

## Neotropical Meliponini: *Paratrigonoides mayri*, new genus and species from western Colombia (Hymenoptera, Apidae, Apinae) and phylogeny of related genera

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### Abstract

*Paratrigonoides mayri* **gen. nov.**, **sp. nov.**, from the Cauca Valley region of Antioquia, Colombia, is described. It resembles *Paratrigona*, especially species of the *P. lineata* group. The new genus is recognized by a combination of bidentate mandibles, the keirotrichiate area of tibia III not depressed on the posterior edge (plesiomorphies), yellow markings flanking the frontal median line and two spots below the lateral ocelli, supraclypeal area partly covering antennal sockets, and by the upper part of the preoccipital ridge lamellate and bordered by a row of robust hairs (autapomorphies). The result of a cladistic analysis suggests *Paratrigona* + *Aparatrigona* form the sister-group of *Paratrigonoides* **gen. nov.**

**Key words:** stingless bees, new genus, taxonomy, Neotropics

### Introduction

Recently, generic revisions and regional accounts of stingless bees (e.g. Roubik 1992; Camargo & Moure 1994, 1996; Camargo 1996; Roubik *et al.* 1997; Ayala 1999; Camargo & Pedro 2003, 2004, 2005; Pedro & Camargo 2003; Eardley 2004) have significantly increased knowledge about this group and have resulted in the description of four new genera. The new genus proposed here, *Paratrigonoides* **gen. nov.**, comes from the Cauca Valley, NW Colombia, a region where only recently have collecting efforts been intensified. The phylogenetic relationships of this new taxon are studied in relation to the genera of Meliponini that present a broad and flattened keirotrichiate area, these constitute a derived clade, one that is exclusively Neotropical.

## Materials and Methods

The terminology employed here follows Camargo & Pedro (2004, 2005). Abdominal terga and sterna are indicated with TII–TVIII and SII–SVIII, considering the fusion of the first abdominal tergum (the propodeum) with the thorax. The propodeal disc is called the metapostnotum. The legs are designated with Roman numerals—I, II, III.

To facilitate comparisons, the generic diagnosis follows the character combinations considered in previous work, principally that of Camargo & Pedro (2004, 2005), with the addition of the item **r** which refers to the labium and galea. Distinctive or autapomorphic characters are indicated in boldface letters. Measurements are indicated in millimeters.

The matrix of 14 taxa and 32 characters (Table 2) was analysed using maximum parsimony in PAUP\* 4.0b10 (Swofford 2001) (branch and bound or heuristic search, with equal weightings, unordered characters, Acctran optimization, rooted or unrooted) to produce minimum-length trees. The figures were generated using MacCLADE 3.05 (Maddison & Maddison 1992). Photomicrographs were taken with a Pentax MZ-M using the Leica MZ8 stereo microscope.

### *Paratrigonoides*, gen. nov.

**Type species; *Paratrigonoides mayri* sp. n.**

**Diagnosis. Worker. a**—Body length between 4.5 and 4.7 mm. **b**—integument matte-microreticulate on head and thorax; metapostnotum alveolate. **c**—Body dark ferruginous except vestiture and markings described below; mesoscutum black; wing membrane hyaline. **d**—Yellow markings pronounced on head, thorax and base of all tibiae. On the head, yellow markings on paraocular areas, clypeus, supraclypeal area and frons; **frons with oblong mark on each side of median line and smaller mark anterior to lateral ocellus** (Fig. 1). On the thorax, yellow markings as follows: a transverse stripe on pronotum, entire pronotal lobe, one stripe each side of mesoscutum, axilla and distal margin of scutellum. **e**—Vestiture: erect hairs on body uniformly pale-whitish, slightly more yellowish on tarsi; in addition, a fine silvery gray micropilosity, branched, decumbent, covering face and mesoscutum; erect hairs lacking on lower half of face; **row of robust setae, branched at apices, along preoccipital lamella, on upper part of occiput** (Fig. 2); metapostnotum glabrous; setae on abdominal sterna branched; **f**—Head ca. 1.09 x wider than long, slightly wider than thorax; maximum interorbital distance slightly greater than length of eye; inner orbit of eye somewhat convergent below; superior alveolar tangent slightly below middle of face; vertex rounded, not forming post-ocellar carina; malar space very short, approximately  $\frac{1}{4}$  diameter of third flagellomere; **preoccipital ridge having fine lamella on the upper part, curving forward** (Fig. 2); side rounded; gena, seen from side, narrower than compound eye. **g**—Clypeus ca. 1.96 x wider than long, convex; epistomal suture, between subantennal sutures a widely open V;

**supraclypeal area widened, forming, at each side, a flange, partly covering antennal sockets.** **h**—Labrum normal. **i**—Mandible bidentate (Fig. 5). **j**—Scape ca. 0.80 x as long as latero-ocular distance, slightly narrower than diameter of third flagellomere; pedicel as wide as long; third flagellomere slightly longer than wide. **k**—Pronotum short, ca. 0.76 x length of scutellum; anterior margin normal, not emarginate. **l**—Scutellum short, 2.07 x wider than long; posterior margin semicircular, barely extending beyond metanotum viewed from above; basal fovea lacking. **m**—Forewings shorter than body length, ca. 2.7 x length of tibia III; pterostigma ca. 4.2 x longer than wide, slightly wider than diameter of third flagellomere; marginal cell ca. 3.86 x longer than wide, lanceolate, open slightly at apex; bifurcation between M and Cu coinciding with cu-anal vein; submarginal angle between Rs and Rs + M, slightly acute, ca. 80°; angle between M and Rs + M obtuse, ca. 120°; first abscissa of M ca. 0.82 x length of first abscissa of Cu; submarginal cells weakly veined, first r-m almost obsolete [as in *Paratrigona lineata* (Lepeletier)]; second cell Cu and first M closed—first vein m-Cu weak, although evident; hind wing with jugal and vanal lobes subequal; hamuli 5. **n**—Tibia III subtriangular, ca. 2.5 x longer than wide [as in *P. lineata*, although slightly wider]; postero-distal edge slightly rounded; corbicula occupying distal half, gently depressed, more strongly concave at apex; corbicular setae simple, only two or three having some ramification; internal surface with very wide keirotrichiate area, with a narrow posterior rim, glabrous, not depressed, approximately 1/10 greatest width of keirotrichiate area; tibial comb and penicillum normal. **o**—Basitarsus III ca. 0.6 x as wide as tibial width and ca. 0.51 x its own length, apex 1.47 x basal width; posterior margin sinuous, postero-distal edge projecting slightly, rounded; internal surface without basal sericeous area, hairs irregularly distributed. **p**—Metapostnotum relatively protuberant, the basal disc slanted at ca. 45° and posterior half vertical. **q**—Abdomen short and wide, approximately oval viewed from above. **r**—Labium very long, approximately twice head length; galea slightly longer than length of tibia III. **s**—Nest unknown.

***Paratrigonoides mayri* sp. nov.**

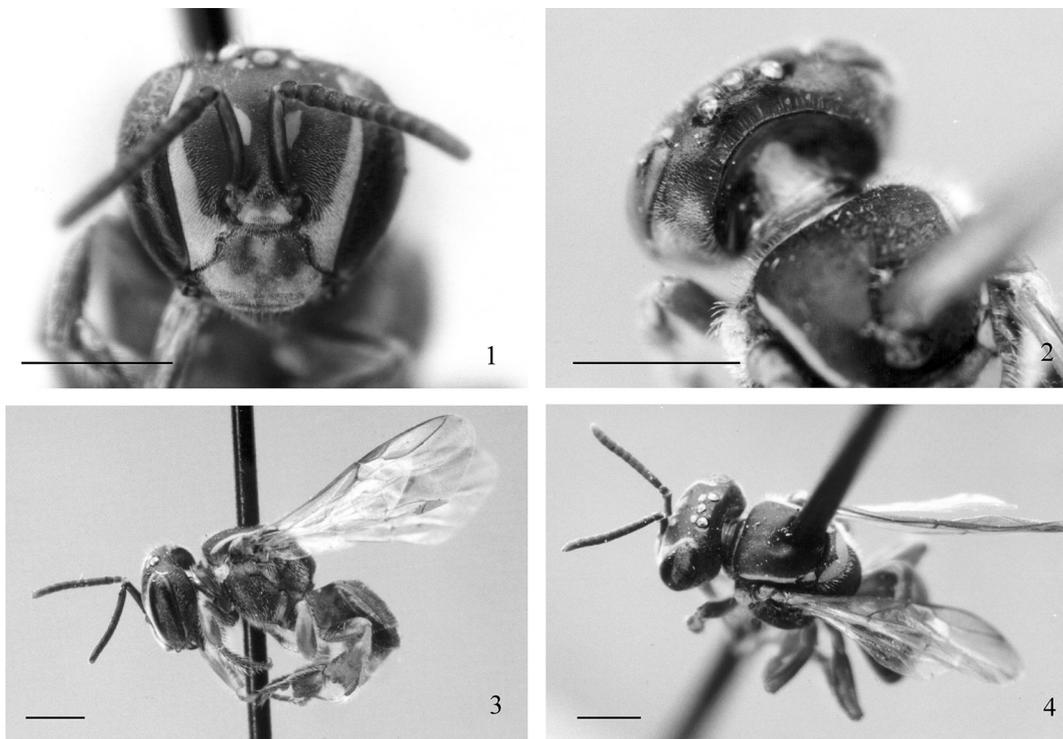
**Diagnosis. Worker.** See discussion and boldface characters under foregoing description of the genus.

**Holotype.** Worker (Table 1, Figs. 1–5).

**Dimensions.** Total length ca. 4.66 mm; anterior wing length, from apex of costal sclerite to wing tip, 4.14 mm (including tegula, 4.75 mm); maximum head width 1.94 mm.

**Integument color.** Body predominantly dark-ferruginous, except yellow markings described below; mesoscutum dark; legs and wing veins ferruginous, wing membrane hyaline. Yellow markings pronounced on head, thorax and tibial base of all legs. Paraocular mark widened below, filling space between epistomal suture and ocular orbit, with small gap near antennal socket, continuing above to tangent of superior orbit,

terminating in short truncation (Fig. 1); clypeus with massive somewhat anchor-shaped mark (as in *P. lineata*); supraclypeal area with widened trapezoidal marking, filling the area to level of mid antennal sockets; on frons, oblong marking each side of median line, closer to antennal sockets than to ocelli and small circular mark beneath lateral ocelli; gena having small band at inferior orbit. Pronotum with transverse band, pronotal lobe entirely yellow, with barely translucent median area. Mesoscutum banded on each side, from anterior edge to axilla, each as wide as  $5/8$  diameter of third flagellomere; axilla yellow; scutellum with wide postero-marginal band, notched on anterior median line (Fig. 4). On tibiae I and II, yellow marks extend to median line, along basal two-thirds; on tibia III, following posterior margin to little past middle.



**FIGURES 1–4.** *Paratrigonoides mayri* gen. nov., sp. nov. **1**, head, frontal view; **2**, head, detail of preoccipital carina; **3–4**, profile and dorsal view. Scale = 1.0 mm.

**Vestiture.** Pale-whitish erect hairs on entire body, slightly yellowish on tarsi; paraocular area, clypeus, supraclypeus and inferior face having silvery decumbent micropilosity; upper one-half of face with sparse erect hairs, increasing in length toward vertex; between ocelli, ca. 18 hairs little longer than diameter of median ocellus and slightly serrate; slightly longer on lower gena; scape somewhat micropilose, with some small erect hairs, one-fourth its diameter; a row of robust setae, branched at apex, along preoccipital lamella (Fig. 2), the longest slightly shorter than diameter of median ocellus. Mesoscutum with sparse erect hairs; scutellum with erect finely plumose hairs, longest at

posterior edge, approximately one-half scutellum length; ventral hairs of the mesepisternum, up to approximately 0.30 mm in length. Metapostnotum glabrous. Abdominal terga II to V mostly glabrous, some micropilosity at sides and premarginal bands of terga III–V, more abundant and more branched on VI and VII, especially along margin of latter, and as long as the diameter of median ocellus; sternal erect hairs branched, those at edges having recurved tips backward.

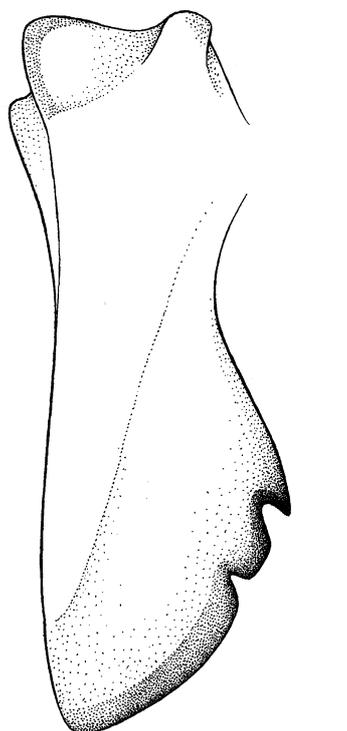
**Integument.** Matte-microreticulate on head and thorax, more densely on face and mesoscutum (ca. 10–15 piligerous micro-punctures per ocellar diameter slightly finer than in *P. lineata*); genae slightly smoother and more shining; metapostnotum, particularly in the disc, with marked alveoli (7–8 per ocellar diameter), pentagonal or hexagonal, delimited by fine carinulae. Outer surface of tibia III smooth and shiny, somewhat tessellated at base. Abdominal terga smooth and shiny, in particular on II and III, superficially microreticulate.

**Form and proportions** (measurements in Table 1). Head 1.09 x wider than long, 1.70 x wider than clypeo-ocellar distance. Eyes 2.62 x longer than wide, converging slightly below. Malar space very short, one-fourth diameter of third flagellomere. Clypeus length 0.51 x its maximum width, 0.42 x clypeo-ocellar distance. Mandibles 0.69 x clypeo-ocellar distance in length, having two denticles on inner apical edge, the internal one truncate on apex (Fig. 5). Labrum 2.64 x wider than long, normal, convex, apical margin slightly arched. Supraclypeal area widened, forming, at each side, a flange, partly covering antennal sockets. Scape 0.79 x alveo-ocellar distance in length, normal, diameter approximately that of third flagellomere. First flagellomere somewhat longer than wide. Inter-ocellar distance 1.48 x greater than ocello-orbital, 2.12 x diameter of median ocellus. Upper preoccipital ridge having fine lamella curving upward (Fig. 2). Scutellum 2.7 x wider than long, distal margin semicircular, slightly over-roofing the apex of metanotum. Tibia III subtriangular, 0.79 x head width, 2.51 x longer than wide (as in *P. lineata*, but somewhat wider and with the postero-distal edge slightly more rounded). Basitarsus III 1.94 x longer than wide, posterior margin sinuous, slightly expanded at apex and postero-distal edge slightly projected, rounded. Forewing 2.54 x longer than wide, 2.13 x head width.

**Type material.** Holotype, worker, from Colombia “S. Jeronimo (Ant.) en Bacharis [*sic*] sp, Feb. 1978, A. Molina P.” [San Jerónimo, Antioquia, NW Medellín, 6°25'N/75°43'W]; paratypes, 5 workers, with the same locality label, in addition to one worker taken by malaise trap, from “Colombia: Bolivar, Los Colorados, Alto el Mirador, 400 m, 9°54' N, 75°07' W” [ca. 400 km N of San Jerónimo], anonymous. Holotype deposited in USNM (Smithsonian Institution) Washington, D. C., paratypes deposited in the National University, Medellín, STRI (Smithsonian Tropical Research Institute, D. W. Roubik collection), and Departament of Biology of the Faculty of Philosophy, Science and Letters of Ribeirão Preto, University of São Paulo (RPSP, Camargo collection).

**TABLE 1.** Measurements (mm) of the holotype *Paratrigonoides mayri*, **gen. nov., sp. nov.**

1. total length	4.66
2. head width	1.94
3. head length (from clypeal apex to vertex)	1.77
4. compound eye length	1.44
5. compound eye width	0.55
6. superior interorbital distance	1.09
7. maximum interorbital distance	1.30
8. lower interorbital distance	0.97
9. median ocellus diameter	0.18
10. distance between lateral ocelli	0.34
11. ocello-orbital distance	0.23
12. interalveolar distance	0.37
13. alveolus-lateral ocellus distance	0.87
14. alveolar diameter	0.16
15. clypeus length	0.48
16. clypeus width	0.94
17. clypeo-ocellar distance	1.14
18. length of malar space	0.03
19. length of scape	0.69
20. scape diameter	0.11
21. pedicel length	0.15
22. length of first flagellomere	0.14
23. width of first flagellomere	0.13
24. length of third flagellomere	0.13
25. width of third flagellomere	0.12
26. mandible length	0.79
27. mesoscutum length	1.24
28. mesoscutum width	1.33
29. scutellum length	0.42
30. scutellum width	0.87
31. forewing length to apex of costal sclerite	4.14
32. forewing length including tegula	4.75
33. forewing width	1.63
34. length of first abscissa of M	0.76
35. length of first abscissa of Cu	0.93
36. length of tibia III	1.53
37. width of tibia III	0.61
38. length of basistarsus III	0.72
39. width of basistarsus III	0.37



**FIGURE 5.** Mandible, detail of denticles. Scale = 0.5 mm.

**Etymology.** The species of this new genus is named in honor of Ernst Mayr, one of the central architects of the synthetic theory of evolution, born on 5 July, 1904, deceased on 3 February, 2005, at 100 years of age.

### **Phylogenetic relationships**

Fourteen genera were included in the analysis (Table 2). The character posterior margin of keitrichiate area very narrow, flat, not depressed is shared exclusively by the Neotropical taxa, *Partamona* Schwarz, *Parapartamona* Schwarz, *Nogueirapis* Moure, *Scaptotrigona* Moure, *Nannotrigona* Cockerell, *Meliwillea* Roubik *et al.*, *Paratrigona* Schwarz, *Aparatrigona* Moure and *Melipona* Illiger. It is within this group, considered monophyletic (*e.g.*, Roubik *et al.* 1997; Pedro & Camargo 2003), that the new taxon is placed. Thus, for an analysis of possible phylogenetic relationships, such a group is used as the ingroup and, as an outgroup we used the more basal genera, *Plebeia* Schwarz, *Mourella* Schwarz, *Schwarziana* Moure and *Friesella* Moure. This Neotropical group (to which *Scaura* Schwarz and *Schwarzula* Moure also belong) also has a very wide keitrichiate area, the same as the ingroup, but with the posterior edge depressed and clearly defined, as a step or sulcus. The character matrix was prepared using, in addition to

features already studied by Roubik *et al.* (1997) and Pedro and Camargo (2003), characters such as the yellow marks on head, thorax and legs, the kind of setae, and integumental texture, as described below.

**TABLE 2.** Matrix of characters for *Paratrigonoides* **gen. nov.** and species of related genera.

	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	3	3	3			
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
<i>Paratrigonoides mayri</i> <b>sp. nov.</b>	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	3	0	0	0	1	1	4	0	0	0	0	0	0	1	0	0	0	
<i>Paratrigona lineata</i> (Lepeletier)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	1	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	
<i>Aparatrigona impunctata</i> (Ducke)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	4	0	1	0	1	0	0	0	0	1	0	1	0	1	0	0	0	
<i>Partamona peckolti</i> (Friese)	0	0	0	1	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	2	3
<i>Parapartamona vittigera</i> Moure	1	0	0	1	1	1	1	1	1	1	1	0	0	0	1	2	0	0	1	0	0	1	0	0	0	0	1	1	1	2	1		
<i>Nogueirapis mirandula</i> (Cockerell)	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	
<i>Scaptotrigona xanthotricha</i> (Moure)	1	1	1	0	1	1	1	1	1	0	1	0	0	2	1	6	1	0	1	0	1	3	1	1	2	1	0	1	1	0	1	2	
<i>Nannotrigona testaceicornis</i> (Lepeletier)	1	1	1	0	1	0	0	0	0	1	0	0	0	0	7	0	0	0	0	0	2	0	0	2	1	0	0	1	0	1	0	1	2
<i>Meliwillea bivea</i> Roubik, Lobo & Camargo	1	1	1	0	1	1	1	1	1	1	0	0	2	1	0	0	0	1	0	0	0	1	1	0	0	0	1	1	0	0	1	0	2
<i>Melipona marginata</i> Lepeletier	0	0	0	0	0	0	2	1	0	0	1	0	0	0	4	3	0	2	0	0	5	0	0	0	0	0	0	1	0	0	4		
<i>Plebeia droryana</i> (Friese)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
<i>Mourella caerulea</i> (Friese)	0	0	1	0	0	0	0	0	0	0	1	1	3	0	5	3	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	
<i>Schwarziana quadripunctata</i> (Lepeletier)	0	0	0	0	1	0	0	1	0	0	1	1	3	0	2	3	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1		
<i>Friesella schrottkyi</i> (Friese)	0	0	0	0	0	0	1	0	0	1	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

- 1) Clypeus, yellow markings—0 = present; 1 = absent.
- 2) Paraocular area, yellow markings—0 = present; 1 = absent.
- 3) Supraclypeal area, yellow markings—0 = present; 1 = absent.
- 4) Frons, yellow marking on frontal line—0 = absent; 1 = present.  
This refers to the supraclypeal band that extends to the base of the frontal line. In some species of *Partamona* all of the supraclypeal triangle is yellow and, in some *Nogueirapis*, the band reaches the median ocellus. In *Parapartamona* there are only one or two small yellow marks next to the base of the frontal suture.
- 5) Pronotum, yellow markings—0 = present; 1 = absent.
- 6) Mesoscutum, lateral yellow bands—0 = present; 1 = absent.
- 7) Axillae, yellow markings—0 = present; 1 = absent.
- 8) Scutellum, yellow marking—0 = on apical margin; 1 = absent; 2 = entire.
- 9) Tibia III, yellow marking on base—0 = present; 1 = absent.
- 10) Plumose hairs on frons and paraocular areas—0 = present; 1 = absent.  
Branched or plumose hairs include apressed micropilosity, covering the face as in

*Paratrigonoides* **gen. nov.**, to long branched hairs that form tufts on the frons, as in *Melipona*, *Mourella* and *Schwarziana*. Further resolution of this character, considering distribution and size of the hairs, did not result in clear character states, due to continuous variation.

- 11) Erect, simple hairs on the upper one-half of the frons—0 = absent; 1 = present.
- 12) Metapostnotum—0 = glabrous; 1 = hirsute.
- 13) Vestiture on abdominal sterna—0 = simple; 1 = branched.
- 14) Abdominal sterna hairs, form—0 = almost straight or only bending at tip; 1 = sinuous at tip; 2 = multi-sinuous; 3 = recurved at tip.
- 15) Tomentum of abdominal terga—0 = absent; 1 = present.
- 16) Frons, integument—0 = smooth and shiny, having piligerous micropunctures; 1 = rugulate, semi-glossy, piligerous punctures; 2 = finely micro-alveolate (alveoli 0.3 x ommatidial diameter), semi-glossy; 3 = finely micro-alveolate, opaque, alveoli well-defined (alveoli 0.3 x ommatidial diameter); 4 = micro-alveolate, semi-glossy, alveoli well-defined (alveoli 1.0 x ommatidial diameter); 5 = alveolate, semi-glossy, alveoli irregular with rugulose spaces, equal or greater than punctures diameter (ca 1.5 x ommatidial diameter); 6 = alveolate (ca. 1.0–2.0 x ommatidial diameter), semi-glossy, spaces irregular; 7 = macro-alveolate (ca. 4.0–5.0 x ommatidial diameter), alveoli approximately hexagonal, regular, deep and lined by fine lamellae.
- 17) Abdominal terga, integument—0 = smooth-shiny; 1 = micro-alveolate, matte; 2 = superficially micro-reticulate, matte; 3 = strongly tessellated, shiny.  
In *Scaptotrigona*, the integument is micro-alveolate, as in *Paratrigona*, although with fine hairlets emerging from each alveolus.
- 18) Mandible, number of teeth—0 = 2; 1 = 4.
- 19) Mandible, contour between denticles—0 = in a V or U; 1 = in a flat arc, denticles well separated; 2 = in a straight line, denticles tiny and well separated.
- 20) Galea, length—0 = short (shorter than tibia III); 1 = long (longer than tibia III).
- 21) Supraclypeal area, form (between antennal alveoli)—0 = normal; 1 = expanded, partly covering antennal sockets.
- 22) Preoccipital ridge—0 = upper part without clear limits; rounded at sides 1 = forming a keel above, rounded at sides; 2 = as keel above and forming lamellar ridge at sides; 3 = forming translucent carina above, followed at sides by large dent ending in a tooth; 4 = lamellate-carina above, rounded at sides; 5 = forming lamellar carina above (as character state 4, but closer to foramen magnum), rounded at sides.

With the exception of *Friesella*, which has the basal or 0 state for 22, the remaining genera of the outgroup—*Plebeia*, *Mourella* and *Schwarziana*—share state 1 (keel above, rounded at sides). That coding may create doubts about polarity, although all remaining Neotropical meliponines, with the exception of *Cephalotrigona* Schwarz and the African groups, display rounded preoccipital ridges, indicating the plesiomorphic state.

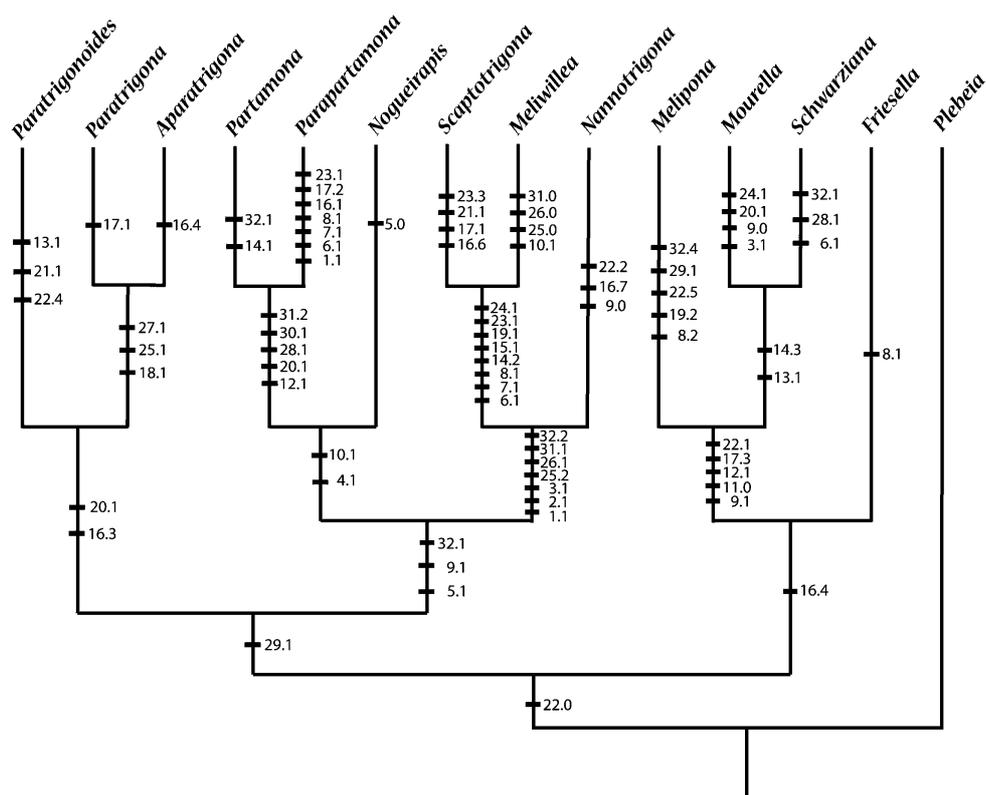
- 23) Malar space—0 = short, < 1.0 x diameter of third flagellomere; 1 = long, ca. 1.5 x diameter of third flagellomere.  
Character states are not discrete for this trait, thus the indication of a particular state is tentative in some taxa, and variation among species also exists in some genera, *e.g.* *Paratrigona* (see Camargo & Moure, 1994).
- 24) Length of eye—0 = long, > superior interorbital distance; 1 = short, clearly shorter than superior interorbital distance.
- 25) Scutellum, length—0 = short-rounded, maximum extension seen from above, covering base of metapostnotum; 1 = long-flattened, covering one-half or more of metapostnotum; 2 = long-triangular, covering almost all metapostnotum.
- 26) Scutellum, basal fovea in a V or U—0 = absent; 1 = present.
- 27) Scutellum, lateral margin next to axillary suture—0 = normal; 1 = expanded.
- 28) Median cell, form—0 = nearly an obtuse triangle (vertex, formed by the first abscissa of M and Rs + M, largely open and approximately aligned with the cell center); 1 = nearly triangle-rectangle (vertex forming 90°, or open slightly, displaced to the apical one-third of cell).  
Codification of *Schwarziana* leaves some doubt, with the cell vertex displaced to the apical one-third of cell, but largely obtuse.
- 29) Posterior margin of keirotrichiate area on inner surface of tibia III—0 = clearly depressed in step or sulcus; 1 = not depressed, in same plane as keirotrichiate area.
- 30) Corbicula, form—0 = somewhat concave; 1 = strongly concave, scoop-shaped.
- 31) Tibia III, form—0 = subtriangular, somewhat expanded at apex; posterior margin slightly arched, slightly pointed on postero-distal edge; maximum width approximately at distal one-fourth; 1 = subtriangular, broadening to postero-distal edge, widest at apex; 2 = scoop-shaped, very wide, rounded in apical two-thirds; maximum width in distal one-third.
- 32) Basitarsus III, form—0 = subrectangular, posterior margin sinuous; expanded slightly at middle; 1 = rectangular, sides nearly parallel; 2 = pentagonal, medially expanded, forming a bulge near middle of posterior margin; 3 = bulging, posterior margin somewhat resembling the contour of a pear, sinuous at base and rounded on posterior distal margin.

## Discussion

At first, *Paratrigonoides* **gen. nov.** appears to resemble genus *Paratrigona*, primarily species of the *P. lineata* group (see Camargo & Moure 1994), considering the combination of yellow markings, matte-reticulate integument of the head and thorax, covered with fine, branched and depressed micropilosity, and by the keirotrichiate area with the posterior margin narrow and not depressed. Yet the taxon is distinguishable from *Paratrigona* and

all other meliponine genera by the characters (autapomorphies) indicated above: yellow markings flanking the frontal median line and below the lateral ocelli, preoccipital ridge with a narrow lamellate carina having a row of robust hairs, and an extensive supraclypeal area, covering a portion of the antennal sockets. Added to the foregoing are the presence of only two mandibular teeth and a short scutellum. In *Paratrigona* + *Aparatrigona*, the mandibles possess four teeth, the preoccipital ridge is rounded and lacks a carina, and the scutellum is long, projecting well beyond the metanotum.

All phylogenetic analyses produced the same principal results. *Paratrigonoides* **gen. nov.** consistently appeared as sister group of *Paratrigona* + *Aparatrigona*. From these, for discussion purposes, one tree was selected as having the fewest homoplasies in characters that were considered most important (length 82, CI = 0.646, HI = 0.354, RI = 0.638, RC = 0.412; Fig. 6). Including the African genus *Plebeina* as outgroup did not result in differing placement of *Paratrigonoides*.



**FIGURE 6.** One of the ten minimal-tree cladograms considered of *Paratrigonoides* **gen. nov.** and related Neotropical Meliponini.

Although *Paratrigonoides* **gen. nov.** was always related to *Paratrigona* + *Aparatrigona*, there was no synapomorphy that unequivocally justified this position. The

chief character that produced the association was 16.3 (integument of the face matte-reticulate); however, that character is polymorphic and difficult to code in an evolutionary sequence. There exists variation among species within a single genus, and some character states considered here are not discrete. On the other hand, when 16.3 is considered in conjunction with other characters and their states, micropilosity fine, decumbent-plumose, covering the entire face and intercalated with sparse, erect hairs on the frons, which is shared by the three taxa, a true homology is suggested. That is, the combined characters may have arisen evolutionarily only once. Micropilosity was not coded in the character matrix because of some of the same problems mentioned concerning character 16.

Another point that may be considered consistent with the hypothesis of monophyly of the above mentioned three taxa, although in terms of negative evidence, is the fact that *Paratrigonoides* **gen. nov.** does not belong to any of the groups formed by other genera, in all of the character set and polarity options, indicated by phylogeny and parsimony, that were performed.

Considering the collection of taxa included in the analysis, some interesting points emerge. First, character 29.1 (posterior margin of the keirotrichiate area on the inner surface, tibia III not depressed) was initially taken to define the ingroup, as already proposed (*e.g.* Roubik *et al.* 1997; Pedro & Camargo 2003), but now appears as a homoplasy, with two independent origins, including the separate origin in *Melipona* (Fig. 6). That result was due to the consistent association of *Melipona* with *Mourella* + *Schwarziana*, primarily by character 11.0 (absence of simple, erect hairs on the frons). That character alone, however, had little significance, but when combined with long pilosity, dense and plumose, covering the frons, characters shared by the three genera, lent more plausibility to the hypotheses suggested in Fig. 6. Second, the sister group status between *Mourella* and *Schwarziana* also derived from a good character (14.3): hairs on the abdominal sterna, especially on the distal margins of sterna III–V, with recurved tips, forming regular rows of hooks. Character 13.1 (plumose hairs on abdominal sterna) is homoplasious and appears also in *Paratrigonoides* **gen. nov.** Finally, the four crown groups presented in Fig. 6 were stable in all 10 options of tree topology that were produced by PAUP\*. What varied, then, were relationships in the basal or more ancestral branches. As indicated in Fig. 6, three basalmost groups are separated by a single character state each, and two of three such traits are homoplasious. Future studies performed with a greater variety of characters and taxa are needed. For the present work, our analysis concludes with the placement of *Paratrigonoides mayri* **n. gen., n. sp.**, as sister to the *Paratrigona* + *Aparatrigona* clade.

In the past 15 years five new stingless bee genera have been described. In addition to *Paratrigonoides*, there are monospecific *Papuatrigona* Michener & Sakagami, 1990, from New Guinea, and *Trichotrigona* Camargo & Moure, 1983, *Melliwillea* Roubik, Lobo & Camargo, 1997, and *Camargoia* Moure, 1989, with three species, from the Neotropics. However, the diversity of Meliponini is far from being known in its totality.

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