, *Tetragonula* has been reported from Sumatra, Sulawesi, Moluccas, Papua, East Kalimantan, West Kalimantan, and North Kalimantan (Sakagami et al. 1990; Syafrizal et al. 2014; Sadam et al. 2016; Syafrizal et al. 2020; Syaifudin and Normagiat 2020). The clear distinction among the 10 species is based on body length and eye width (Figure 14, Table 2), suggesting that these characters can be used to distinguish *T. drescheri* and *T. fuscobalteata*, which are morphologically similar and were previously only distinguishable using male genitalia and body part measurements (Samsudin et al. 2018). Furthemore, the finding that *T. fuscobalteata*, from South Kalimantan, is smaller than *T. drescheri* agrees with the report of Samsudin et al. (2018).

In addition to morphological features and morphometric measurements, we provide important characters of nest entrances and brood cell arrangements of stingless bees from meliponiculture in South Kalimantan, Indonesia. This study is the first to report the unique and the substantial variation in the entrances of stingless bee species from meliponiculture in South Kalimantan, Indonesia. We found four types of entrance openings belonging to *T. laeviceps*, which are dominated by irregular openings and ornamented with various types of propolis. The shape, color, and rigidity of the nest entrance of stingless bees vary between species. Nest entrance properties of stingless bees are related to many factors, such as age of bee genetics, nest age, and the microenvironment, such as rainfall, predation, sunlight, microclimate, parasites, and symbionts. The size of nest entrance of stingless bees also varies (Kelly et al. 2014).

The structure of nest entrances is highly influenced by bee genetics, nest age, and the microenvironment, such as rainfall, predation, and sunlight. These influences could explain some of the variations in the nest entrances of South Kalimantan stingless bees (Table 3). The variations in entrance color that were observed in the nests of *T. laeviceps* are caused by different resin sources in each sampling site. The other variations in the entrances of *T. laeviceps* nests are probably driven by the polyphenism phenomenon in which similar genotypes generate two, three, or more distinct phenotypes. This phenomenon is influenced by environmental conditions and drives a phenotype shift in the neurochemical and hormonal pathways related to nesting behaviors (Simpson et al. 2011). Furthermore, Alves et al. (2018) stated that the nest entrances of *T. sapiens* and *T. fuscobalteata* are tube like with several variations in texture, length, and diameter. Variation in nest entrances is related to the defense and foraging activities of stingless bees.

Apart from the variations in nest entrances, the brood cell arrangement of *T. laeviceps* in Kalimantan is also surprisingly varied: semi-cluster brood cells were observed in Tanah Laut District, South Kalimantan, whereas clusters were observed in Hulu Sungai District, South Kalimantan. Some of these arrangements for *T. laeviceps* are different from those of previous observations of *T. laeviceps* from Vietnam, which only show a cluster brood cell arrangement. The hypothesis of stigmergy, in which previous worker constructions stimulate the building behavior of stingless bee workers, could apply to cell building by these stingless bees. Slight changes in the building behavior of the first builder are followed by other builders, thereby generating a different structure of the brood cells (Oldroyd and Pratt 2015). In such cases, architectural modifications could also occur after a taxon diverges from an ancestor or an unassociated species converges because of similar nest sites and materials. Our findings provide a hint to the possibility of the existence of a species complex in Kalimantan stingless bees as found in the sibling species of *T. hockingsi* and *T. carbonaria* in Australia, which are extremely similar in morphology but have different brood cell arrangements. As a possible solution, in addition to morphology, morphometric measurement and nest structure analysis can be complemented by DNA barcoding as a promising tool to recognize the sibling species.

In conclusion, we found that meliponiculture activities in South Kalimantan were developing in the five regencies surveyed. The species of stingless bees exploited were varied for each meliponiculture area. Based on the morphological characters, morphometric measurements, nest entrance properties, and brood cell characterization, the stingless bees were identified as *T. laeviceps, T. fuscobalteata, T. drescheri, T. melanocephala, T. biroi, H. apicalis, H. itama, H. canifrons, G. thoracica,* and *L. terminata*. To the best of our knowledge, this paper is the first to report about stingless bee species from meliponiculture in South Kalimantan, Indonesia. Furthermore, it is also the first to report that *H. canifrons* were kept in meliponiculture in Kalimantan Island, Indonesia. Further research is needed to preserve and utilize one of Indonesia's important biodiversity resources.

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