Stingless Bees of the Genus *Trigona* (Subgen. *Geniotrigona*) (Hymenoptera, Apidae), with Description of *T. (G.) incisa* sp. nov. from Sulawesi[1]

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Abstract   *Trigona incisa* sp. nov. is described based on workers from Sulawesi as a second species of the subgenus *Geniotrigona*.   The unknown male of *T. (G.) thoracica* is described and some taxonomic comments are given on *Geniotrigona*, including its probable affinity with *Trigonella* and *Heterotrigona*.

Introduction

Geniotrigona Moure, 1961, was erected as a monobasic genus for the reception of *Trigona thoracica* Smith, 1857, the largest Malesian stingless bee species with long malar space.   *Geniotrigona* is regarded as a subgenus of the genus *Trigona* Jurine, 1807, in our system (Sakagami, 1975), although it was included in the subgenus *Tetragona* Lepeletier et Serville, 1828, in a lumping system (Sakagami, 1975, 1982; Schwarz, 1948; Wille & Michener, 1973; Wille, 1979).   In this paper, *T. incisa* sp. nov. is described synoptically compared with *T. thoracica* as a second species of *Geniotrigona* based on workers from Sulawesi (Celebes).   The so far unknown male of *T. thoracica* is also described and the taxonomic position of *Geniotrigona* is commented on.

Trigona (Geniotrigona) incisa sp. nov.

(Figs. 2, 4, 7, 8, 10, 27, 29–30, 45, 48, 53–54, 60)

Worker.   Robust.   Concolorously blackish.   Short appressed hairs sparser, paler and less woolly than in *T. thoracica*.   Occiput medially incised, malar space

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1)   Contribution to the knowledge of the Indopacific stingless bees XII, and contribution No. 37 of Sumatra Nature Study (Entomology).

longer than flagellar width but much shorter than in *T. thoracica*, second mandibular tooth distinct though slender.

Body 5.8±0.5 mm, wing with tegula 7.7±2.0 mm ($n=10$).

Coloration　Concolorously black to brownish black, mesosomal dorsum not reddish brown as in *thoracica*, mandible apically, flagella frontally, antennal socket and hind tibia occasionally paler.　Wings distinctly more infuscated than in *thoracica*, veins and pterostigma dark brown.

Pilosity　Erect, spinous and black hairs on occiput 200 μm, less stout than in *thoracica* (Figs. 1–2).　Ocellocular area and frons down to upper extremity of frontal carina with fine, simple and appressed dark brown hairs and surface clearly visible instead of bearing denser, ochraceous and poorly plumose hairs as in *thoracica*. Face and supraclypeus with hairs dense, dark brown, plumose and fairly covering surface although far sparser than paler and very dense toment-like hairs in *thoracica* which cover face, paraocular area and clypeus rather homogeneously (often detached) and poorly plumose only partly; paraocular area below with brown ocher hairs, denser, longer (75 μm), more conspicuously plumose and covering surface completely.　Clypeus with hairs dense, homogeneous, short (25 μm), brown, appressed and poorly plumose.　Gena similar but hairs simple and less covering surface, below sparser and longer (50–75 μm) as on malar area.

Mesoscutum and mesoscutellum with dense, erect, dark brown and simple or poorly plumose hairs (50 μm), admixed with sparse, black and erect spinous hairs, instead of bright yellow ocher, conspicuously plumose and woolly hairs admixed with stouter, spinous hairs as in *thoracica*.　Metanotum with dense, homogeneous and plumose hairs, fine and greyish white instead of yellow ocher and woolly as in *thoracica*.　Meso- and metapleuron with dense, whitish to pale yellow, short (75 μm) and plumose hairs, denser on metapleuron above while sparser on mesopleuron below, admixed with sparser and longer hairs, shorter (250 μm), stouter and brown to dark brown above and longer (400 μm), finer and nearly whitish below, instead of bearing homogeneously dense, bright yellow ocher, woolly hairs with brown spinous hairs as in *thoracica*.

Propodeum laterally with dense, whitish, plumose hairs, not bright yellow ocher, extremely dense and woolly as in *thoracica*, median glabrous area narrower than in *thoracica* and shaped invert-triangularly (Figs. 10–11).

Legs with hairs black, trochanters and femora below whitish, not yellowish as in *thoracica*.　Hairs on outer surface of midtarsi distinctly plumose posteriorly. Corbicular surface basally with simple hairs (100–300 μm) mixed with longer (300 μm) and apically plumose hairs, apically with sparse, simple and stouter hairs. Posterior corbicular fringe 250 μm, nearly entirely (=not apical part alone) plumose; posterior parapenicillum bristle-like, apical hairs curved distinctly but not exaggeratedly as in *thoracica* (Figs. 44–45).

Metasomal tergum 1 (T_1) with finest and brownish hairs (±2.5 μm) very sparsely, seen as if glabrous.　T_2 similar but laterally with marginal band (±7.5
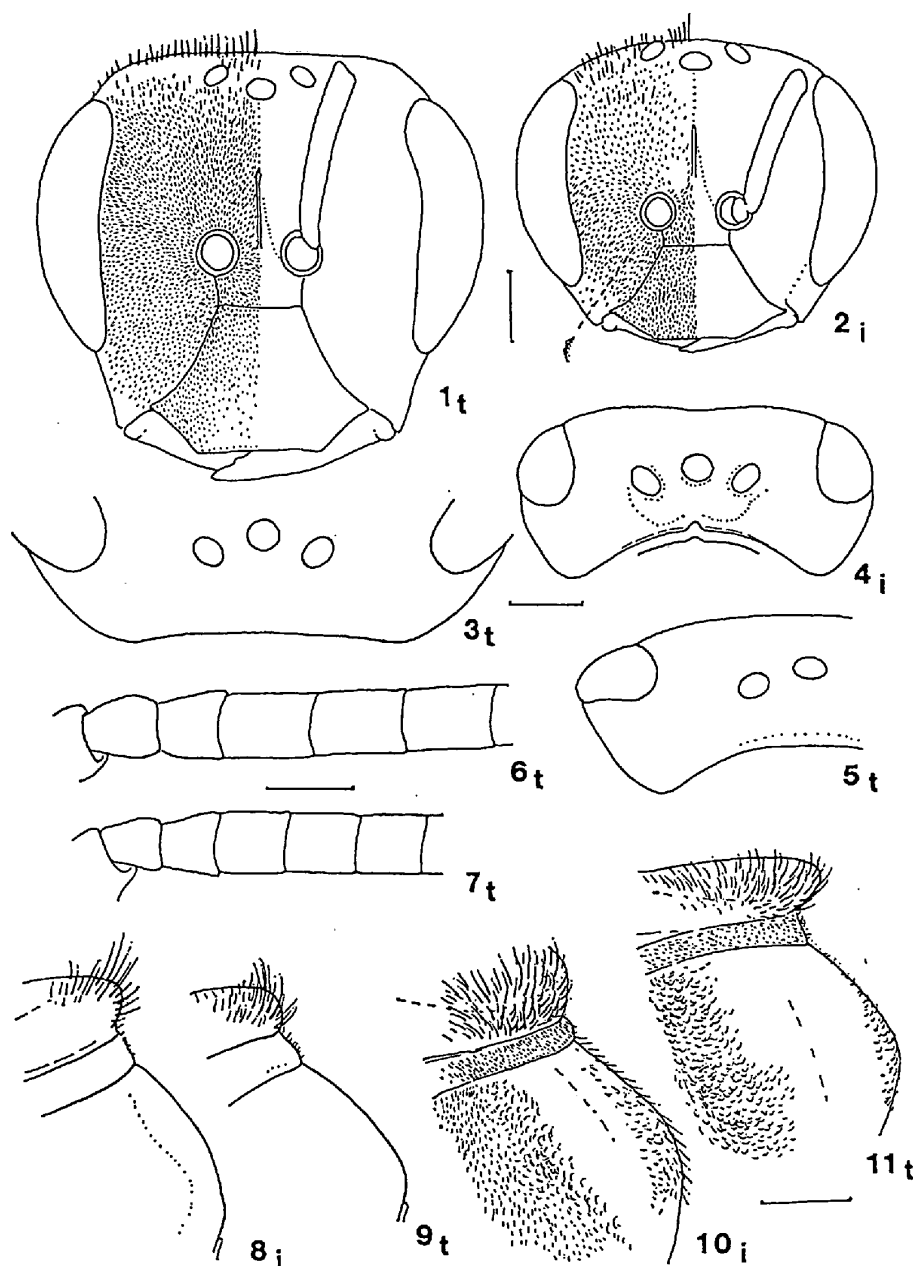
Figs. 1-11.   Workers of *Trigona thoracica* (t) and *T. incisa* sp. nov. (i) —— 1-2, Head seen frontally; 3-5, vertex seen dorsally (3-4, vertex oriented horizontally; 5, occipital line oriented as in Fig. 4; variation of occipital incision shown in Fig. 4 with two extremes); 6-7, basal flagellomeres of left antenna; 8-9, propodeum seen laterally; 10-11, ditto seen obliquely.   Scale=0.5 mm in Figs. 1-5, 8-11; 0.25 mm in Figs. 6-7.   Erratum Fig. 7t→Fig. 7i

μm wide) consisting of dense, finest hairs. T_3 and particularly T_4 with marginal bands wider (250 μm) and entire, discs also with hairs slightly denser. $T_{5,6}$ with hairs homogeneously denser and longer (max. 100 μm), not partly plumose as in *thoracica*; laterally with sparse, spinous and black hairs, long, erect hairs on pos-
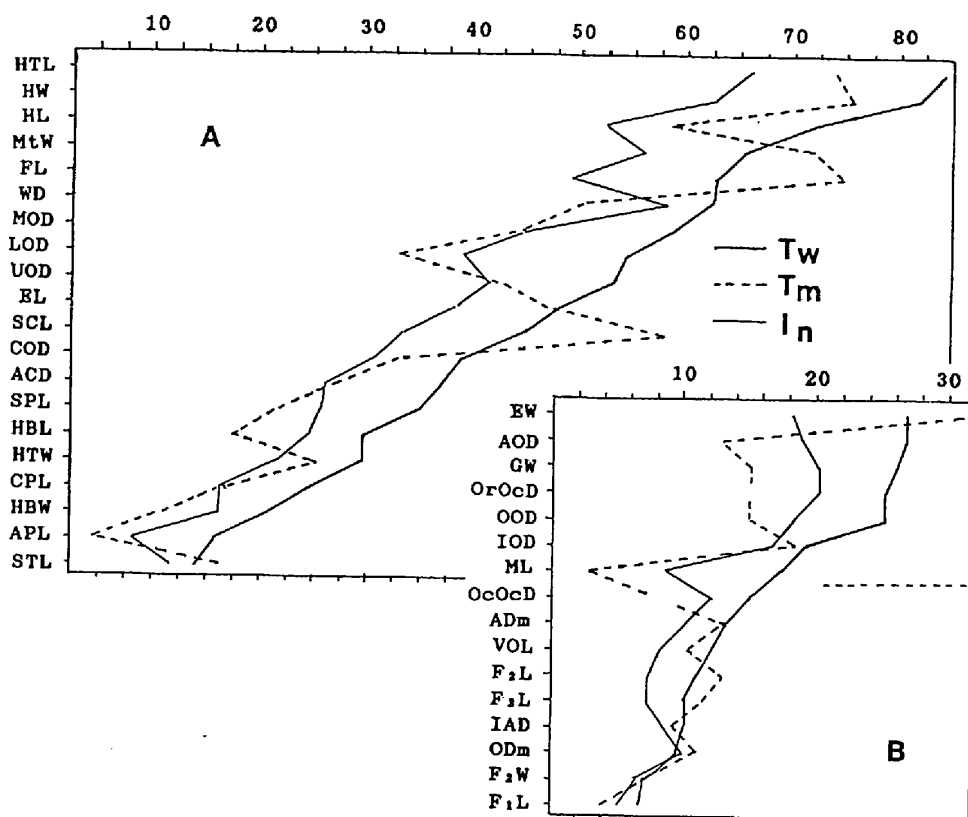
Fig. 12. Comparison of metric characters in *T. thoracica* (worker and male, Tw, Tm) and *T. incisa* sp. nov. (worker, In). Characters are arranged, in both A (25 units=1 mm) and B (40 units=1 mm), according to the descending order in Tw. Explanation of each character is given in the text.

terior parts of sterna brownish, not black and stouter as in *thoracica*.

Sculpture   Ignoring micropunctures bearing hairs, surface generally smooth and shining.   On apical terga, areas around punctures bearing hairs rather widely depressed as in *thoracica*.

Metric characters (Fig. 12)   Given with mean±SD ($n=10$ or in *incisa* partly $n=5$ or 7) for *thoracica/incisa*, arranged in the descending order in *thoracica* (L, W=maximum length and width, D=minimum distance).

A (25 units=1 mm); HTL (hind tibia L) $84.5\pm0.9/65.9\pm2.4$, HW (head W) $82.0\pm1.3/62.6\pm1.9$, HL (head L) $72.1\pm2.3/52.1\pm2.0$, MtW (metasoma W) $65.2\pm2.9/55.8\pm1.2(5)$, FL (flagellar L) $62.8\pm1.5/48.8\pm0.4(5)$, WD (wing diagonal=D between M–Cu bifurcation and inner tip of marginal cell) $62.3\pm0.9/58.3\pm1.6$, MOD (maximum interorbital D) $58.8\pm1.7/45.2\pm1.7$, LOD (lower interorbital D) $54.2\pm1.4/38.9\pm1.0$, UOD (upper interorbital D) $53.1\pm1.4/41.2\pm0.9$, EL (eye L) $47.5\pm1.1/38.1\pm1.6$, SCL (mesoscutum L) $44.5\pm0.7/33.4\pm0.9$, COD (clypeocellar D) $38.6\pm1.4/30.8+1.1$, ACD (alveoclypeal D, alveolus=antennal socket) $37.0\pm0.8/26.1\pm1.0$, SPL (scape L) $34.9\pm0.8/25.7\pm0.8(5)$, HBL (hind basitarsus L) 29.6

$\pm 1.0/24.5\pm 1.0$, HTW (hind tibia W) $29.6\pm 0.9/21.8\pm 1.0$, CPL (clypeus L) $24.6\pm 0.5/16.2\pm 1.4$, HBW (hind basitarsus W) $20.0\pm 0.7/16.0\pm 0.9$, APL (apical part of clypeus L=L of part exceeding lower interorbital line) $15.8\pm 1.1/8.0\pm 0.7$, STL (mesoscutellum L) $14.1\pm 0.8/11.6\pm 0.7$.

B (40 units=1 mm): EW (eye W, seen laterally, not maximally) $26.4\pm 0.9/18.2\pm 0.6$, AOD (alveorbital D) $26.4\pm 0.9/18.8\pm 0.4(5)$, GW (gena W, seen laterally) $26.0\pm 1.2/20.4\pm 1.5$, OrOcD (orbitoccipital D) $25.1\pm 0.7/21.3\pm 0.9(7)$, OOD (ocellocular D) $25.1\pm 0.7/18.1\pm 0.7$, IOD (interocellar D) $18.2\pm 0.9/16.3\pm 0.9$, ML (malar length, minimum) $17.6\pm 0.7/8.5\pm 0.5$, OcOcD (ocelloccipital D) $15.3\pm 0.5/12.9\pm 0.8(7)$, ADm (transverse diameter of alveolus) $12.5\pm 0.4/10.3\pm 0.4(5)$, VOL (verticorbital L=tangential L between summit of head and supraorbital line) $12.1\pm 0.7/8.2\pm 0.4$, $F_{1,2,3}$ L, F_2W (flagellomere 1, 2, 3 L, flagellomere 2 W) $7.1\pm 0.22/5.2\pm 0.2(5)$, $11.2\pm 0.4/7.5\pm 0.3(5)$, $10.4\pm 0.3/7.5\pm 0.3(5)$, $7.3\pm 0.2/6.5\pm 0.4$, IAD (interalveolar D) $10.3\pm 0.7/8.7\pm 0.4(5)$, ODm (transverse diameter of median ocellus) $9.4\pm 0.5/8.2\pm 0.3$.

Structure Seen laterally vertex gently rounded, not flat and obliquely raised postward as in *thoracica*. Gena slightly wider than eye, not as wide as eye as in *thoracica*; scape above not exceeding median ocellus as in *thoracica*. Seen dorsally (Figs. 4–5), gena distinctly extended postward; occipital margin distinctly incurved and raised, and, unlike in *thoracica*, medially more or less distinctly incised triangularly; postocellar area greatly elevated than flatter as in *thoracica* (Figs. 4–5).

Seen frontally (Figs. 1–2), contour of vertex gently curved and laterally seldom angulate, not horizontal and laterally not rounded but appreciably angulate as in *thoracica*; lateral ocellus on contour, not below as in *thoracica*; anterior tangent of median ocellus on or slightly above supraorbital line, not below as in *thoracica*. Frontal carina weak but distinct as in *thoracica*. Inner orbit below convergent slightly but more than in *thoracica*.

Malar space much shorter than in *thoracica* (Figs. 1–2, 60–61). Flagella distinctly shorter than in *thoracica* with shorter basal flagellomeres (Figs. 6–7). Mandible bidentate, outer notch narrowed, inner notch deeper, and inner tooth more distinct than in *thoracica*, though slender (Figs. 53–55).

Hind tibia with inner margin less curved than in *thoracica* (Figs. 44–45), below posterior slope of longitudinal elevation steeper and sparsely haired than gentler and glabrous as in *thoracica*, and posterior glabrous area narrower than in *thoracica* (Figs. 47–48); width of longitudinal haired elevation and glabrous area 10:8 in *incisa* and 10:13 in *thoracica*. Submarginal cells traceable as in *thoracica* (Figs. 26–27). Metasoma relatively shorter and wider than in *thoracica*.

Specimens examined (all from Sulawesi (Celebes)). Holotype 1 worker, Modoinding, Minahasa, N. Celebes, vi. 26–27, 1941, native collector, ded. F. DUPONT; Paratypes 2 workers, same data with holotype; 3 ww, Todyamboe, 900 m, C. Celebes, vii. 1936, L. J. TOXOPEUS; 9 ww, Wuasa, Kab. Poso, Sulteng, Sulawesi, x. 10. 1984, K. WATANABE; 3 ww, Lorei Lindu Nat. Park, C. Sulawesi, C. v. ACHTERBERG,

1985 (1 w, Gn. Tokosa, 2,100–2,200 m, xii 8; 2 ww, Lake Tambing, xii 5–9, Mal. Tarp 5, Swamp). Holotype, another w from Modoinding, 2 ww from Todyamboe and 3 ww from Lorei Lindu in Rijksmuseum van Natuurlijke Historie, Leiden, 1 w in Museum Zoologicum Bogoriense, Bogor, and all others tentatively with SFS.

### *Trigona* (*Geniotrigona*) *thoracica* Smith, 1857

(Figs. 1, 3, 5–6, 9, 11, 13–26, 28, 31–33, 35–36, 39–40, 42–44, 47, 55, 61)

Male. New to science. Coloration after full pigmentation unknown. Head transverse, vertex raised medially, malar space much shorter than in worker. Modified sterna 5 and 6, and highly modified hind leg similar to those of *Trigona* (*Heterotrigona*) *itama* and *T.* (*Trigonella*) spp.

Body 8.6±0.4 mm, wing with tegula 7.8±1.0 mm ($n=6$).

Coloration (based on two darkest ♂♂ from nest). Black. Flagella frontally and apex of scape frontally blackish brown, alveolus, scape frontally, supraclypeus below alveolus, clypeus, pronotum, mesopleuron partly, metapleuron mostly, mesoscutellum apically, metanotum, propodeum laterally, terga basally, sterna and legs brown to pale brown. Femora, tibiae and basitarsi above partly darker to blackish, claws apically black. Mandible brown, medially deeper, apex narrowly black. Wings transparent, distinctly brownish, veins blackish, pterostigma dark brown.

Pilosity Brown even in deepest-pigmented individuals. Erect hairs on vertex less stout than in ww (=worker), medially to 450 μm and curved apically, laterally ±250 μm and rather straight (Fig. 13). Hairs shorter (125–175 μm) and sparser on ocellocular area, becoming denser and longer (to 375 μm) on frons. Head above with no admixture of stout hairs as in ww. Hairs on face, supraclypeus (50 μm), clypeus and paraocular area (125 μm) short, appressed and simple or
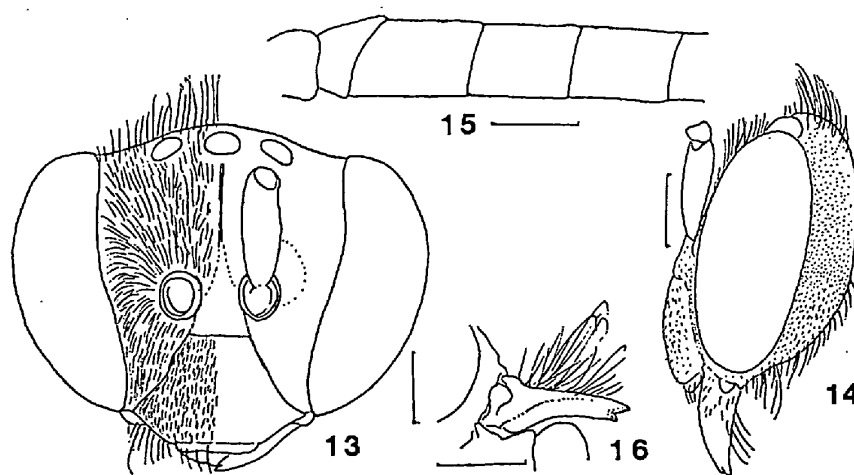
Figs. 13–16. Male of *T. thoracica.* —— 13–14, Head seen frontally and laterally; 15, basal flagellomeres of left antenna; 16, left mandible. Scale=0.5 mm.

poorly plumose, around alveolus, denser, more plumose and completely covering surface (Figs. 13–16). Labrum with erect and simple hairs (175 μm) (Fig. 13), maximum hairs of mandibular beard 625 μm, slightly curved apically (Fig. 16). Gena with appressed hairs, above 50 μm, poorly plumose and moderately dense; below 75 μm, distinctly plumose and denser, though not covering surface completely (Fig. 14).

Mesoscutum with long (anteriorly 325 μm, centrally 200 μm), simple and erect hairs and short (100 μm), long-branched, woolly hairs, both combined incompletely covering surface; mesoscutellum similar, apical fringe not particularly long, to 300 μm; metanotum with rather dense, long-branched hairs. Mesopleuron with curved, long-branched, and woolly hairs moderately densely, surface visible except uppermost part, below and metapleuron with hairs simple and less curved. Propodeum laterally with dense, plumose hairs concealing surface, medially broadly glabrous as in ww.

Mid tibia above densely and homogeneously with short (25–75 μm) and simple hairs, posterior fringe simple, 125–175 μm, rarely 200 μm. Hind tibia above (Fig. 33) with homogeneously dense and simple appressed hairs (75 μm); apicomedially sparser, mixed with longer semierect hairs, posterior fringe sparse, 100–125 μm; below with wide longitudinal band of very dense setae ($\pm$50 μm), anterior slope glabrous, with sparse, 175–250 μm bristles on apical part (Fig. 35), postmarginal slope glabrous with very sparse and short (75 μm) hairs. Hind basitarsus above (Fig. 33) with sparse hairs (75 μm), posterior hairs to 175 μm, that below homogeneously with dense and stout bristles, sparser basally, while denser and longer (to 175 μm) apically (Fig. 35).

$T_{1,2}$ glabrous, T_2 with narrow marginal band consisting of dense, minute (30 μm) and appressed setae. T_3 similar but band broader, medially occupying about 1/2 of disc and laterally more. T_4 nearly entirely pubescent. T_5 with hairs longer (100 μm) and woolly, laterally with simple bristles ($\pm$150 μm). T_6 with bristles also on disc. Sterna on apical halves with dense and appressed hairs (25–50 μm), on S_2 sparser medially and on other sterna variously differentiated as described below.

Sculpture. Head with dense, homogeneous and minute micropunctures; interspaces dimly shining, slightly wider on ocellocular area with obscure etchings. Mesosomal dorsum with punctures finer and sparser, and interspaces smooth and shining. Tergal glabrous part virtually smooth and shining, though with very superficial lineolation, marginal haired band densely micropunctate, premarginally with sparse punctures 25 μm in diameter.

Metric characters. Presented as in ww (n=7). Difference from ww often conspicuous as shown in Fig. 12.

A (25 units=1 mm): HW 75.6$\pm$0.7, FL 74.6$\pm$1.2, HTL 74.0$\pm$0.9, MtW 71.7$\pm$2.4, HL 58.7$\pm$0.7, SCL 57.9$\pm$1.0, WD 50.4$\pm$1.2, EL 47.0$\pm$0.9, MOD 44.7$\pm$1.2, UOD 43.0$\pm$0.8, COD 33.1$\pm$0.4, LOD 32.8$\pm$0.6, ACD 27.3$\pm$0.4, HTW 25.3$\pm$0.7, SPL 21.9$\pm$0.6, HBL 17.8$\pm$1.0, CPL 16.8$\pm$0.4, STL 16.2$\pm$0.8, HBW 11.4$\pm$

1.0, APL 4.4±0.5.

B (40 units=1 mm): EW 31.1±2.8, IOD 18.6±0.5, OOD 15.1±0.6, GW 15.1±0.5, ADm 13.0±0.5, F_2L 12.9±0.6, AOD 12.7±0.4, ODm 11.4±0.4, F_3L 11.3±0.4, F_4L 10.7±0.4, VOL 10.4±0.7, IAD 9.4±0.5, F_2W 7.0±0.0, ML 2.7±0.2.

Structure. Head seen laterally, vertex rounded, not raised postward as in ww, and gena and malar space much narrower (Fig. 14). Seen dorsally postocellar line slightly behind supraorbital line, postocellar area gently raised, occiput not carinate; area surrounding median ocellus narrowly, and area postlateral to lateral ocellus evenly depressed. Seen frontally, head transverse, much shorter and vertex much raised medially than in ww (Figs. 13, 1); lateral ocellus oblique, not attaining summit and the lower rim slightly below supraorbital line; eye very large, outer orbit conspicuously rounded, inner orbit distinctly convergent below and gently sinuous. Frons flat, face medially longitudinally depressed, frontal sulcus attaining slightly below median ocellus. Supraclypeus and clypeus mildly convex. Antennal scape not attaining median ocellus (Fig. 14). Flagellomeres except F_1 distinctly longer than width (Fig. 15). Mandible bidentate (Fig. 16).

Mesoscutum fairly convex, mesoscutellum seldom projecting beyond metanotum Seen laterally, propodeum basally oblique, gently flexing midway. Mid tibia above very gently convex; mid basitarsus slender, posterior margin basally divergent, apically parallel with anterior margin; mid distitarsi normal (Fig. 39), with relative length 8:7:5:11: claw 5; claw not geniculate (Fig. 40). Hind tibia above gently convex, anterior margin gently outcurved, posterior margin linear but distinctly rounded subapically, apical margin rounded and mildly pointed midway (Fig. 33); below broadly flat (Fig. 35), anterior and posterior semiglabrous areas narrowly sloped, the former mildly ridged at boundary with median longitudinal area with dense setae. Hind basitarsus triangular, postapically roundly pointed, anterior margin forming a differentiated plane as in *Trigonella*, though not demarcated with ridges as in the latter; hind distitarsi anomalously shortened (Fig. 33), with relative length 3:2:2:9: claw 3+6; claw extraordinarily geniculate (Figs. 42–43).

Metasoma slightly elongate but not cylindrical, apical terga ($T_{6,7}$) not modified. Basal margins of S_{3-5} incurved gently, not steeply and angulately as in *Trigonella* (Sakagami & Inoue, 1987). S_3 (Fig. 17) with gradulus not evanescent, sinuate; medially not interrupted, and submedially without appendage; pregradular area very narrow medially; hairs (max 150 μm) on postgradular area moderately dense, though slightly sparse medially, not forming distinct patches; hairs on submedian area near apical margin stout but short and recurrent, issuing from transparent sheaths contrasting on dark background; apical margin medially gently and broadly extended, transverse with no modification. S_4 (Fig. 18) similar but gradulus reduced except for median part; median area glabrous and medioapically semimembranous, submedian recurrent hairs forming dense, subapical patch. S_5 (Fig. 19) short; apodemal lobe rectangular, pregradular area nearly obsolete but
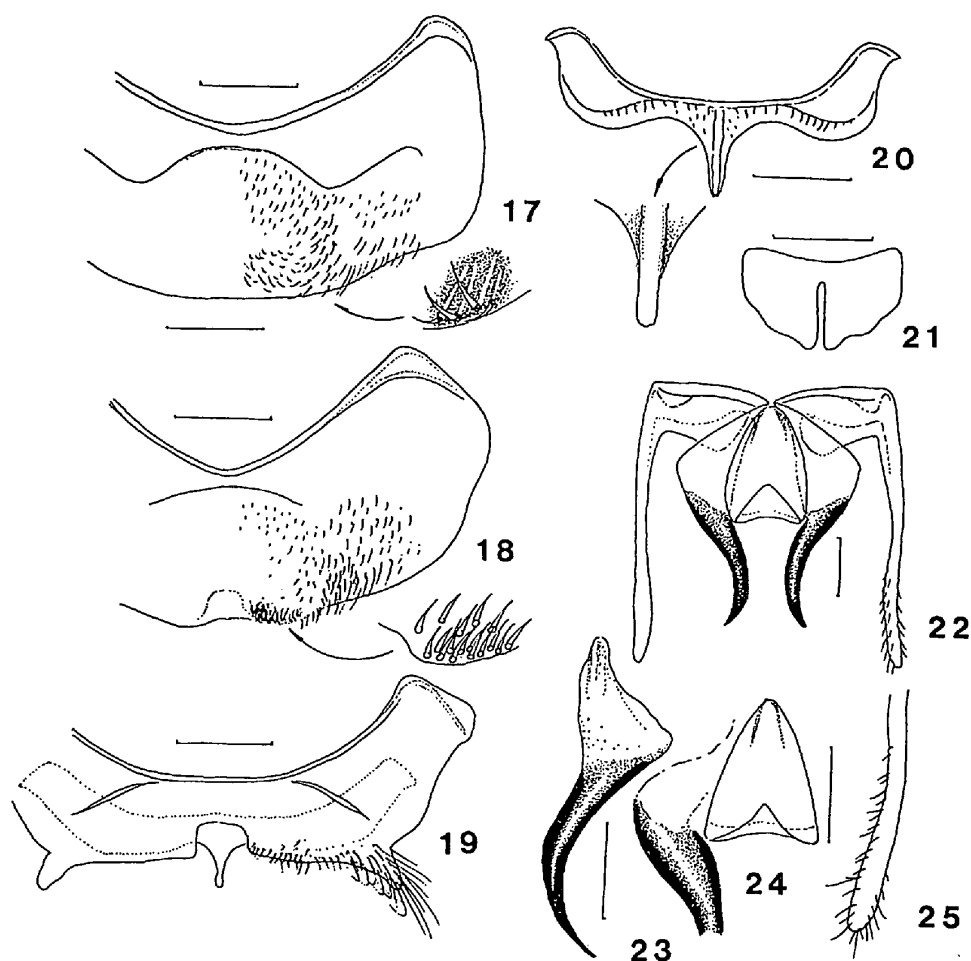
Figs. 17–25.   Male terminalia of *T. thoracica*. —— 17–18, Sterna 3 and 4; 19, sternum 5, with sternum 6 below; 20, sternum 6; 21, sternum 7; 22, genitalia; 23, penis valve; 24, spatha, 25; gonostylus.   Scale=0.5 mm in Figs. 17–19, 0.25 mm in Fig. 20–25.

gradulus represented by thin, submedian appendage, apical margin transverse with large, rectangular, median notch less developed than in *Trigonella* and lateral process shorter than in *T. itama* and *Trigonella*; hairs confined to apical margin and subapical area, longer on lateral process, 250 μm. S_6 (Figs. 19–20) similar to that of *Trigonella*, with basal margin widely transverse medially; median body with sparse hairs on depressed area behind gradulus, apical process triangular, slender apically, straight seen laterally, not rod-like and slightly bent as in *Trigonella*. S_7 (Fig. 21) homogeneously transparent and semicircular, gradulus reduced, with deep and narrow apical emargination (possibly variable among individuals).   Male genitalia very similar to those of *Trigonella* and *Trigona itama* (Fig. 22) with gonostylus approximately straight, subtly sinuate; subapically slightly dilated and apically tapering, bearing sparse hairs on apical 1/3 (Fig. 25); penis valve distinctly shorter than gonostylus, relatively slender and mildly curved (Fig. 23), connecting bridge

longer than in *Trigonella*, comparable to that in *T. itama*; spatha elongate-triangular with lateral margin outcurved, transparent, slightly longer than in *T. itama* and much longer than in *Trigonella* (Fig. 24).

Specimens examined. Seven ♂♂ taken from a colony collected in Wanariset, East Kalimantan, Indonesia in December and reared at Herbarium Bogoriense, Bogor by Mr. G. G. HAMBALI (SAKAGAMI *et al.*, 1983). *T. thoracica* is known from Burma, Thailand, Malaya, Singapore, Sumatra and Borneo (SCHWARZ, 1939; SAKAGAMI, 1975).

Taxonomic Comments on *Geniotrigona*

First, the taxonomic status of *Geniotrigona* is redefined according to the discovery of a second species *T. incisa*. Secondly, the systematic affinity of *Geniotrigona* with *Heterotrigona* and *Trigonella* is discussed based on the newly described male of *T. (G.) thoracica*. Thirdly, an evolutionary note on *T. incisa* is added to.

Geniotrigona was characterized by short mesoscutellum and propodeum and particularly by unusually long malar space possessed by *T. thoracica*, the type species (MOURE, 1961). Each Indo-Pacific subgenus of the stingless bees of *Trigona – Tetragona* complex (SAKAGAMI, 1975) is distinguished successively from the remainder by features in workers parenthesized below: *Lepidotrigona* (head and mesosoma densely tessellate and posterior corbicular fringe consisting of simple hairs alone without admixture of plumose hairs) — *Homotrigona* (hind basitarsus below without oval disc bearing fine sericeous hairs) — *Heterotrigona* (mandible unidentate instead of bidentate) — *Lophotrigona* and *Platytrigona* (propodeum medially haired) — *Tetragonula* (with *Tetragonilla*, SAKAGAMI & KHOO, 1987) (mesoscutellum emphatically projecting beyond metanotum and propodeum) — *Tetrigona* and *Odontotrigona* (mandibular teeth strong) — *Trigonella* (small, hind basitarsus less than 1/2 as wide as hind tibia, malar space narrower than flagellar width, and submarginal cells indistinct) — *Geniotrigona* (see above). The above distinction of *Geniotrigona* from other subgenera does not essentially change by the addition of *T. incisa* but the features itemized as diagnostic of *Geniotrigona* (MOURE, 1961) are supplemented or modified as below:

a) Tomentous pubescence on head and mesosoma sparser and less woolly in *incisa* (Figs. 1–2).

b) Inner orbits slightly convergent below in *incisa* than subparallel as in *thoracica*. Upper alveolar tangent at mid-face but slightly below in *incisa*: Ratio of "distance from upper alveolar tangent and summit of head" to "distance between upper alveolar tangent and lower clypeal margin"=22/23 in *thoracica* and 17.5/16 in *incisa* (Figs. 1–2).

c) Clypeus shorter in *incisa* (L: W=10: 20). Frontal carina weak but present in both species.

d) Malar space longer than flagellar width in both species but distinctly shorter
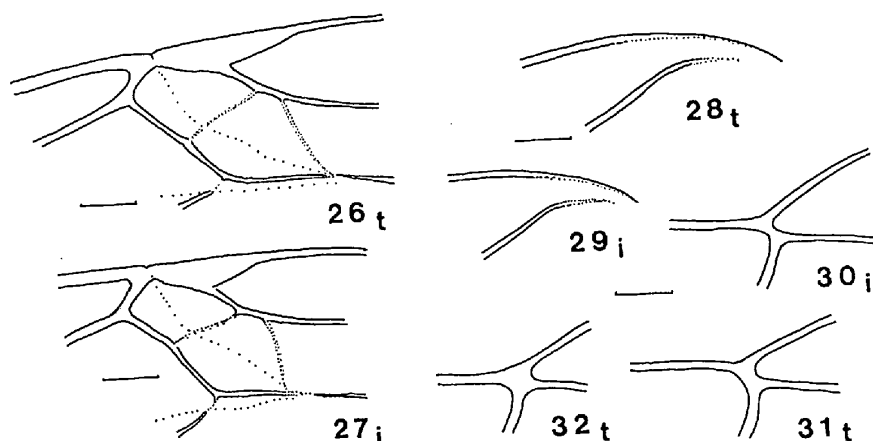
Figs. 26–32. Wing venation of workers of *T. thoracica* (t) and *T. incisa* sp. nov. (i). —— 26–27, Submarginal cells; 28–29, apex of marginal cell; 30–32, relation of M–Cu bifurcation to origin of cu–an. Scale=0.5 mm in Figs. 26–27, 0.25 mm in Figs. 28–32.

in *incisa* ($ML/F_2W=17.6/7.3$ in *thoracica*, 8.5/6.5 in *incisa*) (Figs. 1–2, 60–61). Gena slightly wider in *incisa* ($EW/GW=26.4/26.0$ in *thoracica*, 18.2/18.8 in *incisa*). Outer mandibular tooth more developed in *incisa* than in *thoracica*, but inner tooth opposite (Figs. 53, 55).

e) Occiput less raised but distinctly incised in *incisa* (Figs. 4–5). $OcOcD/OrOcD=15.3/25.1$ in *thoracica* and 12.9/18.8 in *incisa*.

g) Bifurcation between M and Cu either shortly before (Figs. 30–31), or nearly coincided with the orgin of cu–an (Fig. 32) in both species. This character should be removed from previous keys (MOURE, 1961; SAKAGAMI, 1975).

Discovery of the male of *thoracica* exposed remarkable structural similarities in apomorphic features of hind legs and apical sterna among 3 Malesian subgenera, *Heterotrigona* (SCHWARZ, 1939; also SAKAGAMI & INOUE, unpubl.), *Trigonella* (SAKAGAMI & INOUE, 1987) and *Geniotrigona*. Below these subgenera are abbreviated as *H*, *T* (*Tm=T. moorei*, *Tl=T. lieftincki*) and *G*.

Apomorphies in hind legs involve two different tendencies. First, the hind tibia which is above relatively flat with rather sparse and uneven hairs, which are longer and plumose toward the posterior margin, is regarded as a plesiomorphic state while the tibia gently convex with dense, even and simple hairs as an apomorphic state (SAKAGAMI, 1978; SAKAGAMI & ITO, 1981). Many stingless bee subgenera possess the former state but in the Malesian subgenera *Lepidotrigona* (SAKAGAMI, 1975) and the *laeviceps* group and *gressitti* group of *Tetragonula* (SAKAGAMI, 1978) exhibit the latter. In the present case *Tm* is plesiomorphic, *G* and *H* are apomorphic and *Tl* intermediate. The second apomorphy in hind legs covers all anomalies deviating from the normal structural plan, e.g., subapical convexity of anterior tibial margin, narrow and triangular basitarsus, anterior margin of hind basitarsus forming a narrow, demarcated plane, exaggeratedly shortened distitarsi (Figs. 33–38), and elongate, peculiarly geniculated claw (Figs. 37–38, 41–43). On these char-

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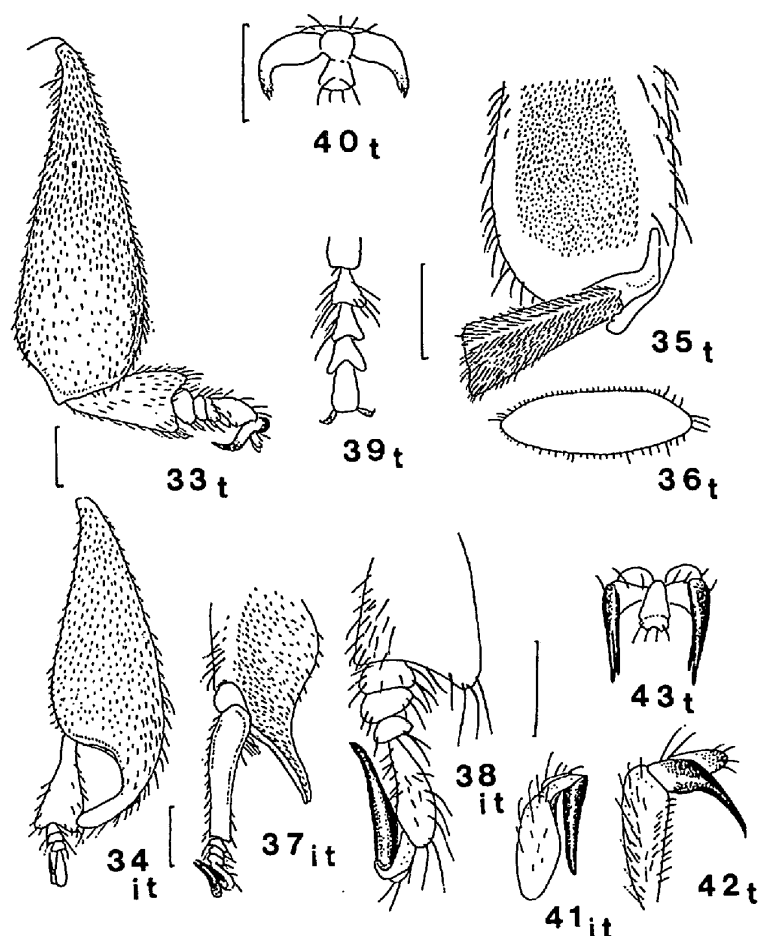
Figs. 33–43. Male hind tibia and tarsi of *T. thoracica* (t) and *T. itama* (it) with mid tarsi.
—— 33–34, Left tibia and tarsi, outer surface; 35, left tibia and basitarsus, inner surface;
36, left tibia, cross section, outer surface below; 37, left hind tibia (apical half) and tarsi
seen frontally; 38, left tarsi, outer side; 39–40, mid distitarsi and claw seen frontally;
41–43, hind tarsal claw seen laterally and frontally. Scale=0.5 mm in Figs. 33–37, 39;
0.25 mm in Figs. 38, 40–43.

acters, deviations from the normal pattern proceed in the ascending order of $Tl<$
$Tm<G<H$. H is further provided with a bizzare postapical tibial process (Figs.
34, 37). Whether these modifications relate to any functions is unknown. Prob-
ably basitarsus is operated by a strong musculature located within tibia, because
in dead specimens basitarsus is invariably bent acutely from tibia unlike the posi-
tions illustrated (Figs. 33–34). It is conceivable but not yet proved that the whole
structure represents an adaptive syndrome to seize the virgin queen in mating.

Male genitalia of three genera themselves do not differ much one another, with
gonostylus not robust and the apical 1/3 provided with sparse but distinct hairs
(Figs. 22, 25; present in H though not shown by Schwarz, 1939), and spatha not
reduced. This pattern prevails in other Malesian subgenera (Sakagami, unpubl.)
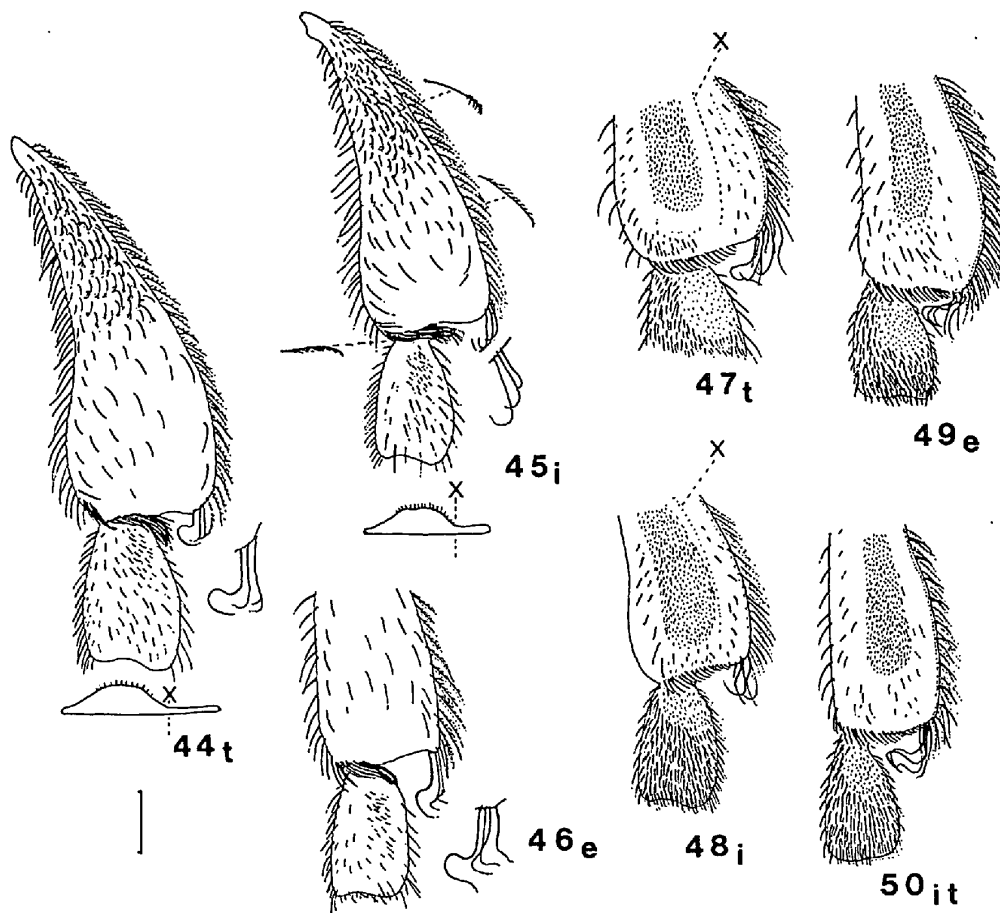
Figs. 44–50. Worker hind tibia and basitarsi of *Trigona thoracica* (t), *T. incisa* sp. nov. (i), *T. erythrogastra* (e) and *T. itama* (it). —— 44–46, outer surface, 44–45 with cross section; 47–50, inner surface (×=posterior end of inner longitudinal elevation). Scale=0.5 mm.
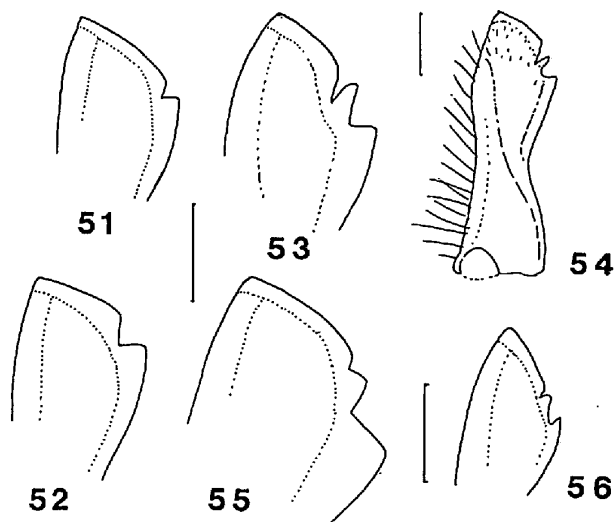

Figs. 51–56. Left worker mandible of *Trigona itama* (51), *T. erythrogastra* (52), *T. incisa* sp. nov. (53–54), *T. thoracica* (55), and *T. moorei* (56). Scale=1 mm in Fig. 54, 0.25 mm in others.

but not in the most predominant subgenus *Tetragonula*, which is characterized by robust penis valve and virtually reduced spatha (SAKAGAMI & INOUE, 1987). On the other hand, sternum 6 (S₆) of *H, T* and *G* is intermediate between the plesiomorphic platelike state seen in *Lepidotrigona* (SAKAGAMI, 1975) and *Homotrigona* (SAKAGAMI, 1963) and the strongly screlotized slender structure with a prominent apical process realized in many groups (SAKAGAMI, 1975, 1978; and SAKAGAMI, unpubl.), *i.e.* in the three subgenera the platelike pattern is still retained in the apodemal part while the apical process is already fairly conspicuous but not so acutely bent as in the latter pattern. This state suggests that S_6 in the three subgenera represents a stage intermediate in the process of transformation from the plesiomorphic state represented by *Lepidotrigona* and *Homotrigona* to that shown by the other subgenera. Corresponding to modifications of S_3–S_5, which are also in general stronger in the three subgenera than in the two last-mentioned ones, probably indicate an integral trend of changes in these parts. On the other hand, it is unknown whether "normal" sterna in many subgenera represent secondary simplifications of prior modifications or the absence of such modifications accompanied by specialization of S_6.

In any event, it is likely that the three subgenera, *H, G* and *T*, form a monophyletic group within the Indo-Pacific *Trigona–Tetragona* complex, sharing two apomorphous syndromes in hind legs and terminalia in males, and also dense and stout bristles on vertex and relatively wide hind basitarsus (wider than 1/2 tibial width) and similar hind tibial pilosity (Figs. 44–50) in workers. On the other hand, the phyletic relationship among three subgenera cannot yet be settled. *H* and *G* are more apomorphous than *T* in male hind legs but both *H* and *T* are more apomorphous against *G* in apical sterna. Probably one of these two trends is really homologous and the other homoiologous. At the present two alternative dichotomies, (*H–G*)–*T* and (*H–T*)–*G* are equally likely. Structurally *H* is more specialized than the other two in two additional apomorphies: occurrence of postapical process in male hind tibia and reduction of outer mandibular tooth. Comparing mandibular teeth between *T. thoracica, T. incisa* and *T. moorei*, secondary reduction of the outer tooth is compensated by development of the inner tooth (Figs. 51–56).

Finally, the evolutionary position of *T. (G.) incisa* is tentatively commented on. At a first glance, morphometric differences, particularly in head, of *T. thoracica* and *T. incisa* seem to be enormous. However, these are regarded as an outcome of allelomorphic differentiation. The difference is very similar to the intraspecific difference between queen and worker of a bumblebee, *Bombus diversus* (SAKAGAMI & KATAYAMA, 1977) (Figs. 57–61). This resemblance is persuasive to assume speciation of the two *Geniotrigona* species through allelomorphic differentiation. Comparing the two species with those of other Oriental *Tetragona* groups, *T. incisa* is in general less differentiated than *T. thoracica*. Probably *T. incisa* remained undifferentiated except for the occipital structure since arrival of its ancestor at Sulawesi. Among various bee groups, stingless bees are considered most difficult to cross the ample water barriers (MICHENER, 1979). It is also well known that Sulawesi has
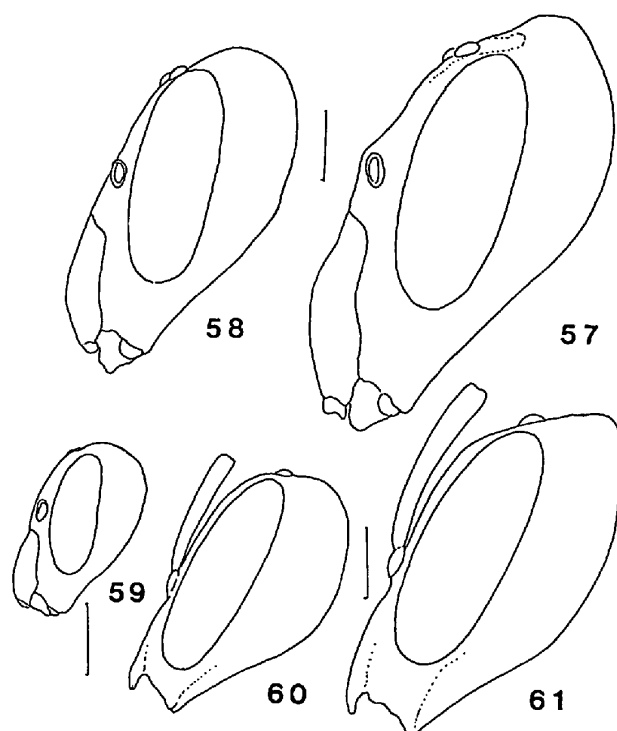
Figs. 57-61. Head seen laterally of *Bombus diversus* Smith (57, queen, 58-59, large and small workers), *Trigona incisa* sp. nov. (60) and *T. thoracica* (61). Scale=1 mm in Figs. 57-59, 0.5 mm in Figs. 60-61.

been isolated throughout the Pleistocene from the continental islands lying on Sunda shelf (AUDLEY-CHARLES, 1981). This relation is reflected in rich stingless bee fauna in Malaya (M), Sumatra (S) and Borneo (B) and similar species compositions among these islands (Number of known species 29/M, 24/S, 28/B; Sørensen's quotient of similarity=0.81/MB, 0.83/MS, 0.77/BS) against a very poor fauna in Sulawesi (at present only 5 or 6 known species) (SAKAGAMI & INOUE, unpubl.).

Among these species only *T. incisa* is endemic there. On the other hand, *T. thoracica* is widespread from Burma to Sumatra and Borneo without subspeciation. It is inferred that the ancestor of *T. incisa* arrived at Sulawesi much older than the Pleistocene either realizing a difficult dispersal across the Makassar Straits or through a land bridge formed in the mid Miocene or during the late Pliocene and Quaternary, although the latter possibility is at the present no more than a speculation (AUDLEY-CHARLES, 1981). The discovery of the male of this species is requested to clarify its origin better.

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