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Description of the male of *Lepidotrigona nitidiventris* (Smith, 1857), redescription of the female holotype and additional morphological data on the workers (Hymenoptera: Apidae: Meliponini)

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Abstract: We describe for the first time the male of *Lepidotrigona nitidiventris* (Smith, 1857), emphasizing the structure of the male genital capsule and metasomal sterna four through seven. Our identification of the male as *L. nitidiventris* is based on our examination of the worker holotype (type locality Mt. Ophir, Peninsular Malaysia) which we found to match workers from the same nest as males found in western Thailand. The species belongs to the *L. nitidiventris* species group, comprising *L. latipes* (Friese), *L. palavanica* (Cockerell), *L. trochanterica* (Cockerell), with *L. nitidiventris* as the type species of the genus. No males of these species were previously known. We examined the holotype workers of the three other species and confirm all four as clearly different species. We propose, however, that the obviously smaller *L. palavanica* should not be included in the large-sized group of *Lepidotrigona*.

Keywords: Genitalia - morphology - stingless bees - taxonomy - Malaysia - Thailand.

INTRODUCTION

Stingless bees (Meliponini) are advanced eusocial insects (Michener, 1974; Quezada-Euán, 2018) and are among the most important pollinators in tropical and subtropical habitats (Roubik, 1989; Heard, 1999). Honey and propolis from stingless bees have been valuable for medicinal purposes since ancient times (Dardón & Enríquez, 2008; Umthong *et al*., 2009; Vit *et al*., 2013; Campos *et al*., 2014; Ávila *et al*., 2018). In Thailand, *Lepidotrigona* Schwarz, 1939 is one of the most important genera not only because of their pollination activities but also because their honey has a higher sugar content compared to other Thai stingless bees, the honey of which is often rather sour (Chuttong *et al*., 2016). *Lepidotrigona nitidiventris* (Smith, 1857) was designated as the type species of the subgenus *Lepidotrigona* (under the genus *Trigona*) by Schwarz (1939). *Lepidotrigona* can be differentiated from other Old World genera of meliponines classified in *Trigona* sensu lato by the tessellate miscrosculpture on the head, mesosoma, and apical metasomal terga, and by the greatly expanded metatibia of workers (Schwarz, 1939). After Rasmussen & Cameron (2010) determined that Old World *Trigona* are genetically divergent from New World *Trigona* sensu stricto, *Lepidotrigona* was elevated to generic level; thus *L. nitidiventris* is the type species of the genus. *Lepidotrigona* has been divided into three groups based primarily on size (Schwarz, 1939; Rasmussen, 2008, 2013). This classification was followed by Attasopa *et al*. (2018). The groups are the small *L*. "*ventralis*", the mid-size *L*. "*terminata*" and the large *L*. "*nitidiventris*" groups according to the length of body and forewing. Species level separation involves a combination of body size, colour of integument on metasomal terga, colour of hairs on the head and mesosoma (Schwarz, 1939; Sakagami, 1975). There are also differences among species and species groups in the male genitalia (Attasopa *et al*., 2018) although males are not known for all species. As is

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often the case with stingless bees, morphometrics is often necessary to confirm species identity (Sakagami, 1975; Koch, 2010; Hurtado-Burillo *et al*., 2016; Rattanawanne *et al*., 2017; Attasopa *et al*., 2018; Ndungu *et al*., 2018).

Among the three species groups within *Lepidotrigona*, the *L. nitidiventris* group (Rasmussen, 2008) has the largest body size. The members of the group are very rare and its taxonomy still mostly unresolved. Moreover, some species names in the *L. nitidiventris* group have been used differently by different authors. For instance, *L. palavanica* (Cockerell, 1915) was considered as a synonym of *L. nitidiventris* by Schwarz (1939), while Rasmussen (2008) considered it as a separate species within the *L. nitidiventris* species group. Another example is *L. trochanterica* (Cockerell, 1920), assumed to be a variety of *L. nitidiventris* by Schwarz (1939), but raised subsequently to full species level by Rasmussen (2008). In Thailand, so far only one species of this group has been reported, namely *L. nitidiventris*, based on workers. Workers of the species have been reported throughout many countries in South East Asia by many authors [see citations in Rasmussen (2008) which also includes non-taxonomic papers]. However, no male in the species group has yet been described.

In the course of studies on the nest entrance architecture and feeding behaviour of meliponines in Thailand (e.g. Bänziger, 2018), HB found workers and some males emerging from nests with the same trumpet-like nest entrance as built by *Lepidotrigona* (Bänziger *et al.*, 2011: figs 8, 9). The workers were readily recognized by their large size and faint yellowish wings as belonging to the *L. nitidiventris* group. Because of the importance of these males, a detailed examination of the holotype of *L. nitidiventris* was carried out by KA and compared to workers of the nest in mention. Here we re-describe the holotype worker of *L. nitidiventris* and describe the male of the species for the first time. Data on the taxa of the *L. nitidiventris* species group are also briefly analysed and differences among the species are provided along with a discussion.

MATERIALS AND METHODS

Two nests of the species, labelled as UP45 and UP88, were found around 6 km away from each other near Umphang, Tak Province, western Thailand. Workers (females) and males were captured when exiting nest UP88. No males were seen exiting nest UP45. Specimen preservation and male genitalia dissection methods follow the procedures of Attasopa *et al*. (2018). One male and one worker from nest UP88 were deposited in the Muséum d'histoire naturelle de Genève, Switzerland (MHNG), the remaining specimens are with HB at the Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University (BCMU). The type material of *L. nitidiventris* was borrowed from the Oxford University Museum of Natural History, Oxford, United Kingdom (OUMNH). Types of other species of the group were borrowed from the Natural History Museum, London, United Kingdom (NHMUK) and Museum für Naturkunde, Berlin, Germany (ZMB) (details below). The holotype of *L. nitidiventris* and Thai specimens were examined morphologically under a Nikon SMZ1500 stereomicroscope and measurements were taken with an ocular micrometer (calibrated with a stage micrometer). The metatibial ratio, as used in our analysis, is the maximum width of the metatibia compared to its maximum length (see fig. 1C in Attasopa *et al*., 2018). Images were taken at PCYU (the Packer Collection at York University, Toronto, Ontario, Canada, using a Visionary Digital BK plus with a Canon 40DSLR camera and processed with Photoshop CS6 (Adobe Inc.). The illustration of the 7th sternum was prepared following Attasopa & Warrit (2012). The specimens collected in Thailand were identified as *L. nitidiventris* by comparison with the holotype and using the original description of the species by Smith (1857). The word "hairs" without additional structural description refers to simple hairs; specialized hairs are noted as plumose hairs, robust hairs, etc. We use the word "setae" for small strong sclerotized portion on terminalia such as apical setae on S5 (as figs 2A2-C2 in Attasopa *et al*., 2018). Terminology and measurements follow Michener (2007) with some terms and additional measurements as in Attasopa *et al*. (2018) and the term metapostnotum refers to what is often called the propodeal triangle. Flagellomere, and metasomal sternum and tergum represented by F, S, and T, respectively, with the number following the letter indicating which segment. The terminology for the surfaces of legs follows Aguiar & Gibson (2010).

TAXONOMY AND RESULTS

Order: Hymenoptera
Family: Apidae
Subfamily: Apinae
Tribe: Meliponini
Genus: *Lepidotrigona* Schwarz, 1939

***Lepidotrigona nitidiventris* (Smith, 1857)**
Figs 1-17

Holotype Worker (female): Figs 1-3

Type material examined: OUMNH; worker holotype; MALAYSIA; labelled as follows: "Holo-/ type", "M. OPHIR/ 79", "*Trigona nitidiventris* ./ Smith" "*Tr. nitidiventris*/ Smith J. Pr. L./ Soc. T. 2 p 50/ Malacca M. Ophir" (see inset to Fig. 3).

Diagnosis: *Lepidotrigona nitidiventris* is the type species of the genus and also the nominate species of the species group which comprises the largest species of the genus. Workers differ from those of *L. ventralis*

and the *L. terminata* groups by a combination of body size (more than 5.5 mm) and apically expanded metatibia (spoon-like: as wide as approximately half its length, more than 0.46 times). In the other two groups the body length is usually less than 5.5 mm, and the metatibial ratio less than 0.45 times. *Leipidotrigona nitidiventris* also differs in the faintly yellow-tinged wings which are pale brownish grey in the other two groups. *Lepidotrigona nitidiventris* has robust hairs on the anterior and posterior margins of the mesoscutum and mesoscutellum, whereas the hairs are not robust on those areas in the *L. ventralis* group. *Lepidotrigona nitidiventris* can be differentiated from *L. latipes* by their brown tegula and black T2-T6, whereas they are yellowish brown and reddish brown, respectively, in *L. latipes*. The pale yellowish-brown vertex hairs in *L. nitidiventris* separate it from *L. trochanterica*, where those hairs are all black. *L. palavanica* differs from *L. nitidiventris* in being much smaller in body size and metatibial ratio.

Re-description of the species:

Structure: Body length 6.62 mm. Head wider than long (width 2.57 mm, length 1.95 mm); eye width (in side view) 0.67 mm; gena width 0.32 mm; interocellar distance 0.44 mm; ocellocular distance 0.38 mm; inner orbits slightly converging below, upper interorbital distance 1.51 mm, lower interorbital distance 1.46 mm; scape length excluding basal bulb 0.99 mm, with basal bulb 1.09 mm; 1st flagellomere length 0.16 mm; 2nd flagellomere length 0.24 mm, width 0.17 mm; 3rd flagellomere shorter than 2nd; malar space length 0.13 mm; length of longest hair on vertex 0.2 mm. Length of longest hair on mesoscutum 0.16 mm; length of longest hair on mesoscutellum 0.11 mm; forewing length 5.84 mm, width 2.32 mm; forewing diagonal 1.89 mm, length of 1st submarginal cell 0.41 mm, length of 2nd submarginal cell 0.87 mm; 1st recurrent vein before mid-length of posterior margin of 2nd submarginal cell. Metatibia length 2.51 mm, width 1.27 mm; metabasitarsus length 0.95 mm, width 0.66 mm.

Coloration of integument: Head black except as follows: apex of mandible dark brown; basal bulb and extreme base of scape, and base of F1 yellow; rest of flagellum dark brown. Mesosoma black except tegula, pronotal lobe, and sides of metanotum all brown; all legs black except all trochanters, procoxa, metacoxa ventrally, profemur ventrally, and posterior portion of metabasitarsus brown, tarsomeres 3 to 5 yellowish brown; wings hyaline to pale yellow, wing veins yellowish brown except C, R, M, and Rs brown. Metasomal terga black except basal depression and posterior margin of T1 whitish brown; metasomal sterna yellowish brown.

Pubescence: Facial hairs mostly plumose, densely appressed and whitish yellow; hairs of lower edge of labrum and mandible pale brown, hairs of vertex robust and pale yellowish-brown, longest hairs on vertex approximately 1/5 times as long as scape. Mesoscutum and mesoscutellum hairs minute yellowish white; hairs of anterior and posterior areas of mesoscutum and mesoscutellum robust, yellowish brown; mesoscutellum with some dark brown hairs intermixed, longest hairs on mesoscutum and mesoscutellum approximately 1/6th and 1/9th as long as scape, respectively; margins of mesoscutum and mesoscutellum with distinct band of short, plumose, scale-like yellow hairs, bands on mesoscutum wider anteriorly and posteriorly; mesepisternum, metepisternum, and pronotal lobe with whitish-yellow, plumose hairs, intermixed with long white hairs on mesepisternum ventrally; hairs on lateral surface of metanotum and propodeum plumose, yellowish white; metapostnotum bare; coxae and trochanters as well as ventral surface of profemur with yellowish-white hairs, rest of profemur with brown hairs intermixed with black hairs distally; tibiae with black hairs except metatibia with whitish-brown keirotrichia posteriorly; protarsi with brown hairs except probasitarsus with black hairs intermixed; meso- and metatarsi with black hairs intermixed with few brown hairs. T1 with minute, sparse, pale whitish-brown hairs except basal depression and posterior margin lacking hairs. Posterior margin of T2-T6 as well as visible portions of T5 and T6 with minute pale brown hairs intermixed with dark brown hairs on posterior half of T5 and T6; S1-S6 minute with sparse yellowish-brown hairs.

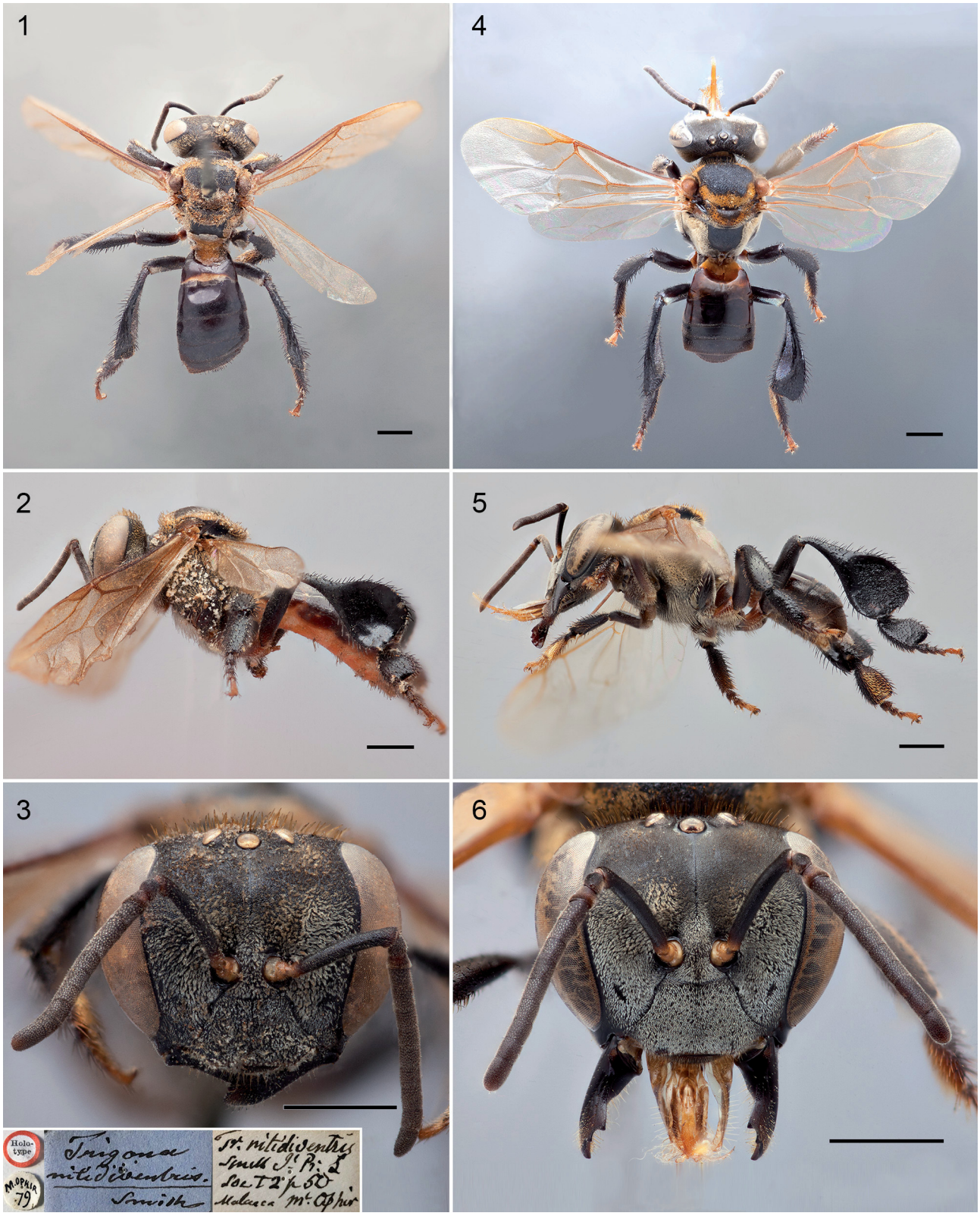
Surface sculpture: Head and mesosoma with fine, dense punctures, slightly larger on mesoscutellum; metapostnotum with larger crowded punctures all over, diameters 1.5-2 times those of head; all legs with sparse, shallow and fine punctures; lateral part of T1, posterolateral parts of T1-T4 and complete T5 and T6 with sparse shallow, fine punctures; posterior margin of T2-T4 and complete T5 and T6 with minute, shallow punctures; S1-S6 with fine shallow punctures all over.

Worker (female): Figs 4-6

Material examined: BCMU-LNW01; nest UP45; 2 workers; THAILAND, Tak Province., Umphang District; 5.V.2011; leg. prep. H. Bänziger. – All remaining specimens with the same labels except as follows: BCMU-LNW02; nest UP45; 2 workers; 19.VI.2012. – BCMU-LNW03; nest UP45; 2 workers; 21.III.2016. – BCMU-LNW04; nest UP88; 3 workers; 7.V.2016. – MHNG-LNW05; nest UP88; 1 worker; 7.V.2016.

Variation: N=10, measured as range (average±SD). As in holotype except as follows:

Structure: Body length 5.69-6.56 (6.17±0.22) mm. Head width 2.58-2.87 (2.77±0.08) mm; head length 1.84-2.03 (1.96±0.05) mm; eye width (in side view) 0.63-0.68 (0.66±0.01) mm; gena width 0.3-0.42 (0.37±0.04) mm; interocellar distance 0.42-0.48 (0.45±0.02) mm;



Figs 1-6. *Lepidotrigona nitidiventris*, worker. (1-3) The Malaysian holotype, including its label at the bottom left of (3). (4-6) Thai worker, BCMU-LNW04 (HB-W1). Dorsal habitus (1, 4), lateral habitus (2, 5), head, frontal view (3, 6). Scale bars: 1 mm.

ocellocular distance 0.38-0.42 (0.4±0.01) mm; upper interorbital distance 1.51-1.61 (1.56±0.03) mm, lower interorbital distance 1.46-1.56 (1.52±0.03) mm; scape length excluding basal bulb 0.99-1.05 (1.03±0.02) mm, with basal bulb 1.09-1.2 (1.17±0.03) mm; 1st flagellomere length 0.16-0.18 (0.17±0.01) mm; 2nd flagellomere length 0.2-0.23 (0.21±0.01) mm, width 0.16-0.18 (0.17±0.004) mm; malar space length 0.14-0.15 (0.14±0.005) mm; length of longest hairs on vertex 0.2-0.25 (0.21±0.02) mm. Length of longest hairs on mesoscutum 0.17-0.22 (0.19±0.01) mm; length of longest hairs on mesoscutellum 0.13-0.18 (0.15±0.02) mm; forewing length 5.73-6.27 (6.05±0.18) mm, width 2.35-2.52 (2.21±0.74) mm; forewing diagonal 1.94-2.03 (1.98±0.03) mm, length of 1st submarginal cell 0.44-0.48 (0.46±0.01) mm, length of 2nd submarginal cell 0.84-0.95 (0.89±0.03) mm. Metatibia length 2.51-2.67 (2.6±0.05) mm, width 1.23-1.32 (1.27±0.02) mm; metabasitarsus length 0.95-1.07 (1±0.04) mm, width 0.67-0.75 (0.7±0.02) mm.

Coloration of integument: Tegula, wing veins M, Rs, and stigma slightly paler yellow than those of the holotype; mesoscutellum dark brown, sometimes with a brown spot posteromedially; tarsomeres 3 to 5 sometimes dark brown. T1 laterally with two large black triangular spots which occasionally are in contact with each other, rest of T1 sometimes light brown; metasomal sterna vary in darkness of brown.

Pubescence: Hairs of vertex slightly darker than those of the holotype, sometimes intermixed with dark brown hairs. Metasomal sternal hairs sometimes paler than those of the holotype.

Surface sculpture: Punctures on metasomal terga vary in density, otherwise as in holotype.

Male: Figs 7-17

Material examined: BCMU-LNM01; nest UP88; 7 males; THAILAND, Tak Prov., Umphang Distr; 7.V.2016; leg. prep. H. Bänziger; caught leaving the nest [not swarming]. – MHNG-LNM02; nest UP88; 1 male; Tak Prov., Umphang Distr; 7.V.2016; leg. prep. H. Bänziger; caught leaving the nest [not swarming].

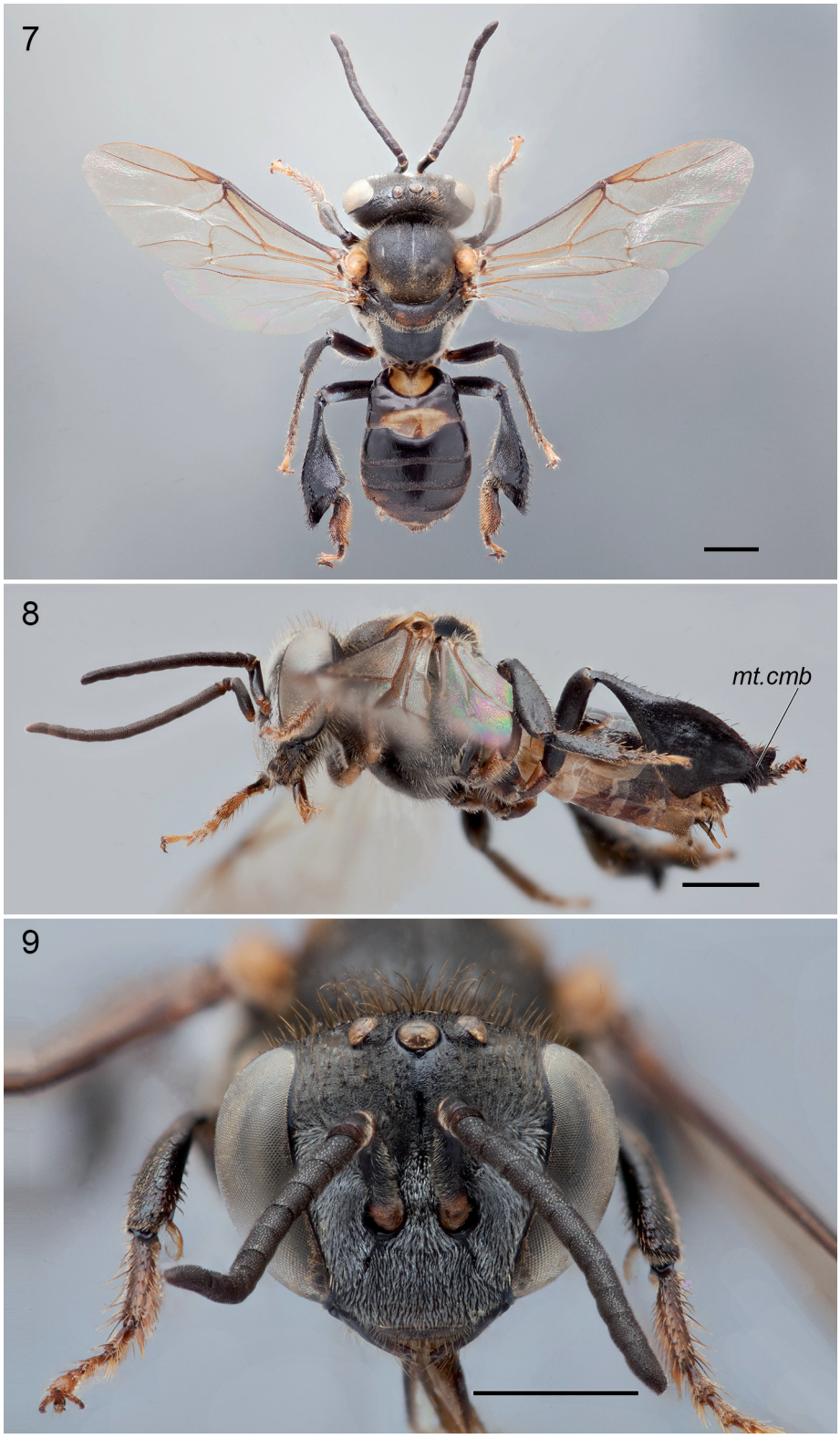
Male terminalia and associated sterna: Dissected from five males (BCMU-LNM01) with the following codes: GP3200, GP3201, GP3205, GP3365, GPKA88.

Diagnosis: Males differ from the males of *L. terminata* and *L. ventralis* group by their overall larger size, shape of the metatibia and of S5 and S6 as follows: male of *L. nitidiventris* with expanded, triangular metatibia with apical margin straight, with a black comb near apicodorsal area (missing in other species where males are known); metatibial hairs dark brown to black (Figs 7, 8). Metatibia of other species simple, rounded apically, without comb, with hairs grey to brown or intermixed with few dark brown hairs. S5 of *L. nitidiventris* has long protruding apical-lateral lobes, but no subapical lobes (Fig. 11), whereas S5 of other known males of the genus have short to very short lateral lobes, two distinct subapical lobes, and strong apical setae. S6 of *L. nitidiventris* with two deep subapical emarginations with long, narrow apical-medial lobes (Fig. 12), S6 of other known males of the genus do not have or have only weakly produced subapical emarginations, and short apical-medial lobes. Genital capsule of *L. nitidiventris* bilaterally symmetrical (Fig. 16), asymmetrical in the known species that belong to the *L. ventralis* group.

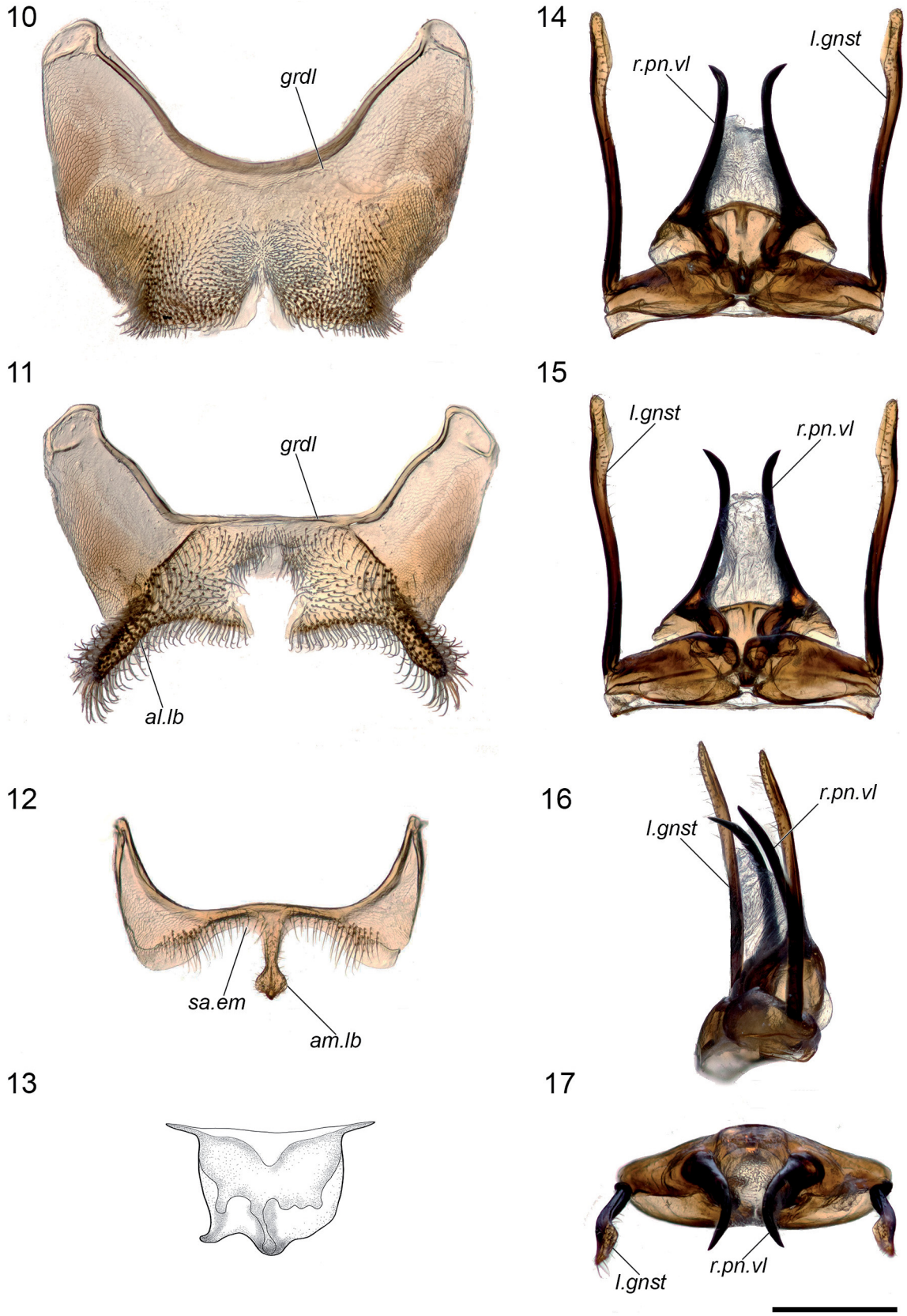
Description: N=8, measured as range (average±SD). As in the worker holotype except as follows:

Structure: Body length 6.19-6.98 (6.56±0.3) mm. Head width 2.4-2.62 (2.55±0.07) mm; head length 1.81-2 (1.89±0.06) mm; eye width (in side view) 0.62-0.72 (0.68±0.04) mm; gena width 0.28-0.37 (0.31±0.03) mm; interocellar distance 0.4-0.55 (0.49±0.05) mm; ocellocular distance 0.3-0.33 (0.33±0.01) mm; inner orbits converging below, upper interorbital distance 1.49-1.56 (1.52±0.02) mm, lower interorbital distance 1.04-1.11 (1.07±0.02) mm; scape length excluding basal bulb 0.75-0.78 (0.78±0.01) mm, with basal bulb 0.88-0.95 (0.93±0.02) mm; 1st flagellomere length 0.14-0.16 (0.15±0.01) mm; 2nd flagellomere length 0.28-0.3 (0.3±0.01) mm, width 0.16-0.17 (0.16±0.004) mm; malar space length 0.02-0.03 (0.03±0.003) mm; length of longest hairs on vertex 0.33-0.43 (0.37±0.04) mm. Length of longest hairs on mesoscutum 0.2-0.24 (0.22±0.01) mm; length of longest hairs on mesoscutellum 0.16-0.18 (0.17±0.01) mm; forewing length 5.6-6.05 (5.86±0.14) mm, width 2.05-2.18 (2.12±0.04) mm; forewing diagonal 1.78-1.97 (1.86±0.06) mm, length of 1st submarginal cell 0.43-0.48 (0.45±0.02) mm, 2nd submarginal cell length 0.77-0.83 (0.8±0.02) mm. Metatibia length 2.48-2.66 (2.57±0.07) mm, width 1.08-1.2 (1.16±0.03) mm; metabasitarsus length 0.7-0.77 (0.73±0.02) mm, width 0.48-0.53 (0.51±0.02) mm. Apex of S1 and S2 entire, S3 with small narrow emargination apicomedially; apical margin of metatibia flat diagonally (not rounded) forming a triangular-shaped metatibia, and with a black metatibial comb on the apex near the dorsal margin.

Coloration of integument: Yellowish-brown area on F1 slightly darker than in holotype. Mesosoma black except tegula and pronotal lobe light brown, mesoscutellum seldom with yellowish-brown spot posteromedially; procoxa and proximoventral area of profemur brown, protrochanter and protarsus yellowish brown, rest of fore leg black; mid and hind legs black except mesotrochanter, and meso- and metatarsomeres 4-5 yellowish-brown, metatrochanter and ventral area of meso- and metafemurs brown, anterodistal and posterior area of metatibia and metabasitarsus sometimes brown, hyaline wings pale yellowish, slightly more brownish tinged than in workers,



Figs 7-9. *Lepidotrigona nitidiventris*, male, BCMU-LNM01 (HB-M1). Dorsal habitus (7), lateral habitus (8), head, frontal view (9). *mt.cmb* – metatibial comb. Scale bars: 1 mm.



Figs 10-17. *Lepidotrigona nitidiventris*, male terminalia and associated sterna, BCMU-LNM01 (HB-M1), GPKA88. (10-13) S4-S7, ventral view. (14-17) Genital capsule. Dorsal aspect (14), ventral aspect (15), lateral aspect (16), caudal aspect (17). *al.lb* – apicolateral lobe, *am.lb* – apicomedian lobe, *grdl* – gradulus, *l.gnst* – left gonostylus, *r.pn.vl* – right penis valve, *sa.em* – subapical emargination. All figures are shown at the same scale. Scale bar: 0.5 mm.

wing veins yellowish brown except C and R, dark brown. Metasomal terga black except basal depression of T1 brownish white or vary to light brown, T6 and T7 sometimes dark brown; S1-S7 light brown.

Pubescence: Hairs of vertex long whitish brown, longest hairs approximately half of scape length; scape with thin white hairs medioventrally. Hairs of mesoscutum and mesoscutellum mostly whitish brown with brown hairs intermixed on mesoscutellum posteriorly, the longest hairs on mesoscutum and mesoscutellum approximately 3/10 and 2/9 as long as scape, respectively; posterolateral margin of mesoscutum with thinly scattered whitish-yellow plumose hairs, which vary in density, sometimes to the point that the plumose hairs are missing altogether laterally; pronotal lobe, mesepisternum, metepisternum, lateral surface of propodeum, and metanotum with short, plumose, yellowish-white hairs intermixed with yellowish-white simple hairs, the simple hairs longest on mesepisternum ventrally; coxae and trochanters with long white hairs; femurs with white hairs ventrally and with short dark brown hair dorsodistally; protarsi with light brown hairs intermixed with few dark brown hairs; pro-, mesotibiae, and metatarsus with dark brown hairs intermixed with few whitish-brown hairs; metatibia with black or sometimes dark brown hairs, and with a black comb restricted to the apical angle, as well as with yellowish-white keirotrichia posteriorly. Metasomal tergal hairs as those of the holotype except lateral and posterior area of T4-T5, T6 and T7 posteriorly with black hairs; S1-S3 with short brown hairs.

Surface sculpture: As for the holotype but punctures smaller and denser on mesoscutum.

Terminalia and associated sterna: S4 emarginate apicomedially forming an apex with two broad shallow lobes, S4 gradulus almost touching anterior margin of sternum anteromedially; area posterior to gradulus with short hairs, the hairs denser on lateral lobes, and with a brown spot laterally (Fig. 10). S5 with long protruding apicolateral lobe posterolaterally oriented, and with deep emargination apicomedially, gradulus transverse medially, touching anterior margin of sternum; S5 with hairs on posterior area from gradulus, longer on posterior margin and apicolateral lobe; S5 brown marked laterally, darker on the apicolateral lobe (Fig. 11). S6 biconcave with long apicomedial lobe, narrowing distally with spatulate apex, apical emarginations with long hairs (Fig. 12). S7 convex apicomedially and bisinuate apicolaterally, with small asymmetrical subapicolateral lobes, the left lobe appearing to be slightly more protruding than the right one (Fig. 13). Gonostylus longer than penis valve, tip expanded widest at approximately apical 1/6, genital capsule and apical 1/3 of gonostylus light brown except penis valve and the remainder of gonostylus black. Penis valve narrow, first weakly curved ventrally mainly at mid-length, slightly curved lateroventrally towards apex (Figs 14-17).

Additional type material examined:

***Lepidotrigona latipes* (Friese, 1900)**

Type material examined: ZMB; worker holotype; MALAYSIA [Malacca, not Singapore, see discussion]; labelled as follows: “India/ Singapore/ 1890”, “Trigona/ latipes/F. /1909 Friese det.”, “Type”, “Coll Friese”, “HOLOTYPE/ Trigona/ latipes Friese/ Examined C Rasmussen ’07”.

***Lepidotrigona palavanica* (Cockerell, 1915)**

Type material examined: NHMUK 013379686; worker holotype; PHLIPPINES; labelled as follows: “Type”, “Trigona/ palavanica/ CKll. TYPE.”, “B.M. TYPE HYM. 17B.1120”, “3839”, “P. Princess/ Palawan/ Baker”, “Brit: Mus 1933-567.”.

***Lepidotrigona trochanterica* (Cockerell, 1920)**

Type material examined: NHMUK 013379685; worker holotype; MALAYSIA, labelled as follows: “Type”, “B.M. TYPE HYM. 17B.1102”, “Trigona/ trochanterica/ CKll. TYPE.”, “Sadakan/ Borneo/ Baket”, “Brit Mus./ 1933-567.”.

DISCUSSION

Our finding that the holotype worker of *L. nitidiventris* matched the workers from the two nests from western Thailand came as a surprise because of the geographic distance between the type locality and the new sites. In our previous study (Attasopa *et al*., 2018), we found that each of the small *Lepidotrigona* species are present only within a radius of some 300-500 km, whereas the distance between the Malaysian type locality and the Thai sites of *L. nitidiventris* is about 1500 km. Admittedly, *L. nitidiventris* is much larger, nearly twice the forewing length, and it is well-known that flying distance in meliponines is correlated partially with forewing length (e.g. Araújo *et al*., 2004), as it is in general with bees as a whole (Greenleaf *et al*., 2007). However, Bänziger (2018) found that in lachryphagous meliponines, e.g. the minute *Lisotrigona furva* Engel, the flying distance is four or more times that of *Tetragonula iridipennis* (Smith) although this species is larger – possibly an adaptation to a mobile and ephemeral source in tear drinkers. So there can be exceptions to the rule. Rathor *et al*. (2013) and Rasmussen (2013) found *Tetragonula gressitti* (Sakagami) in Northeast India, a distance of more than 2000 km from the type locality in southern Vietnam (Dalat). Unfortunately, due to the rarity of both species, no DNA analyses have yet been possible for corroboration of the conspecificity of the geographically distant samples of *L. nitidiventris* or *T. gressitti*. Nevertheless, there are DNA-based studies which show that South American *Scaptotrigona xanthotricha* Moure

has only weak molecular isolation over a distance of nearly 2000 km (Duarte *et al*., 2014). With a body length of 6-7 mm this species is comparable in size to *L. nitidiventris*.

Males of *L. nitidiventris* can be compared to the males of the other two *Lepidotrigona* groups: the mid-sized *L. terminata* (sensu Schwarz, 1939: fig. 15) and the small-sized *L. satun* Attasopa & Bänziger, 2018, *L. doipaensis* (Schwarz, 1939), and *L. flavibasis* (Cockerell, 1929) (Attasopa *et al*., 2018: figs 5A, 7B, 8B) the metatibia lacks a comb near the apicodorsal area. In *L. nitidiventris* the metatibia is unique in having an apical comb and in being triangular in-shape (Figs 7, 8). In contrast, the males of the other two species groups lack the comb and have a narrower shaped metatibia. Another good character to separate *L. nitidiventris* from all the other known males of the genus is S5: in *L. nitidiventris* it lacks the subapical lobes but has long apicolateral lobes (Fig. 11), whereas all other known males have subapical lobes with apical setae but only short lateral lobes [Schwarz, 1939: fig. 16B; Attasopa *et al*., 2018: fig. 2 (A2, B2, C2)].

Concerning the other three species of the *L. nitidiventris* group, we make the following comments. When Schwarz (1939) treated *L. palavanica* he was not sure whether it was a variety of *L. nitidiventris* because he had not studied the type of the former species. He knew the species only from Cockerell's (1915) description. However, according to our examination of the *L. palavanica* type, this taxon is much smaller than any species of the *L. nitidiventris* group and the metatibial ratio is only 0.45, clearly smaller than the ratio found in species of the *L. nitidiventris* group. Therefore, *L. palavanica* should not be considered as a member of the *L. nitidiventris* group as it is closer in size and metatibial shape to species of the *L. terminata* group, to which it might belong. Phylogenetic analyses are required to determine the make-up of subgroups within the genus and it would seem that discovery of the males of more species will be valuable in providing useful characters.

Our examination of the holotypes of *L. latipes* and *L. trochanterica* reveals them to be large bees (body length more than 5.5 mm) with a high metatibial ratio (more than 0.46). Consequently, they belong to the *L. nitidiventris* group. Our examination of their holotypes indicates that *L. latipes* and *L. trochanterica* clearly differ from each other as well as from *L. nitidiventris* as stated in the diagnosis of the latter species.

The type locality of *L. latipes* poses a problem. The label of the holotype, viz. "India/ Singapore/ 1890", does not make much sense. Friese's (1900) description of the species was in Latin. For the type locality he wrote (in German): "1♀von *Malacca* (Singapore)" [Friese's italics; also, "von" meaning "from"]. This is problematic because Singapore, both a town and an island, is 200 km southeast of Malacca. We interpret Singapore (written by Friese in parentheses) as the broader geographic-political designation of the locality in Friese's time, not the actual collecting site. In those times, Malacca was part of the so-called Straits Settlements, a British Crown Colony from 1867 to 1947. They consisted of Penang, Malacca, Dinding, and Singapore. Singapore was the Seat of Government of the Straits Settlements. We understand that Friese used Singapore as the broader, better-known regional name for the Settlements, as we would now use Malaysia for Malacca. Consequently we consider that the type locality of *L. latipes* is Malacca (in peninsular Malaysia), not Singapore.

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