

New stingless bee genus endemic to Central American cloudforests: phylogenetic and biogeographic implications (Hymenoptera: Apidae: Meliponini)

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Abstract. *Meliwillea bivea* gen.n., sp.n. is the only known stingless bee genus endemic to Central America. External morphology and male genitalia show affinity of *Meliwillea* with *Scaptotrigona*. Its plesiomorphies and current sympatry with *Scaptotrigona* suggest *Meliwillea* is relictual and diverged in montane habitat during the Tertiary, predating the Pleistocene connection between Central and South America which allowed immigration by *Scaptotrigona*. Addition of *Meliwillea* to the list of Neotropical genera changes the phylogenetic position of *Nannotrigona*, making it sister to *Paratrigona* instead of *Scaptotrigona*.

Introduction

Meliponini, the permanently colonial and stingless honey-making bees, are Pan-tropical, with endemic genera in tropical Oriental, African, Indoaustralian and American regions. Restricted distribution of higher meliponine taxa within the Neotropics, where three-quarters of the world's ≈ 500 species occur, had previously been known from South American examples (Camargo & Moure, 1983; Camargo & Wittmann, 1989; Michener, 1990). We therefore were surprised to discover an endemic meliponine bee from Central America that did not correspond to any modern genus. The bee is unusual not only for its taxonomic characters and geographical distribution, but also because it occurs only within a montane habitat, the cloudforests. Our hypotheses are that the new taxon is relictual, related to *Scaptotrigona* (a genus with wide distribution in the Neotropics), and that its recognition is useful for resolving both meliponine phylogenetics and biogeographical relationships between Central and South America.

Methods

Our description of the genus follows the format of Moure (1961), and Michener & Sakagami (1990). Character state analysis was performed using generic traits found reliable by Michener (1990) and Camargo & Pedro (1992a,b), with some modification. Only Neotropical Meliponini sharing a relatively strong apomorphy with the new taxon, the keirotrichiate area

of the inner hind tibial surface flattened and lacking a depressed posterior rim, were analysed. These are *Nogueirapis*, *Nannotrigona*, *Paratrigona*, *Aparatrigona*, *Partamona*, *Parapartamona* and *Scaptotrigona*. *Plebeia*, s.l., constitutes the sister group to these taxa plus *Melipona*, and was used as the outgroup for phylogenetic analysis (see Camargo & Pedro, 1992b). Some taxa that we include (*Nogueirapis*, *Parapartamona* and *Aparatrigona*) are synonymized by Michener (1990) and Michener & Roubik (1993) but are considered as separate entities here due to their restricted distribution or ecological interest. The wide and flattened keirotrichiate area of the worker metatibia, without a depressed posterior rim (a plesiomorphy according to Michener, 1990), was polarized in an alternative manner (Table 1), as suggested by Michener (1982) and by Camargo & Pedro (1992a,b). The large, depressed posterior rim present in *Proplebeia* (a fossil genus described from Dominican amber, originating 15–40 Myr BP), a candidate sister group of *Plebeia*, was interpreted by Michener (1982) as plesiomorphic. He indicated that evolution of the smooth tibial rim 'has progressed toward both narrow (as in modern *Plebeia*) and broad (as in *Tetragona*)'. Camargo & Pedro (1992a,b) work with the hypothesis that a plesiomorphic trait, found in Anthophorinae and resembling that of *Hypotrigona*, is a cylindrical, narrow hind tibia. *Hypotrigona*, along with *Proplebeia*, have a smooth metatibial rim of intermediate extension. We considered three more traits found in the new taxon and among its possible relatives: (i) presence of long, sinuous hairs on the metathoracic coxa and basal metasomal sterna, (ii) a very long malar space, approaching or

Table 1. Characters used for analysis of *Meliwillea*, outgroup and allied taxa.

1	Scutellar fovea 0 = absent, 1 = present
2	Scutellum 0 = round, thick in lateral view, 1 = protruding to metanotum
3	Hindtibial cross section 0 = flat, a narrow, depressed posterior margin of about 1/4 or less width of keitrichiate area (<i>Plebeia</i>), 1 = flat, no depressed posterior margin (<i>Scaptotrigona</i>)
4	Submarginal angle 0 = acute or straight (<i>Plebeia</i>), 1 = obtuse (<i>Partamona</i>)
5	Malar space 0 = short, 1 = large (1/5 length of eye)
6	Gena, at the level of inferior orbital tangent 0 = narrow, 1 = large (as large as eye in profile, <i>Scaptotrigona</i>)
7	Long, sinuous hairs of venter 0 = absent, 1 = present (<i>Scaptotrigona</i>)
8	Tomentum on metasomal terga 0 = absent, 1 = present (<i>Scaptotrigona</i>)
9	Corbicula 0 = little excavated (<i>Plebeia</i> , <i>Scaptotrigona</i>), 1 = broadly excavated (<i>Partamona</i>)
10	Mandibles 0 = bidentate, 1 = quadridentate (<i>Paratrigona</i>)
11	Posterior basitarsus 0 = with posterior margin straight or arched, 1 = with median protuberance (<i>Nannotrigona</i>)

Table 2. Character state matrix for selected American Meliponini and *Meliwillea* gen.n.

Taxon	Character										
	1	2	3	4	5	6	7	8	9	10	11
<i>Plebeia</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Nogueirapis</i>	0	0	1	0	0	0	0	0	0	0	0
<i>Partamona</i>	0	0	0	1	1	1	0	0	1	0	0
<i>Parapartamona</i>	0	0	0	1	1	1	0	0	1	0	0
<i>Paratrigona</i>	0	1	1	1	0	0	0	0	0	1	0
<i>Aparatrigona</i>	0	1	1	0	0	0	0	0	0	1	0
<i>Scaptotrigona</i>	1	1	1	1	1	1	1	1	0	0	1
<i>Nannotrigona</i>	1	1	1	0	0	0	0	0	0	0	1
<i>Meliwillea</i>	0	0	1	1	1	1	1	1	0	0	1

exceeding one-fifth the length of the eye, and (iii) metasomatic terga with tomentose bands, including intercalated short, erect hairs. These are character states restricted to few meliponines.

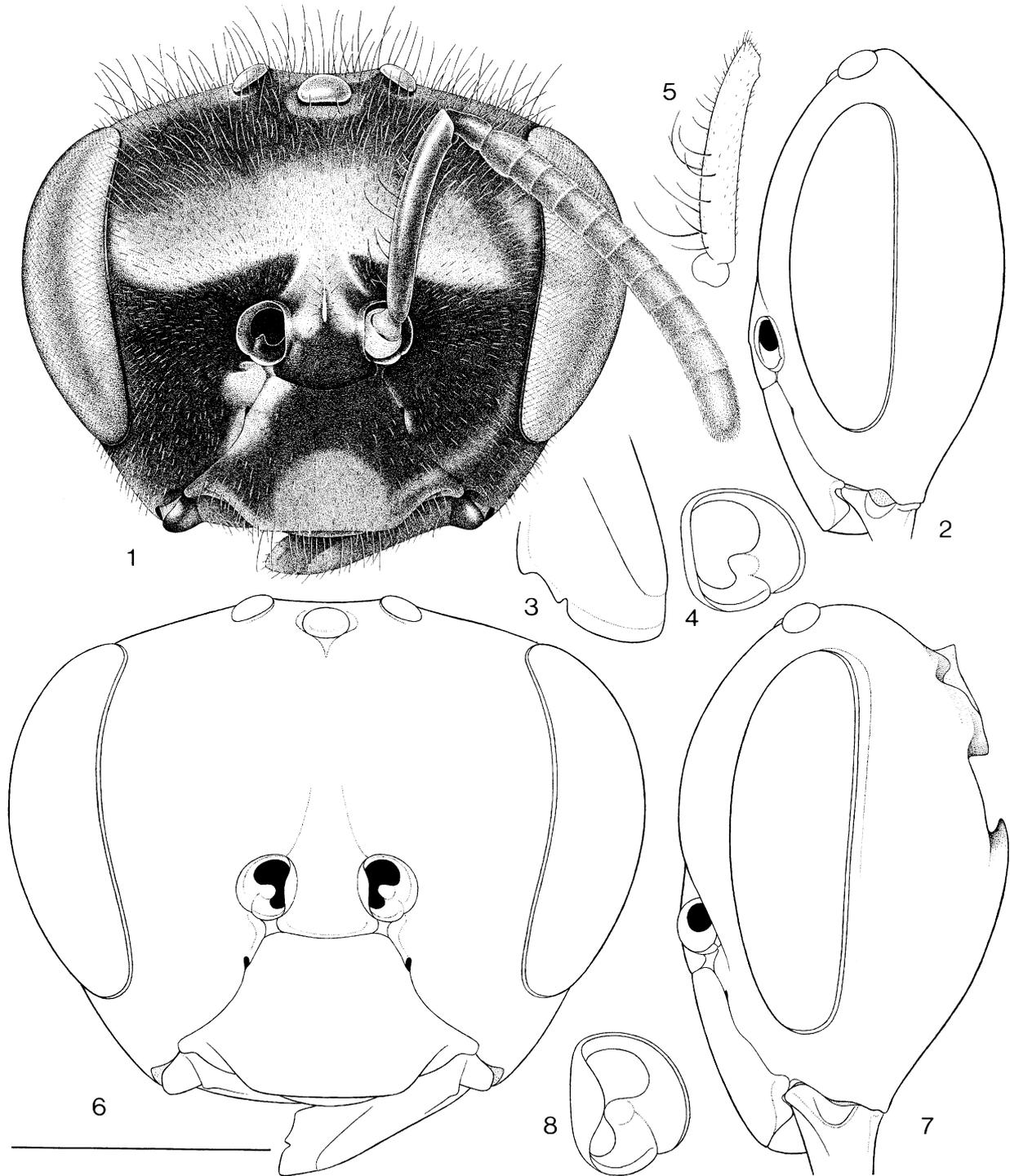
We considered the effects of weighting or excluding certain synapomorphies. A character matrix (Tables 1 and 2) was evaluated with 'phylogenetic analysis using parsimony' – PAUP 3.0. The 'exhaustive search' option was used to construct the different possible trees, using an outgroup (*Plebeia*, characterized by all '0' character states) to root trees, and accelerated transformation character optimization provided in PAUP. All characters were unordered, and were weighted equally. In addition, the scutellar fovea, a highly distinctive character state found in *Nannotrigona* and *Scaptotrigona*, was assigned higher weightings in approximations of tree topology emphasizing this uniquely shared trait; and three traits that were synapomorphies of *Meliwillea* and *Scaptotrigona* were excluded, in an analysis of tree stability.

Meliwillea gen.n.

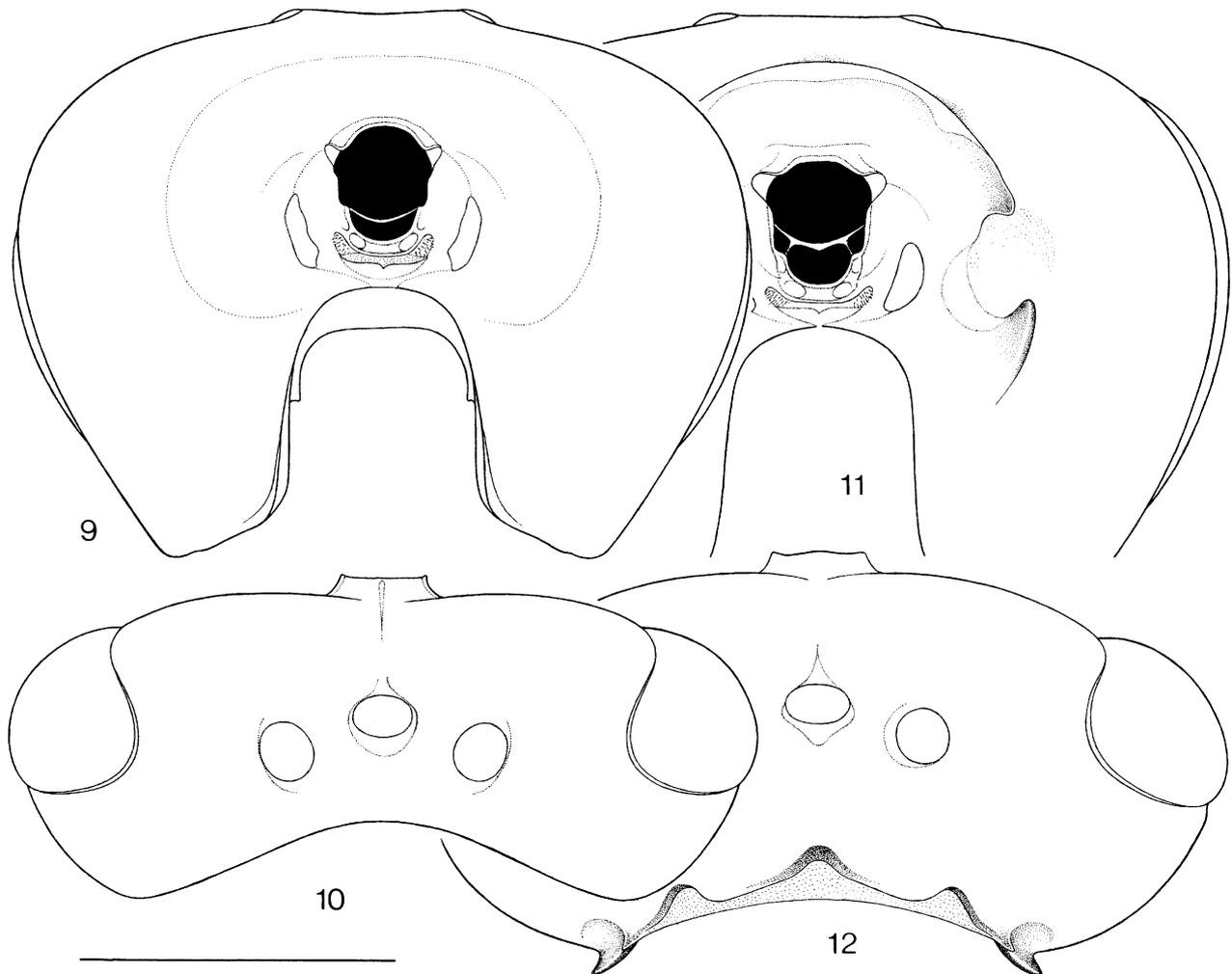
Type species: *Meliwillea bivea* sp.n.

Integument black, shiny; clypeus with uneven punctation; some deeper piligerous punctures, sparse on metasomal terga. Pubescence normal, erect bristles on clypeus, a few pectinate bristles on head, thorax and legs; compound eyes without apparent pilosity. Yellow markings absent. Head slightly wider

than thorax (at mesepisternum); face normal, interorbital maximum larger (1.3 times) than length of eye; inner orbit slightly sinuous, weakly convergent below. Upper alveolar tangent exactly at the middle of face; interalveolar distance much greater (1.8 times) than half of alveolorbital distance. Upper median portion of frons slightly depressed and flattened, forming slight sulcus, with short, elevate-truncate frontal carina between antennal alveoli; frons slightly convex (Figs 1 and 2). Clypeus convex, practically as long as half width; distance from inner rim and the orbit nearly two times diameter of second flagellomere. Mandibles with two small teeth on inner third of apical border (Fig. 3). Malar space long, almost two times diameter of second flagellomere (Fig. 1). Gena, seen in profile, nearly equal to eye width, rounded, lacking preoccipital carina (Figs 2, 9, 10). Labial palpus with 3–4 short, slender bristles on first segment (less than 1/3 length of segment), and with 3–4 smaller bristles on the second segment. Galeae with short, erect bristles. Vertex procurved above superior orbital tangent, scarcely elevated and rounded behind ocelli, lacking carina (Fig. 2); ocello-occipital distance greater (1.3 times) than diameter of median ocellus; interocellar distance (between lateral ocelli) practically equal to ocellorbital distance. Scape slightly shorter than lateral alveolocellar distance. Second and third flagellomeres shorter than their diameters; first flagellomere as wide as long. Notaulus faintly visible; median mesoscutal line and parapsidal lines impressed, forming slight sulcus. Scutellum rounded, reduced, not overhanging metanotal base in profile; from above, barely covering metanotal base



Figs 1–5. *Meliwilllea bivea* gen.n. sp.n., holotype, head, frontal view and profile, with details of the mandible and antennal alveolus, and antennal scape. **Figs 6–8.** *Scaptotrigona barrocoloradensis* (Schwarz) (paratype), head, frontal view and profile. **Fig. 7.** *Scaptotrigona xanthotricha* (Moure), details of the antennal alveolus. Scale line = 1.0 mm, corresponding to Figs 1, 2, 5 and 7; for Figs 3, 4, and 8 the scale is doubled.



Figs 9–10. *Meliwillea bivea*, gen.n., sp.n., paratype, head, posterior and superior views. **Figs 11–12.** *Scaptotrigona xanthotricha*; head, posterior and superior views, details of the preoccipital carina. Scale line = 1.0 mm.

(Figs 13 and 14). Forewing extending well beyond apex of metasoma (slightly longer than length of body); pterostigma moderately large, slightly wider than second flagellomere, six times longer; prestigma shorter, close to $2/3$ width of pterostigma. Length of marginal cell close to 3.3 times width, narrow at base and obtuse-lanceolate at apex. Rs strong to apex; bifurcation between M and Cu anterior to [cu-anal] vein. Submarginal angle obtuse, $110\text{--}120^\circ$. M slightly curved at first m-cu, continuing slender, nearly to wing margin; Cu thick to wing margin. First submarginal cell weakly delimited, Rs very fine, second submarginal cell obtuse, scarcely forming sulcus in membrane indicating vestiges of first r-m. Hindwing normal, lacking vestiges of M beyond r + m (Figs 15 and 16). Hamuli 6–7. Jugal lobe $5/6$ length of vannal lobe. Metathoracic tibia subtriangular, posterior border convex, anterior border concavo-convex, close to 2.3–2.4 times longer than wide; posterior

distal ridge ending in acute angle and distal border, concave; fringing hairs simple and very long with some, especially in the basal third, pectinate. Corbicula strongly concave, occupying distal $3/4$ tibia (Fig. 20). Internal face with keirotrichiate area very wide, reaching distal border, leaving a narrow posterior margin ($1/6$ widest keirotrichiate area width); glabrous, flat, not depressed (Figs 21 and 22). Penicillum and rastellum well-developed with strong bristles. Anterior parapenicillum well-developed, comb-like; posterior parapenicillum unmodified (Fig. 20). Metathoracic basitarsus swollen medially, near 1.6 times longer than wide; half length of tibia; posterior border strongly convex medially, the anterior only somewhat convex; posterior distal margin rounded; inner surface uniformly setose (Figs 20 and 21). Propodeum protuberant (Fig. 13); basal triangle very smooth and shiny, having only weak transverse folds at the base, and entirely



glabrous. Metasoma narrower (nearly 5/6 width) than thorax, ovoid in top view and triangular in cross-section; the first three terga brilliant-tessellate, the last apically rounded.

The name of this genus is in honor of Dr Alvaro Wille, University of Costa Rica, for all that he has contributed to the study of Meliponini.

Meliwillea bivea sp.n.

Worker. Figs 1–5, 9–10, 13–16, 20–22 (Table 2).

Dimensions. Total length \approx 5.4 mm; forewing, from apex of costal sclerite to tip, 6.06 mm, including tegula, 6.8 mm;

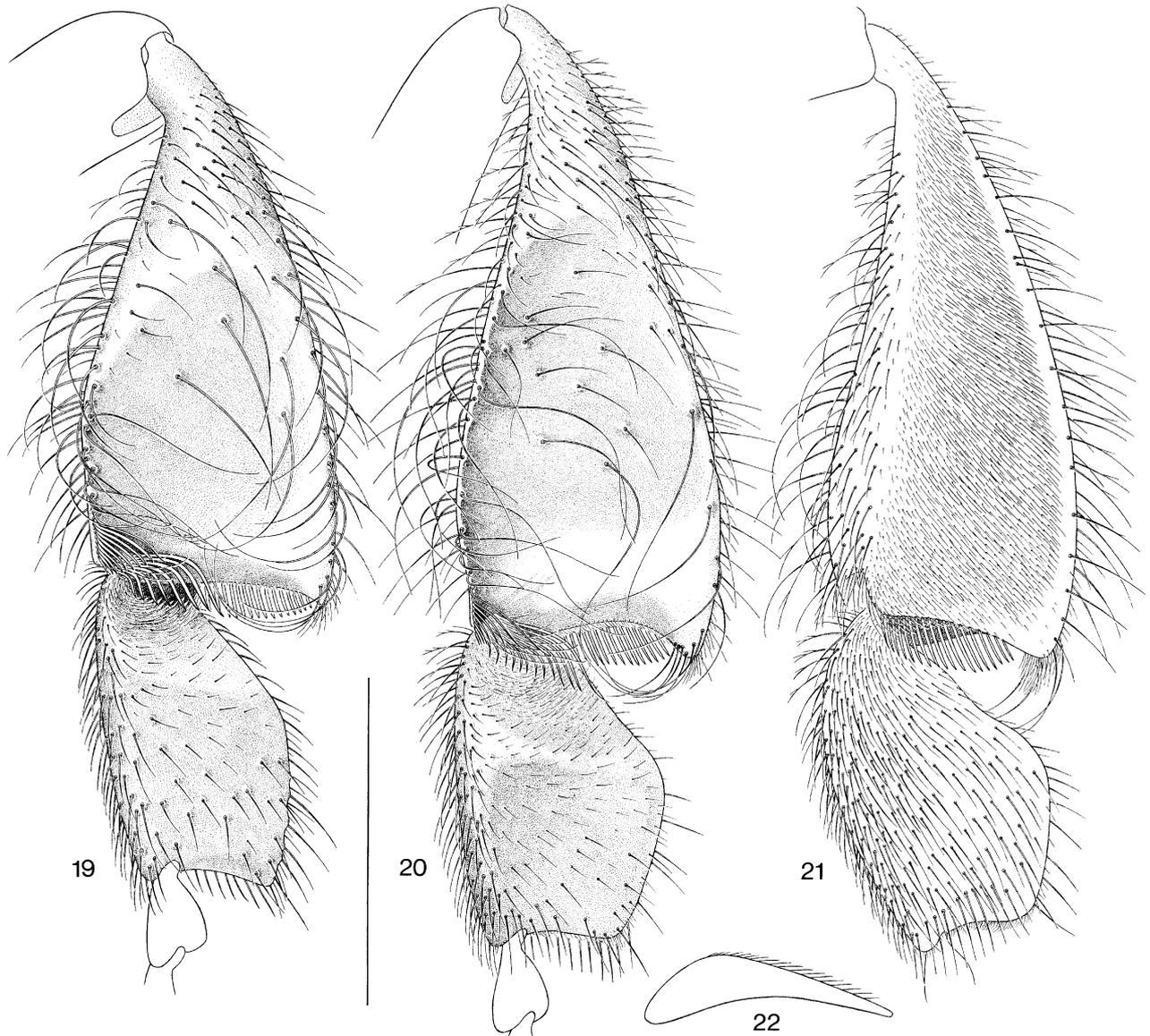
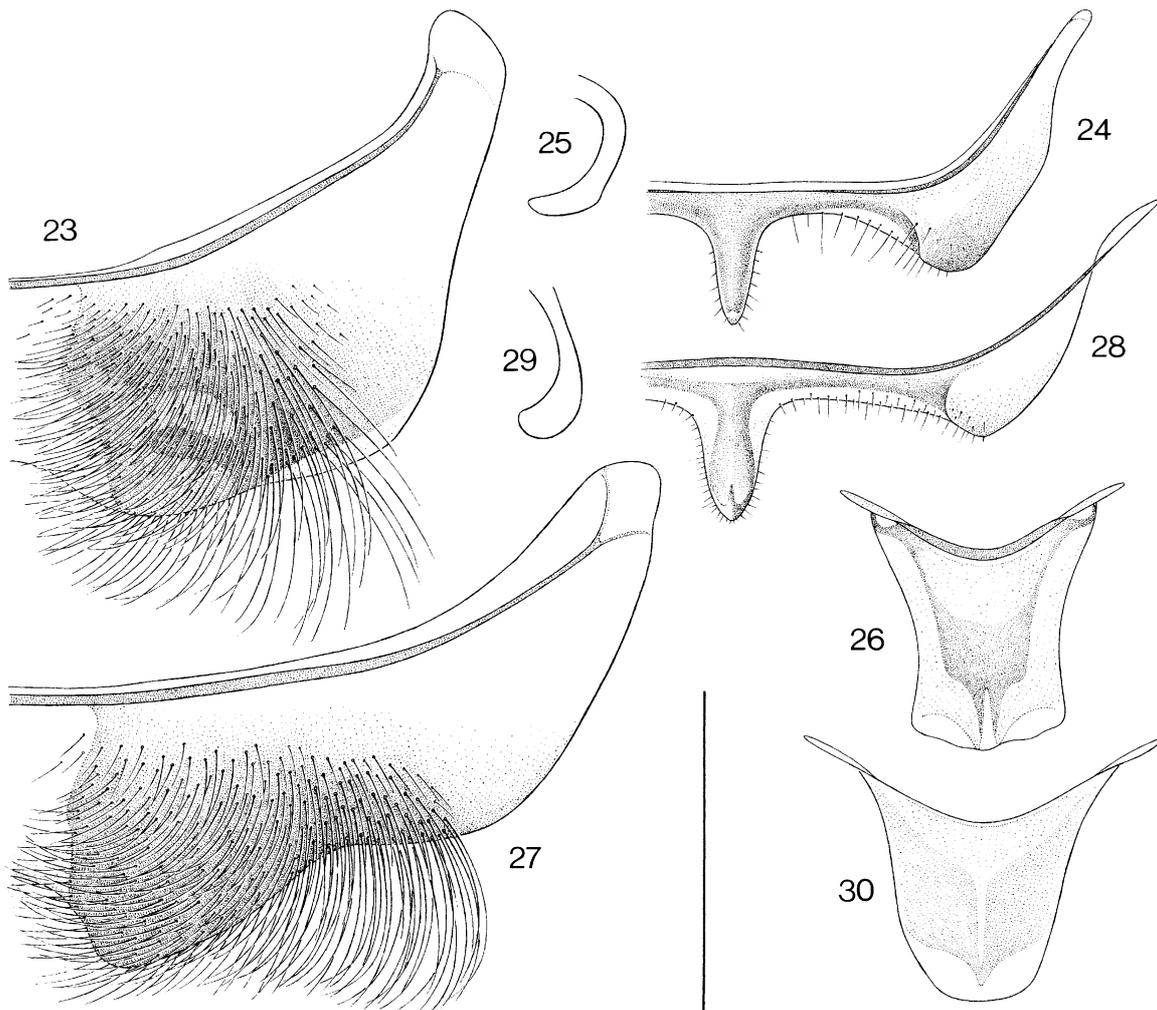


Fig. 19. *Scaptotrigona pectoralis*, metathoracic tibia. **Figs 20–22.** *Meliwillea bivea* gen.n. sp.n., paratype, metathoracic tibia, outer and inner views, and details of keirotrichiate area in cross section. Scale line = 1.0 mm.

Figs 13–16. *Meliwillea bivea* gen.n. sp.n., paratype, thorax, profile and dorsal view, forewing and detail of submarginal angle. **Fig. 17.** *Scaptotrigona pectoralis* (DallaTorre). **Fig. 18.** *Partamona musarum* (Cockerell), details of the submarginal angle of the forewing. Minor scale line = 1.0 mm (Figs 13–15), large scale line = 1.0 mm (Figs 16–18).



Figs 23–26. *Meliwillia bivea* gen.n. sp.n., allotype, male, metasomal sterna, 5 and 6, profile of median process of sterna 6 and 7, respectively. **Figs 27–30.** *Scaptotrigona depilis* (Moure), sterna 5, 6, profile of median process of sternum 6, and sternum 7, respectively. Scale line = 0.5 mm.

maximum head width 2.46 mm; maximum metasomal width 1.94 mm.

Colour. Entirely black, without any vestige of yellow markings; only base of scape, apex of flagellum, mandibular apex, and distitarsi of legs ferruginous; basitarsus and apex of metathoracic tibia darkly ferruginous in holotype (in some paratypes predominantly black). Tegula and costal sclerite blackish. Wings clear-ferruginous, tinged with yellow; veins and pterostigma honey-colored.

Pilosity. Predominantly black; ferruginous on internal surface of basitarsi and entire mesotarsi and distitarsi of all legs; pale ferruginous on venter of metasoma. Bristles on venter of thorax and metasoma sinuous at apex. Erect simple bristles sparse, on clypeus up to 0.20 mm in length, on vertex to 0.26 mm; some pectinate bristles toward occiput. Decumbent micropilosity very short, thin and little evident on inferior portion of face, longer

and more conspicuous in front, not plumose like that of lower face. Scape with 5–6 recurved bristles (slightly pectinate) along the dorsal surface, equal to or longer than scape diameter (Fig. 5); anterior base of scape with very long hair, 0.32 mm (shorter in some paratypes). Anterior portion of mesoscutum with bristles longer than those of vertex (0.32 mm), pectinate and relatively slender; longer at border of scutellum (0.40 mm), with smaller, intercalated pectinate bristles; on mesepisternum as long as those on scutellum, and pectinate, especially on anterior margin; at sides of propodeum intercalated with erect bristles and covering the metanotum, decumbent plumose micropilosity, in the form of a thin tomentum. First and second metasomal terga practically glabrous, with sparse microbristles inserted in conspicuous alveoli along discal band, and premarginal band with decumbent micropilosity; third and following terga with large premarginal bands having semierect bristles intercalated, increasing in size, volume and density toward the apex of metasoma, forming, as the last tergum, a

tuft at each side, with the longest bristles, some pectinate, ≈ 0.24 mm. Margins of terga 3–5, and also intercalated in premarginal bands, with decumbent pilosity, fine and plumose of pale colour, forming thin tomentum, resembling metasomal tomentum of *Scaptotrigona*. Marginal bristles of metathoracic tibia simple, very long (some more than 0.6 mm); at posterior margin intercalated with some shorter bristles, slender and pectinate; pectinate bristles also, principally, on basal third of tibia.

Integument. Predominantly smooth and polished, with slight micropunctuation at bases of micropilosity; on clypeus, piligerous micropunctuation more evident and slightly granular, increasing toward apex, where spaces between micropunctures are the same or smaller diameter than punctures. Basal triangle of propodeum very smooth and polished, with scarcely visible very fine transverse folds at base. Metasomal terga slightly tessellate, less brilliant. Discal band of terga 1–2 with conspicuous sparse punctures (up to 0.03 mm); terga 3–5 with punctuation associated with pilosity of premarginal bands, where punctures smaller and denser, especially at sides.

Form and proportions. (All measurements in mm.) Head wider than long (2.46 : 1.92, length measured between apex of clypeus and vertex), slightly wider than thorax (2.32, measured across mesepisternum), and thorax slightly wider than second metasomal terga (1.94). Eye 2.3 times longer than maximum width (1.34 : 0.57); interorbital maximum (1.74) clearly longer than eye, and superior interorbital distance slightly greater than inferior distance (1.59 : 1.57). Clypeus practically two times wider than long (1.16 : 0.60), close to half length of clypeal-median-ocellar distance (1.22). Malar space very long, approximately two times diameter of second flagellomere (0.29 : 0.15). Inter-alveolar distance close to 4/5 alveolorbital distance (0.34 : 0.43). Scape cylindrical, practically equal to 1/2 length of pedicel and flagellum together (0.86 : 1.74), 7.16 times its diameter (0.12) and nearly 9/10 lateral alveocellar distance (0.94); length of second flagellomere nearly 2/3 its width (0.10 : 0.15); third and fourth flagellomeres practically identical in length and width (0.14 : 0.14 : 0.15 : 0.15). Upper frons slightly depressed, finely sulcate along median line, ending below at supra-clypeal elevation between antennal alveoli, in elevated, truncate carina (see Fig. 1). Distance between lateral ocelli little more than twice diameter of median ocellus and about equal to ocellorbital distance (0.44 : 0.20 : 0.42). Vertex rounded, only slightly elevated between ocelli, and very narrow (0.26), little wider than diameter of median ocellus. Gena, in profile, slightly wider than eye; preoccipital border rounded, without any vestige of carina (Figs 9 and 10). Labrum simple, bulging, distal rim arched. Mandible with two denticles widely separated on inner third of apical border (Fig. 3). Anterior margin of mesoscutum slightly rounded. Scutellum short, bulging (0.50 : 1.08); posterior contour evenly rounded without emargination, only slightly extending beyond base of metanotum (Figs 13 and 14) in dorsal view; basal fovea shaped like 'v' or 'u' absent. Forewing with first submarginal cell weakly defined, second submarginal cell null (Figs 15 and 16). Hamuli 7. Metathoracic tibiae subtriangular,

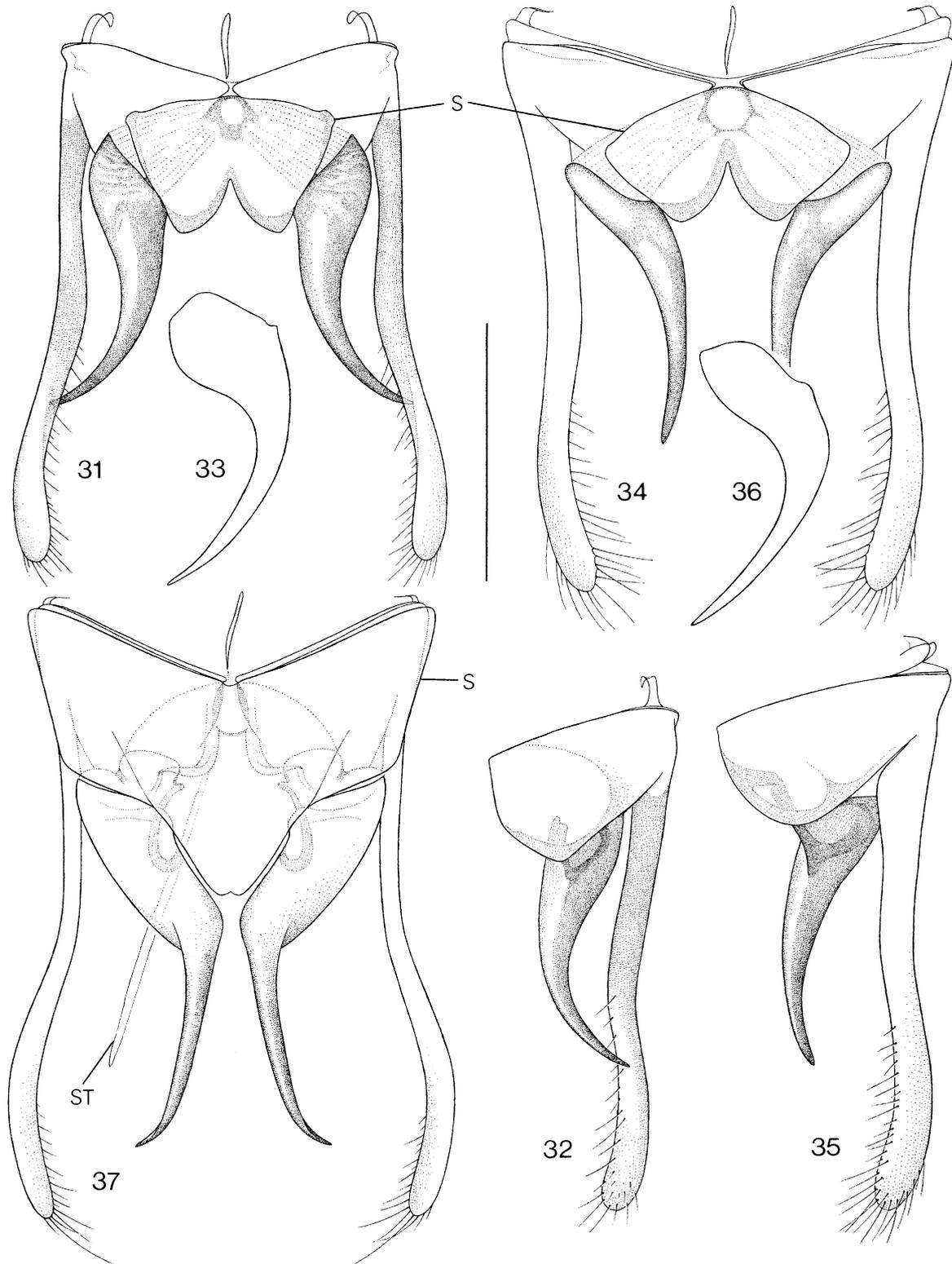
Table 3. Diagnostic measurements (in mm) of holotype and allotype of *Meliwillea bivea* gen.n., sp.n.

	Holotype worker	Allotype male
Head length (clypeal apex to vertex)	1.92	1.84
Head width	2.46	2.34
Thorax width at mesepisternum	2.32	2.01
Second metasomal tergum width	1.94	1.96
Compound eye length	1.35	1.40
Compound eye width	0.57	0.62
Maximum interorbital distance	1.74	1.47
Upper interorbital distance	1.59	1.40
Lower interorbital distance	1.57	1.20
Clypeus length	0.60	0.58
Clypeus width	1.16	0.84
Clypeo-ocellar distance	1.22	1.08
Length of malar space	0.29	0.16
Diameter of third flagellomere	0.15	0.18
Inter-alveolar distance	0.34	0.29
Alveolorbital distance	0.43	0.32
Scape length	0.86	0.66
Pedicel + flagellum length	1.74	2.22
Scape diameter	0.12	0.20
Alveolus-lateral ocellus distance	0.94	0.80
Second flagellomere length	0.10	0.18
Third flagellomere length	0.14	0.18
Fourth flagellomere length	0.14	0.18
Distance between lateral ocelli	0.44	0.32
Median ocellus diameter	0.20	0.24
Ocello-orbital distance	0.42	0.30
Lateral ocellus-occiput distance	0.26	0.20
Scutellum length	0.50	0.52
Scutellum width	1.08	1.10
Posterior tibia length (median)	2.04	1.90
Posterior tibia length (posterior margin)	2.18	–
Posterior tibia width	0.85	0.62
Posterior basitarsus length	1.00	0.90
Posterior basitarsus width	0.60	0.52
Forewing length (paratype)	6.06	5.90
Forewing length (with tegula)	6.81	6.64
Forewing width	2.24	1.95

2.4 times longer (measured from base to median distal margin) than wide (2.04 : 0.85). Corbicula strongly concave, occupying distal 3/4 of tibia (Fig. 20). Metathoracic basitarsi tumescent medially, 1.7 times longer than wide (1.00 : 0.60); posterior margin strongly convex medially (Figs 20 and 21), anteriorly slightly convex; posterior-distal corner rounded. Metasoma semiovoid in top view; contour of basal concavity on first tergum gently rounded.

Male. Figs 23–26 and 31–33 (Table 3).

Dimensions. Total length ≈ 6.3 mm; forewing, from apex of Costal sclerite to tip, 5.9 mm, including tegula, 6.64 mm; maximum head width 2.34 mm; maximum metasomal width 1.96 mm.



Figs 31–33. *Meliwillea bivea* gen.n. sp.n., allotype, male, genital capsule, dorsal view, ventral view and profile of penis valve. **Figs 34–36.** *Scaptotrigona depilis* (Moure), genital capsule, dorsal view, ventral view and profile of penis valve. **Fig. 37.** *Partamona* near *cupira* (Smith), genital capsule, dorsal view. S = spathe, ST = eighth metasomal sternum, present in *Partamona*. Scale line = 0.5 mm.

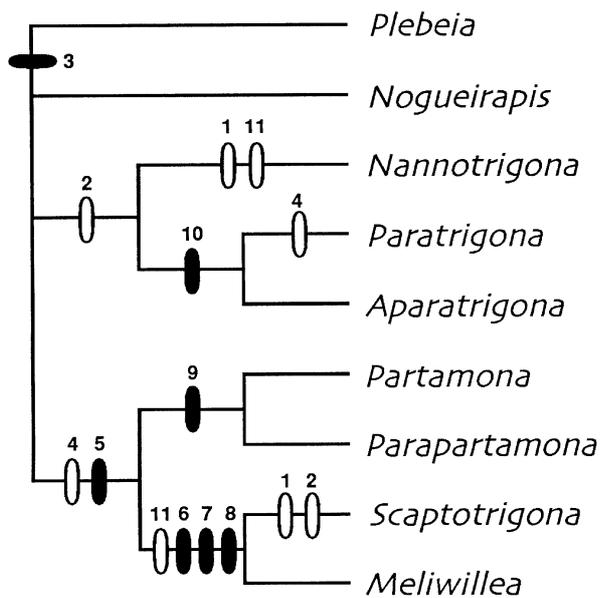


Fig. 38. Minimum tree cladogram of *Meliwillea* and related Neotropical Meliponini, generated from exhaustive search procedure using PAUP. Character states as in Tables 1 and 2; open circles indicate convergence.

Colour. Like worker; metathoracic basitarsus yellow–ferruginous. Wing membranes tinted ferruginous–yellow, slightly darker than in workers; wing veins ferruginous–blackish. One translucent broken band along the midline of sterna 3–5.

Pilosity. Colour like that of worker, hairs denser and longer on face and thorax; pectinate bristles present, especially on tibiae of all legs. Erect bristles on clypeus reaching 0.24 mm, on vertex to 0.54 mm. Scape with bristles longer than its diameter (0.20 : 0.28), slender and recurved forward along entire dorsal surface. Mesoscutum, anteriorly with bristles to 0.40 mm; on distal border of scutellum reaching 0.52 mm. Basal area of propodeum glabrous as in workers. Last metasomal terga, at edges, with strong bristles, recurved inward, reaching 0.40 mm. Metathoracic tibia with short bristles distributed uniformly on external surface; on anterior margin, bristles robust and pectinate, up to 0.24 mm; basitarsus uniformly covered with very short, decumbent pilosity, on outer surface.

Integument. Like worker; punctuation denser on face, especially on clypeus, where punctures are larger (0.02 mm) and without spaces between them, slightly roughening and dulling surface. Metasomal terga slightly tessellate, lacking punctuation on discal bands.

Form and proportions. (All measurements in mm.) Head wider than long (2.34 : 1.84), wider than thorax (2.01); thorax slightly wider than second metasomal tergum (1.96). Eye 2.25 times as long as wide (1.4 : 0.62); interorbital maximum (1.47) slightly larger than length of eye; superior interorbital distance

larger than inferior (1.40 : 1.20). Clypeus 1.44 times wider than long (0.84 : 0.58); clypeocellar distance, 1.08. Malar space little shorter than diameter of third flagellomere (0.15 : 0.18). Interaveolar distance near 8/9 alveolorbital distance (0.29 : 0.32). Scape cylindrical, near 2/7 length of pedicel and flagellum together (0.66 : 2.22), 3.3 times its diameter (0.20) and nearly 5/6 the lateral alveolocellar distance (0.80). First flagellomere shorter than its width (0.09 : 0.22); second and third as long as wide (0.18 : 0.18). Upper face clearly depressed, sulcate along median line; supra-clypeal carina weaker than in workers. Distance between lateral ocelli 1.3 times larger than diameter of median ocellus, and slightly greater than ocello-orbital distance (0.32 : 0.24 : 0.30). Vertex rounded, as narrow (0.22) as diameter of median ocellus. Gena narrower in profile than width of eye; preoccipital rim rounded. Labrum simple, rounded. Mandibles edentate. Mesoscutum, scutellum and wings like worker. Hamuli 6. Metathoracic tibia 3.06 times longer than wide (1.90 : 0.62), margin convex, posterior–distal angle approximately straight. Metathoracic basitarsus strongly swollen on outer surface, 1.7 times longer than wide (0.90 : 0.52); posterior margin strongly convex, posterior–distal edge rounded. Form of metasoma like that of worker. Pre-genital sterna and genitalia, Figs 23–26, 31–33.

Type Material. *Holotype*, worker, COSTA RICA: San José, Braulio Carrillo Nat. Park, 8.xii.1981, (*Roubik*), (NMNH); *allotype*, male, COSTA RICA: Puntarenas, Estación Biol. Las Alturas, Coto Brus, 2000 m, abr. 1993, (*Lobo*), (FFCL: Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto–USP, Camargo collection). *Paratypes*, COSTA RICA: 2 workers, Cerro de la Muerte, Cartago Prov., 2700 m, 27.ii.1978, (*Snyder-Hodges*), (AMNH); the following, collected by (*Roubik*), deposited at USNM, FMUSP: G. B. Fairchild Insect Museum of the University of Panamá, STRI: Smithsonian Tropical Research Institute, *Roubik* collection), InBio: Instituto Nacional de Biodiversidad (Heredia, Costa Rica), and SMKU: University of Kansas, Snow Entomological Museum: 10 workers from the same locality as holotype; 3 workers, Puntarenas Prov., Monteverde 1983, 1989; 63 workers, near Parque Nacional de La Amistad, 2200 m, 1630 m, 21.ii, 2.iv.1992; 50 workers, San José, Zurqui de Moravia, 1600 m, v.1992 (*Hanson*), also 1 worker, iii. 1989; 1 worker, San José, 16 km SE, 1.ii.1989, (*Hanson*), 2 workers, San José Prov., Braulio Carrillo Pk. at S. of tunnel, xii.1981, 1400 m, (*Roubik*); 1 worker, Puntarenas Prov., Las Alturas, ii. 1990, 82°50'W, 8°56'N, 1600 m, (*Lobo*); one male, Zurqui de Moravia, 1600 m, 5.xi.1993, [from nest], (*Lobo*), deposited in IMUCR: Insect Museum of the University of Costa Rica: 12 workers, Puntarenas Prov., San Vito, Estación Biológica Las Alturas, 2000 m, 1992, col. (*Hanson & Godoy*); 10 workers, San José Prov., Zurqui de Moravia, 1600 m, iv.1992, col. (*Hanson*); idem., 1600 m, iv.1992, (*Lobo*); PANAMA: Chiriquí Prov., Cerro Pelota, Santa Clara, finca de R. Hartmann, 1700 m, 22.ii.1992 (*Roubik*); 3 workers, PANAMA: Chiriquí Prov., Santa Clara, 5 km N., Ojo de Agua, 1600 m, 5.iv.1992, 15 workers (*Roubik*); (FFCLRP), worker bearing a yellow 'paratype' label, 'PANAMA', designated by H. F. Schwarz as

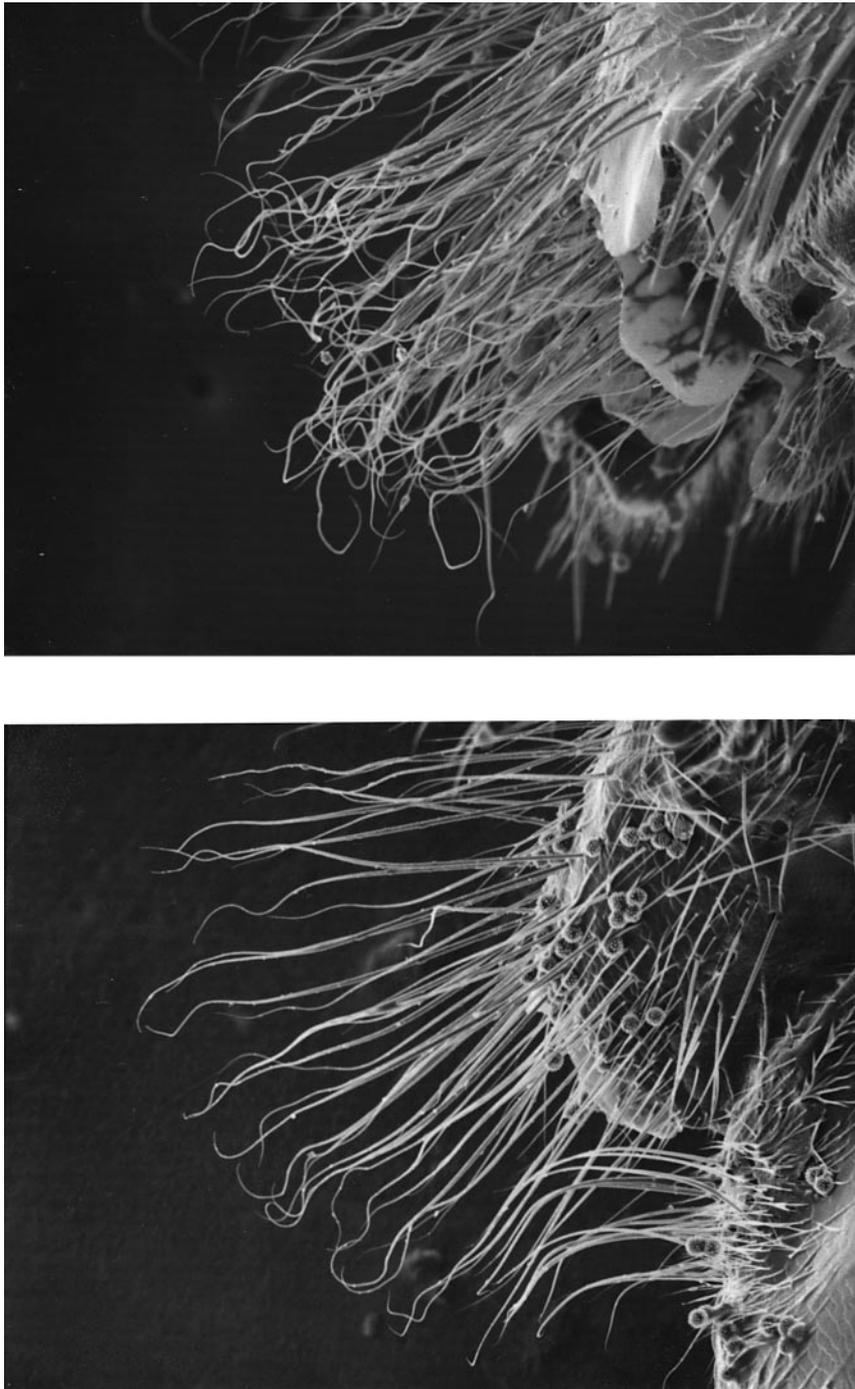


Fig. 39. Sinuous hairs on the metathoracic coxa of *Scaptotrigona luteipennis* (above) and *Meliwillea bivea*. SEM magnification 150 \times .

'*Trigona (Oxytrigona) sarothrum* Schwarz, unpublished' (BMNH).

Etymology. From the Latin, *bivea* signifies 'to have two paths'. This name was chosen because at first inspection this bee appeared to have equally strong affinities with *Scaptotrigona* and *Partamona*.

Bionomics and geographical distribution

Nesting occurs in tree hollows (JALS at Las Alturas, Coto Brus, Costa Rica, 2000 m elevation, and at Zurqui de Moravia at 1600 m). Among individuals collected at Zurqui, El Empalme and Las Alturas, Costa Rica, four were caught in a Malaise trap, thirty visiting flowers of *Miconia* (Melastomataceae) and

two at campfire ashes. At Braulio Carrillo National Park individual foragers were seen flying over a mountain pass intermittently during relatively sunny and calm weather; *Partamona grandipennis* was the only other stingless bee in flight. At 1800 m in Costa Rica, JALS found *Tetragonisca angustula* and *Paratrigona ornaticeps* in the same spot as *Meliwillea*, also at campfire ashes. In Panama, near La Amistad National Park at 1100–2700 m, bees were found visiting small white flowers of composites, and also *Miconia*, as were honey bees (*Apis mellifera scutellata*), and some black meliponines, *Partamona* (*grandipennis* and aff. *bilineata*), and *Scaptotrigona subobscuripennis*. These visits occurred in open and disturbed habitat (pasture) near forest edges. All the above are normally cloudy, rainy and often windy habitats.

To date, this bee species has been recorded only at the mountain range of the Tilarán (Monteverde Field Station), the Talamanca mountain range of Costa Rica and western Panama, and the central Cordillera of Costa Rica, at elevations between 1400 and 2700 m, where relative humidity is 80–100% and daily maximum temperatures usually range from 14 to 22 °C, with minima near 6 °C at 2700 m and annual precipitation is 3000–4000 mm, with 4–5 h daily insolation (Coen, 1991).

In floristic terms, the zone occupied by *Meliwillea* is characterized by some eighty tree species (d.b.h. \geq 10 cm) per hectare. Some of the most common woody plants are *Alnus*, *Billia*, *Brunella*, *Clethra*, *Clusia*, *Cornus*, *Drymis*, *Eugenia*, *Ficus*, *Hedyosmum*, *Magnolia*, *Miconia*, *Ocotea*, *Persea*, *Pinus* (introduced), *Quercus*, *Roupalla*, *Sapium*, *Saurauia* and *Weinmannia*. Common understory plants are very rich and can include Melastomataceae, Piperaceae, Palmae and many epiphytes (Gómez, 1986).

Discussion

Exhaustive search produced a single minimum tree of length 14 (longest tree length = 27), CI = 0.71, RCI = 0.55, RI = 0.77, HI = 0.29 (Fig. 38). *Scaptotrigona* and *Meliwillea* emerged as sister genera, also in trees of lengths 15 and 16. The same minimum length tree resulted from analysis excluding all three synapomorphies unique to *Meliwillea* and *Scaptotrigona* (Table 1). We also included one disproportionately weighted character state, routinely used in meliponine taxonomy (Moure, 1961), considered the hallmark of *Nannotrigona* to *Scaptotrigona* (Michener, 1990)—the scutellar fovea. Doubling or tripling the weight of this character state produced the same, single minimum tree shown in Fig. 38. Greater weightings produced multiple trees, most linking *Nannotrigona*–*Scaptotrigona*, but varying considerably in the placement of *Meliwillea*. With *Meliwillea* excluded from the analysis two minimum trees were found, each showing *Nannotrigona*–*Scaptotrigona* (CI = 0.75, RI = 0.7). Thus, by including the new genus a basic change occurred in tree topology, separating *Nannotrigona* from *Scaptotrigona* and placing the former with *Paratrigona*. Noteworthy are the lack of character state reversions and a preponderance of convergent character states in the cladogram (Fig. 38).

Meliwillea does not possess highly distinctive

autapomorphies, rather, it displays a combination of attributes appearing in various genera (Table 2). Furthermore, *Meliwillea* is easily distinguishable from all other genera and species by the following combination of characteristics, many of which seem plesiomorphic: polished and shining, predominantly black cuticle; absence of yellow markings; two, small, well-separated mandibular teeth (a sympomorph with *Scaptotrigona*); a very long malar space (a sympomorph with *Scaptotrigona*); a short, rounded scutellum lacking a basal fovea and barely extending beyond the base of the metanotum; the submarginal angle of the forewing obtuse, nearly 120°; the inner surface of the metathoracic tibia flat, not depressed and smooth along the posterior margin, and having a uniform keirotrichiate area. The medially swollen metathoracic basitarsus is an autapomorphy. Compared with the sister genus, *Scaptotrigona*, *Meliwillea* differs by absence of a median basal scutellar fovea or pit, absence of a protuberance on the inner margin of the antennal alveolus (Fig. 8), absence of a preoccipital laminar carina, interrupted at the sides (Figs 7, 11, 12), and absence of a gradular carina on the first metasomal tergum. These structures are present only in *Scaptotrigona*.

Certain combinations of body form, such as the head in frontal view (Figs 1–6) and other attributes not shown in our character matrix make us consider the relationship of *Meliwillea* with *Scaptotrigona* to be closer than the formal analysis indicates (see Table 1). These include, among workers, the form of mandibular teeth and the convex median posterior rim of the metathoracic basitarsus. In addition, D.W.R. noticed *Meliwillea* has a strong mandibular gland odour, like the musky, acrid smell characteristic of *Scaptotrigona*; but, with further subjective observation (comparison to live *Scaptotrigona*), the odour proved distinctive. The male of *M. bivea* shows some other similarities with *Scaptotrigona*: the form and pilosity of pregenital sterna, including the translucent patch along the median line of sterna 3–5, and the form of the genitalia – gonocoxites, gonostyli, spatha and penis valve (Figs 23–36). These presumably highly conservative genitalic characters also separate *Meliwillea* and *Scaptotrigona* from other groups that are more or less closely related, such as *Partamona* (see Fig. 37), *Parapartamona*, *Paratrigona*, *Aparatrigona*, *Nogueirapis* and *Nannotrigona* (description of the males in Bravo, 1992; Camargo & Moure, 1994; Michener, 1990; D.W.R. and J.M.F.C. have independently examined males of *Nogueirapis*). Despite a need to include more traits in order to produce stability in any phylogeny of the Meliponini, the close relationship of *Meliwillea* with *Scaptotrigona* is clear.

Biogeographical considerations

Biogeographical patterns of American Meliponini are still poorly known. General discussions consider dispersion without recourse to analytical historical biogeography or phylogenetic hypotheses (Michener, 1979; Camargo et al., 1988; Roubik, 1989). A background of well corroborated biogeographic data for many species, especially those of Central and South America, is essential, thus our comments must be viewed as

preliminary. The primary focus concerns a postulated vicariance event that led to cladogenesis of *Meliwillea*.

Isthmian (Panamanian and Costa Rican) stingless bees, which comprise sixteen to forty-two species in lowland forests (Roubik, 1992, 1993), are represented by no more than three species at higher elevations, above 2000 m (D.W.R., J.A.L., unpublished observations). We believe the monophyletic clade of *Parapartamona-Partamona/Scaptotrigona-Meliwillea* indicates their ancestors existed both in the northern and southern part of the modern Neotropics well before the landmass forming most of the isthmus arose, at 3.3 Myr (Donnelly, 1992; Goldblatt, 1993). *Partamona* and *Scaptotrigona* occur from Brazil to Mexico at sea level to the Andes and highlands of Central America, and at least to 2100 m in Colombia and Ecuador (Schwarz, 1948; Vergara & Pinto, 1981; Coloma, 1986; Ayala, 1992; Bravo, 1992). Sympatry with their proposed sister groups is the product of relatively recent dispersal, following a separation that allowed cladogenesis. We propose the lineage produced the montane *Meliwillea in situ* as mountain building occurred through volcanism and uplifting, during the Tertiary. The large, montane *Partamona grandipennis* has a distribution similar to that of *Meliwillea* (900–2500 m) in the isthmus but shows relatively slight morphological divergence from the strictly montane *Parapartamona* (see Roubik & Michener, 1993; Pedro & Camargo, in press), compared with the degree of difference between *Meliwillea* and its sister group. This comparison indicates a greater age for *Meliwillea*. Endemism of Central American and Mexican meliponines involves species of genera widely distributed in South America. Most seem best regarded as examples of Pleistocene vicariance and divergence, following dispersal across the isthmus (Ayala, 1992; Camargo, 1996; Camargo & Moure, in press). *Meliwillea*, in contrast, is the only genus known exclusively from Central America and because of its abundant plesiomorphies, it is a biogeographical relic. Cloudforest habitat has been more widespread in Central America than it is today. In the mid-Tertiary, and also during post Pliocene glaciations that governed climate during 3 million years, daily maximum temperatures averaged some 7 °C lower, making lowlands, almost to sea-level, resemble cloudforest in temperature as well as in floristic elements (Bush *et al.*, 1991; Goldblatt, 1993). With arrival of *Scaptotrigona*, *Partamona* and other genera from South America, and the return of warmer conditions after the Pleistocene, some *Meliwillea* possibly became extinct (see Platnick, 1976) while montane populations persisted.

The fossil record in amber shows the presence of Meliponini, from the mid Tertiary, in southern Mexico (Wille, 1959) and also in the Antilles (Wille & Chandler, 1964; Cano *et al.*, 1992). The extinct genus, *Proplebeia*, is currently known only from Dominican amber, but Wille's description (1959, 1962) of amber fossil bees from Chiapas, *Nogueirapis silacea*, suggests to us its inclusion within *Proplebeia*, and demands further study.

Early vicariance among meliponines dates to the breakup of a proto-Antillean archipelago, but at what time? Because we are dealing here with endemic Neotropical fauna, the geological time scale necessarily postdates separation of Africa from South America. The earliest Cretaceous (144–130 Myr BP)

appears too early, and there are no known genera of Meliponini shared between Africa and the Americas, despite possible links between south Africa and southern Brazil (Camargo & Wittmann, 1989). Yet the Oligo-miocene, corresponding to the ages of Dominican amber fossils (Cano *et al.*, 1992) seems too late. At 119 mybp, and also the Deseadan of the late Oligocene (28 Myr BP) there was a proto-Antillean island arc across which dispersal by plants and animals evidently occurred (Donnelly, 1992; Goldblatt, 1993 and additional references therein). The isthmus arose *in situ* rather than by accretion of terranes moving in from the eastern Pacific (Donnelly, 1992). Meliponines have only one native species in the Caribbean, *Melipona variegatipes*, endemic to the Lesser Antilles, which closely resembles *Melipona favosa*, of extra-Amazonian South America and Panama, and both seem related to *Melipona yucatanica*, known from Mexico to Costa Rica (Camargo *et al.*, 1988; Nates & Roubik, 1990; Ayala, 1992). *Melipona* is the largest meliponine genus, with about fifty taxa. Although Antillean and Mexican species were likely derived from vicariance events after the Oligocene, earlier contact between Central and South America involved ancestral *Proplebeia* and *Meliwillea*. We suggest these bees were widely distributed between northern South America and Mexico during the earliest opportunity to disperse along a proto-Antillean island arc, in the upper, early Cretaceous period.

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