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The Extinct Fauna of Stingless Bees (Hymenoptera: Apidae: Meliponini) in Dominican Amber: Two New Species and Redescription of the Male of *Proplebeia dominicana* (Wille and Chandler)

JOÃO M.F. CAMARGO,[1] DAVID, A. GRIMALDI,[2] AND SILVIA R.M. PEDRO[3]

ABSTRACT

Seventeen specimens of Meliponini in Dominican Republic amber were studied, including eight workers of *Proplebeia dominicana* and four males, presumably of this same species. Detailed descriptions of two new species, placed tentatively in *Proplebeia,* are included. Characters of the male (mainly shape of sterna 5 and 6) corroborate the hypothesis that *Proplebeia* constitutes a distinct branch within the lineage of Neotropical *Plebeia* (s.s.). We discuss possible phylogenetic affinities among *Plebeia, Proplebeia,* and *Nogueirapis silacea,* the latter in amber from Chiapas, México.

INTRODUCTION

Dominican amber is renowned for the great diversity of organisms in it, and one of the most common insects is a stingless bee, *Proplebeia*. Only one species, *P. dominicana* (Wille and Chandler), has been described, probably because the other meliponines in this amber are so rare and morphologically similar to *P. dominicana* as to have escaped

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notice. Only Michener and Poinar (1996) mentioned the existence of other undescribed species. Indeed, our description of the putative males of *P. dominicana* and two new species is based on nine specimens out of several thousands of *Proplebeia* examined over the past decade by Grimaldi. The abundance and manageable size of amber *Proplebeia* have made them favored subjects for studies on internal ultrastructural preservation (Grimaldi et al., 1994), DNA, and other macromolecules (Cano et al., 1992a, 1992b; Walden and Robertson, 1997; Stankiewicz et al., 1998). *Proplebeia* is certainly one of the most intensively studied of all fossils, but discovery of very similar species indicates that even such fundamental aspects as identity and diagnosis, as well as phylogenetic relationships, require clarification. The numerous studies cited above and below presumably refer to *P. dominicana*, since the new species constitute less than 0.1% of all stingless bees found in Dominican amber.

Proplebeia dominicana was originally placed by Wille and Chandler (1964) in the genus *Liotrigona*, a modern group endemic to Africa and Madagascar (Moure, 1961; Moure and Camargo, 1978; Michener, 1982, 1990; Brooks and Michener, 1988). Moure and Camargo (1978), using the original description of *P. dominicana* and a superficial examination of some specimens (probably a distinct species), suggested the inclusion of *P. dominicana* in the Neotropical genus *Plebeia* (s.s.). Michener (1982), who examined 98 specimens and compared them with *Plebeia* and *Liotrigona*, did not find derived characters (synapomorphies) to support placing *P. dominicana* in one of these two genera. In order to avoid taxonomic ''artificialities,'' he proposed a new subgenus for this species: *Proplebeia*, at that time subordinate to *Trigona* (s.l.). The name proposed by Michener reflected his belief in a close relationship between *Proplebeia* and *Plebeia* (s.s.): ''. . . The placement of *Proplebeia* near *Plebeia* by Michener (1982) still seems reasonable'' (Michener, 1990: 107). Michener (1990) also described other characters from the sting apparatus of *P. dominicana*, which are shared with American genera and not with *Liotrigona* or any other African group.

Michener and Poinar (1996) superficially described male specimens, presumably of *P. dominicana* (in Poinar's personal collection, numbers H10-52 and H10-94).

In the present paper new data on workers and putative males of *P. dominicana* are presented with the description of two new species.

MATERIALS AND METHODS

Seventeen pieces of Dominican Republic amber, each containing one specimen of Meliponini, except the piece AMNH-DR-14-1439 with one complete specimen and two fragments, were examined. The pieces are deposited in the American Museum of Natural History (AMNH—14 pieces), and in the Natural History Museum of the University of Kansas (3 pieces). All specimens came from commercial dealers who exclusively market Dominican amber. As such, it is impossible to know the exact mine from which any one piece originated. Copal—hardened resin from modern trees, only several years to several thousand years old—occurs in the Cotui region of the Dominican Republic, but this material is visually very obvious and no meliponines have ever been found in it. It is derived from the living tree *Hymenaea courbaril*, which occurs throughout the Caribbean and Central America. True amber, which is usually darker, harder, and much more polymerized and inert than copal, comes from mines in the Cordillera Septentrional just north and east of Santiago. It is derived from an extinct *Hymenaea* species possibly most closely related to the east African species *H. verrucosa*.

Unfortunately, published ages of Dominican amber have been unnecessarily confused. Earlier publications have claimed the material to be between Lower Miocene (ca. 23 Ma) to even Upper Eocene (ca. 40 Ma) in age (e.g., Poinar and Hess, 1982; Poinar, 1994a). In particular, mines from the La Toca region have been claimed to be older (Eocene) than other amber deposits in the Dominican Republic (Lambert et al., 1985), but this dating is based on molecular analyses of the amber, which have been shown to be erroneously interpreted (Grimaldi, 1995). In reality, based on the most comprehensive stratigraphic study done thus far (Iturralde

and MacPhee, 1996), Dominican amber is from the lower part of the Mid Miocene to the uppermost part of the Lower Miocene, ca. 15–20 Ma. This date is corroborated by the apparent recency of organismal inclusions, which are not as plesiomorphic as most species preserved in older, Eocene amber from the Baltic (e.g., Grimaldi, 1995, for Diptera; Engel, 2000, for bees). Also, comprehensive unpublished analyses using pyrolysis-gas chromatography (Shedrinsky and Grimaldi, unpubl.) show no consistent variation in Dominican amber regardless of mine source, suggestive of origins that are botanically identical and contemporaneous.

Despite an age that is younger than previously believed, Dominican amber remains a very significant source of fossil insects, one reason being its preservative qualities—probably better than any other amber (Grimaldi et al., 1994). *Proplebeia* bees in this amber have been found with intact internal organs (including crops filled with pollen), as well as subcellular (ultrastructural) details. Dominican amber is also the only significant source of Cenozoic insect fossils in the Caribbean, and has revealed startling examples of extinctions in this region, of which the meliponine bees are a prime example.

The specimens were prepared according to the procedures in Grimaldi (1993). Drawings were made with the aid of a Wild M5A and camera lucida with magnification up to 106×. Measurements were taken with an ocular reticule and are presented in millimeters. Morphological terminology follows Michener (1944, 1990) and Camargo et al. (1967). The term mesosoma refers to the usual segments of thorax plus the first abdominal segment, the propodeum. Segments 2–9 of the abdomen are referred to as 1–8 of the metasoma (T1 = second abdominal tergum, S1 = second abdominal sterna, etc). The legs are indicated with Roman numerals: I, II, III.

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SYSTEMATICS

GENUS *PROPLEBEIA* MICHENER

Figures 1–22

Trigona (Proplebeia) Michener, 1982: 44. Type-species *Trigona (Liotrigona) dominicana* Wille and Chandler, 1964, by original designation.

DIAGNOSIS: Small bees; body length 2.0–4.4 mm. General body form, legs and pattern of wing venation as in *Plebeia* (s.s.). Differs from *Plebeia* principally by broad, smooth, depressed posterior margin of the inner surface of tibia III (⅔ to ⅓ the width of keirotrichiate area; in *Plebeia* ca. ⅙ to ⅕), rastellum with 7–9 long, cylindrical, spinelike hairs, and S6 of male with long, broad median projection (in *Plebeia*, the projection of S6 reduced or absent).

Proplebeia dominicana (Wille and Chandler)

Figures 1–7, 9

Trigona (Liotrigona) dominicana Wille and Chandler, 1964:187–195 (tax., description).

Trigona (Hypotrigona) dominicana; Morris, *in* Zeuner and Manning, 1976: 256 (fossil review).

Trigona dominicana; Wille, 1977: 44 (fossil review, tax. notes); 1979: 269 (tax. notes). – Michener, 1979: 322 (biogeogr., tax. notes).

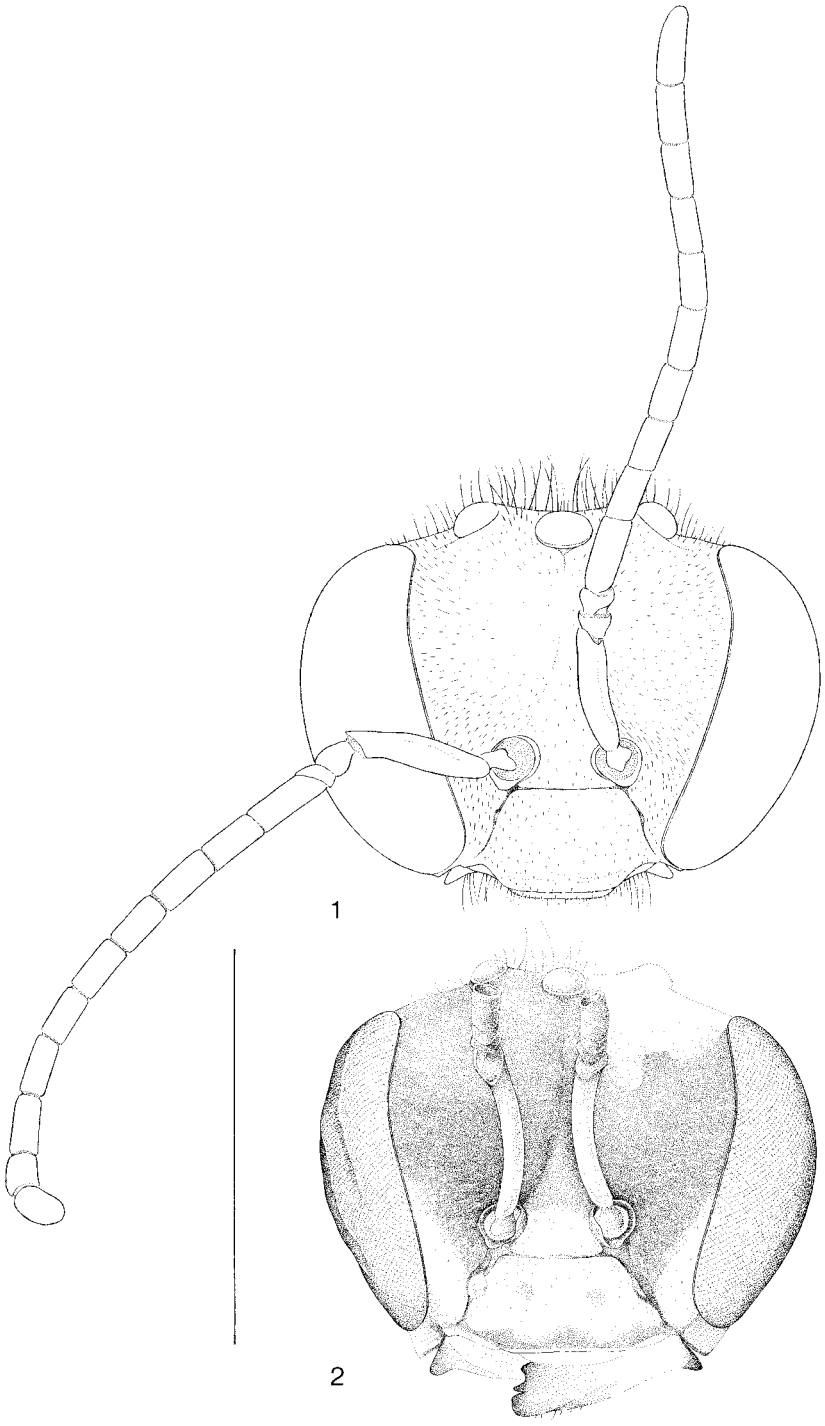
? *Trigona (Plebeia)* black species; Wille, 1979: 269 (tax. notes).

Plebeia dominicana; Moure and Camargo, 1978: 563–564 (tax. notes, new combination).

Trigona (Proplebeia) dominicana; Michener, 1982: 37–45 (not published in this form but stated to be a *Trigona*; tax. notes, new subgenus).

Trigona A, B, C; Michener, 1982: 41–42 (tax. notes).

Proplebeia dominicana; Camargo et al., 1988: 153 (biogeogr. notes). – Camargo, 1989: 44 (tax. notes). – Michener, 1990: 87, 95, 105–107 (tax. notes, phylogeny). – Ayala, 1992: 60 (biogeogr. notes). – Roubik, 1992: 499, 503 (figs. tibia). – Cano et al., 1992a: 249–251 (DNA); 1992b: 619–622 (RNA). – Poinar, 1992: 466–468 (resin collection); 1994a: 537-538 (DNA); 1994b: 73–75 (fossil review, symbiotic and parasitic associations). – Grimaldi et al., 1994: 12–



Figs. 1, 2. *Proplebeia dominicana*; **1.** male, specimen AMNH-DR-14-1178; **2.** worker, specimen AMNH-DR-14-1111. Scale = 1.0 mm.

14 (electron microsc.). – Grimaldi, 1996a: 72–73 (electron micrography); 1996b: 118 (figures, paleoecology). – Michener and Poinar, 1996: 360–361 (fossil review, tax. notes, description of male *P. dominicana*). – Walden and Robertson, 1997: 1075–1077 (DNA). – Carpenter and Grimaldi, 1997: 6 (biogeogr. notes). – Stankiewicz et al., 1998: 642–645 (preservation in resin).

DIAGNOSIS: **Worker**. Body length ca. 3.0 mm; forewing length 2.50-2.75 mm; malar area short, ca. ½ the diameter of scape; yellow stripe on parocular areas extending above the antennal alveolus; emargination between mandibular denticles deep. **Male**. Integument black, smooth, and shiny; body length ca. 3.68 mm; flagellomeres ca. 1.7× longer than wide; S6 with long, wide, median projection, enlarged and bifid apically; S7 with a row of long hairs along the distal margin; gonostyli long, slender, and slightly broadened at apex.

The species was interpreted based on the original description of Wille and Chandler, which is very detailed in relation to both supraspecific and specific characters, and also on additional data provided by Michener (1982). Wille and Chandler presented the measurements, except length of the body and forewing, in units of the eyepiece reticle and there is no indication of the index of conversion into millimeters. In his 1979 paper (p. 269), Wille presented the conversion into millimeters of the depressed posterior rim and keirotrichiate area width of tibia III as 3: 9 units = 0.099: 0.297 mm, which is obviously wrong. If the same proportion is applied to the head width, we have 72 = 2.376 mm (!), which is only a little shorter than the length of the forewing (2.60 mm). However, in another text Wille (1964) indicated on page 123 (footnote) a conversion factor of 1 unit = 0.017 mm, which results in measurements more similar to ours and which were used for comparisons in this study (table 1).

Color of integument, punctation, pubescence, and size of the specimens examined agree perfectly with the description of Wille and Chandler. The yellow stripes on the sides of the mesoscutum (0.06 mm wide) are clearly visible only in specimen DR-14-1179; on the scutellum it is not possible to distinguish a yellow stripe in any of the specimens; thin layers of air bubbles, striations, or the position of cuts in the amber piece hinder a correct judgement. Also, specimen DR-14-1173 is too deformed and discolored. The yellow maculations in the lower parocular areas, clypeus, and supraclypeal area are clearly visible (fig. 2) in all specimens exactly as described and illustrated by Wille and Chandler.

There is disagreement between our specimens and some structural characters mentioned by Michener (1982): the rastellum comprises seven to nine long, well differentiated, and apparently cylindrical bristles (ca. 0.09–0.10 mm), concentrated in the anterior corner of the inner side of the distal border of tibia, behind the tarsal articulation (fig. 4); the penicillum (fig. 3) is normal as in *Plebeia* (s.s.) and *Nogueirapis*, and it is not as long and parallel to the longitudinal axis of the tibia as was indicated by Michener (1982). In the less deformed specimens it is possible to see that the propodeum is not as vertical as it seems in the drawing presented by Michener (1990: 105, fig. 83), the slope being gentle as in *Plebeia* (s.s.). The width of the keirotrichiate area, measured approximately at the middle of the tibia (specimen DR-14-1175), is 0.20 mm and the bare, depressed posterior rim is 0.06 mm wide. The limit between the keirotrichiate area and the depressed posterior rim is clearly defined by a step (fig. 4). The malar area is not linear, its length being approximately equal to half the diameter of the scape.

Wille (1979: 269) referred to some black specimens as *Plebeia* (*s. s.*). Michener (1982: 41), who examined these same specimens, considered them to be *Proplebeia*, possibly a species distinct from *P. dominicana*. However, Michener and Poinar (1996: 354) referred to them only as color morphs of *P. dominicana*. We examined the specimens mentioned by Michener (1982, *Trigona* A, B, C, specimens of Kansas University, Brodzinsky coll.) and consider them conspecific with *P. dominicana*.

DESCRIPTION: **Male.** Based on specimen DR-14-1178, and details of genitalia and pregenital sterna of DR-14-954. Amber piece DR-14-1178 was cut in right angles that allowed examination in several positions. There are some bubbles, fractures, and fis-

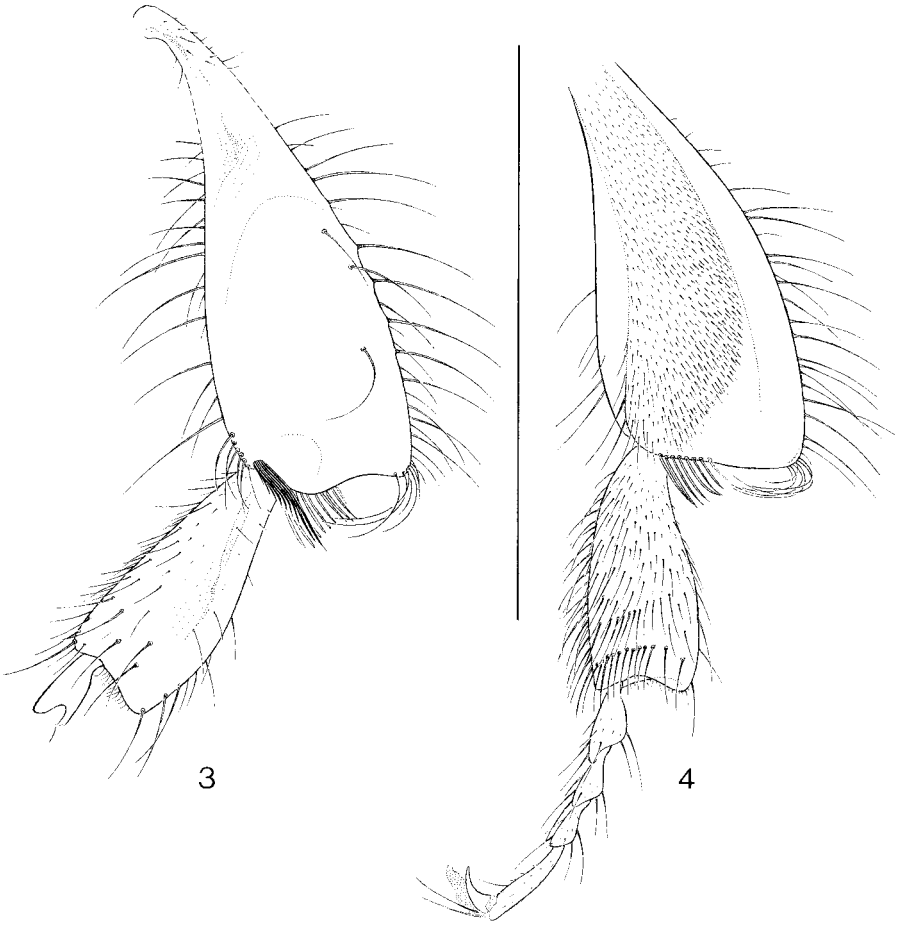
TABLE 1

Measurements (mm) of Select Specimens of *Proplebeia dominicana*

Holotype measurements are from the original descriptions by Wille and Chandler (1964).

	Male DR-14-1178	Worker DR-14-1111	Holotype, worker
1. Head width	1.31	1.30	1.22 (72)
2. Head length	1.00	1.02	—
3. Mesosoma width	1.28	—	—
4. Tergum 2 width	0.98	—	—
5. Eye length	0.84	0.84	0.80 (47)
6. Eye width	0.40	0.36	—
7. Upper interorbital distance	0.75	0.84	0.76 (45)
8. Maximum interorbital distance	0.78	0.89	0.82 (48)
9. Lower interorbital distance	0.50	0.68	0.65 (38)
10. Clypeus length	0.34	0.23	—
11. Clypeus width	0.48	0.54	—
12. Clypeocellar distance	0.64	0.70	—
13. Malar area length	linear	0.04	0.05 (3)
14. Interalveolar distance	0.13	0.16	0.15 (9)
15. Alveolus diameter	0.14	0.14	0.12 (7)
16. Alveolorbital distance	0.10	0.16	0.17 (10)
17. Scape length	0.38	0.40	—
18. Scape width	0.08	0.08	—
19. Length of pedicel plus flagellum	1.66	—	—
20. Alveolus-lateral ocellus distance	0.55	0.58	0.65 (38) (lateral ocellus?)
21. 1st flagellomere length	0.16	—	—
22. 2nd flagellomere length	0.15	—	—
23. 3rd flagellomere length	0.15	0.08	—
24. 3rd flagellomere diameter	0.09	0.08	—
25. Distance between lateral ocelli	0.34	0.26	—
26. Median ocellus diameter	0.14	0.11	0.10
27. Ocellorbital distance	0.11	0.18	0.17 (10)
28. Scutellum length : width	0.28:0.50	0.26:0.44	—
29. Mesoscutum length	—	0.80	—
30. Marginal cell length	0.91	0.92	—
31. Marginal cell width	0.20	0.21	—
32. Forewing length	2.75	2.68 (+tegula 3,12)	2.60
33. Forewing width	0.96	1.08	—
34. Tibia III length	0.92	0.96	—
35. Tibia III width	0.30	0.37	—
36. Basitarsus III length	0.52	0.42	—
37. Basitarsus III width	0.12	0.19	—
38. Hamuli	5–6	5	—
39. Pterostigma length: width	0.44:0.12	0.50:0.12	—
40. 1st abscissa of M	0.38	0.39	—
41. 1st abscissa of Cu	0.54	0.56	—
42. Rs + M + 2nd abscissa M	0.36	0.40	—
43. Total body length	3.68	3.20	2.95

sures, but the bee is well preserved (figs. 1, 5), practically without deformation, which permitted virtually exact measurements to be made. The bubbles over the spiracles (fig. 5) indicate that the bee was quickly immersed by the resin. **Dimensions:** Approximate body length 3.68 mm, forewing length, from apex of costal sclerite to wing tip 2.75 mm (including tegula, 3.00 mm); maximum head width 1.31 mm; metasoma width 0.98 mm



Figs. 3, 4. *Proplebeia dominicana*, tibia III. **3.** outer surface, specimen AMNH-DR-14-1179; **4.** inner surface, detail of the keirotrichiate area and rastellum, specimen AMNH-DR-14-1175. Scale = 1.0 mm.

(figs. 1, 5). **Color of integument:** Black, lacking yellow markings except for one translucent spot on either side of the base of the scutellum (exactly as in worker DR-14-1111). Lower parocular area and distal edge of clypeus somewhat lighter, without yellow markings (specimen DR-14-954 is entirely black). Tarsi of all legs and wing veins light chestnut. Wing membrane hyaline. **Pilosity:** Pale yellow over entire body. Decumbent, minute hairs covering whole face; vertex with unbranched erect hairs, longest hairs 0.16 mm. Mesoscutum with sparse, slender, erect hairs, the longest ones on anterior corners ca. 0.18 mm and those on posterior edge of scutellum ca. 0.20 mm (fig. 5). Pubescence on mesepisterna a little denser than on mesoscutum, increasing in length ventrad (0.12–0.6 mm). Basal area of propodeum glabrous. Posterior edge of tibia III with unbranched hairs (ca. 0.12 mm long). T1-4 without perceptible pilosity, except some minute hairs laterally; sides of T5-7 with erect, unbranched hairs, denser and progressively longer on T6-7; the longest hairs on distal border of T7 0.14 mm. It was not possible to observe in detail the sternal pilosity in any of the specimens; only in DR-14-954 it is possible to see a row of erect unbranched hairs ca. 0.10 mm long, arranged regularly along the distal edge of S5 (figs. 6, 7). **Integument:** Smooth and shiny, except for some sparse piligerous punctures. Punctures of head dense, owing to the dense micropi-

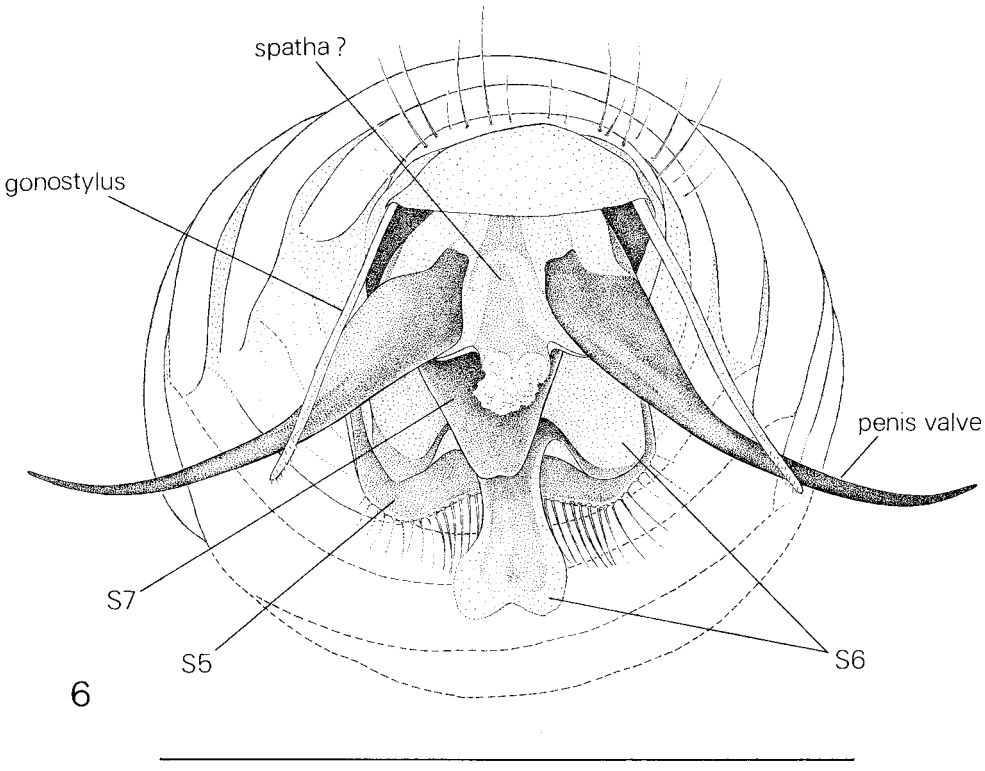
Fig. 5. *Proplebeia dominicana*, male, specimen AMNH-DR-14-1178. Scale = 1.0 mm.

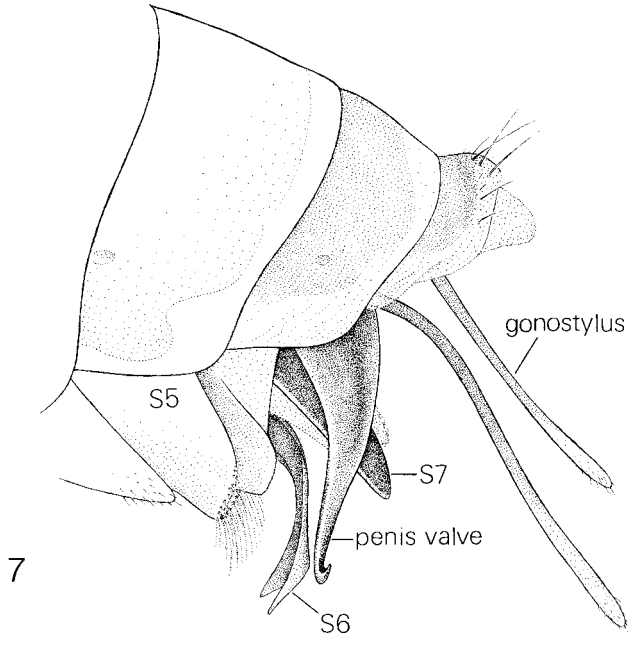
losity, distance between punctures ca. 1 to 2× puncture diameter. Mesoscutum shiny, with large spaces among bases of hairs (3 to 4× puncture diameter). Metasomal terga smooth and shiny. **Form and proportions:** Head wider than long (1.31: 1.00, length measured from apex of clypeus to upper tangent of median ocellus), approximately as wide as mesosoma (1.28, measured across mesepisterna) and wider than T2 (0.98). Eyes 2.1× longer than wide (0.84: 0.40) and convergent below; upper interorbital distance 0.75, maximum distance 0.78, and lower distance 0.50. Malar area linear. Clypeus 1.4× wider than long (0.48: 0.34), slightly convex; epistomal suture almost straight on sides (fig. 1). Labrum normal, slightly convex. Clypeocellar distance 0.64. Interalveolar distance nearly equal to diameter of antennal alveolus and slightly larger than alveolorbital distance (0.13: 0.14: 0.10). Frons slightly depressed along median line. Distance between lateral ocelli ca. 2.4× diameter of median ocellus and 3.1× ocellorbital distance (0.34: 0.14: 0.11). Vertex behind ocelli rounded; preoccipital ridge slightly rounded. Scape length 4.75× its diameter (0.38: 0.08) and ca. $^{2}/_{3}$ distance between antennal alveolus and lateral ocellus (0.55). Flagellum plus pedicel (1.66) ca. 4× length of scape; flagellomeres ca. 1.7× longer than wide (the second one 0.16: 0.09). Scutellum in dorsal view an equilateral arch with rounded apex, 1.8× wider than long (0.50: 0.28) (it is possible that the scutellum is a little deformed because of dehydration in the amber). Forewing 2.9× longer than wide (2.75: 0.96); pterostigma 3.6× longer than wide (0.44: 0.12); marginal cell long and narrow (0.91: 0.20), its apex open; angle between Rs and Rs + M slightly acute (approximately 85°); first abscissa of M ca. $^{5}/_{7}$ length of first abscissa of Cu (0.38: 0.54), and practically as long as Rs + M + second M. First submarginal cell almost entirely open, second abscissa of Rs forming a small projection. Second submarginal cell completely absent. Hamuli, 5–6. Tibia III subtriangular, 3.1× longer than wide (0.92: 0.30) slightly biconvex, posterodistal corner rounded. Basitarsus III 4.3× longer than wide (0.52: 0.12), flattened, lateral margins subparallel, distal edge in right angle. Details of the genitalia and pregenital sterna as in figures 6, 7. S5 unmodified, except for slightly concave distal border (with a transverse row of hairs); S6 with long, wide median projection [= apical process (Michener, 1990)], enlarged and bifid apically (figs. 6, 7); visible portion of S7 strongly sclerotized. Genitalia of specimen DR-14-954 is in triggered conformation, with penis valves directed laterally (as occurs during copulation in extant Meliponini), making study of certain structures difficult; gonocoxites not entirely visible nor is an unequivocal spatha. Penis valves very long (0.67 long per 0.11 wide at base), rather arched and pointed apically; gonostylus long and slender, exposed portion 0.61 long, 0.02 wide at its slightly broadened apex (figs. 6, 7).

MATERIAL EXAMINED: Four males, AMNH-DR-14-1178, DR-14-954, DR-14-1174 and DR-14-812; eight workers, AMNH-1 DR-14-1111, DR-14-1173, DR-14-1175, DR-14-1176, DR-14-1179 (these selected as particularly well preserved) and three unnumbered ones from the Natural History Museum of the University of Kansas, Snow Hall (Brodzinsky coll.); all from the Dominican Republic, as described under Materials and Methods.

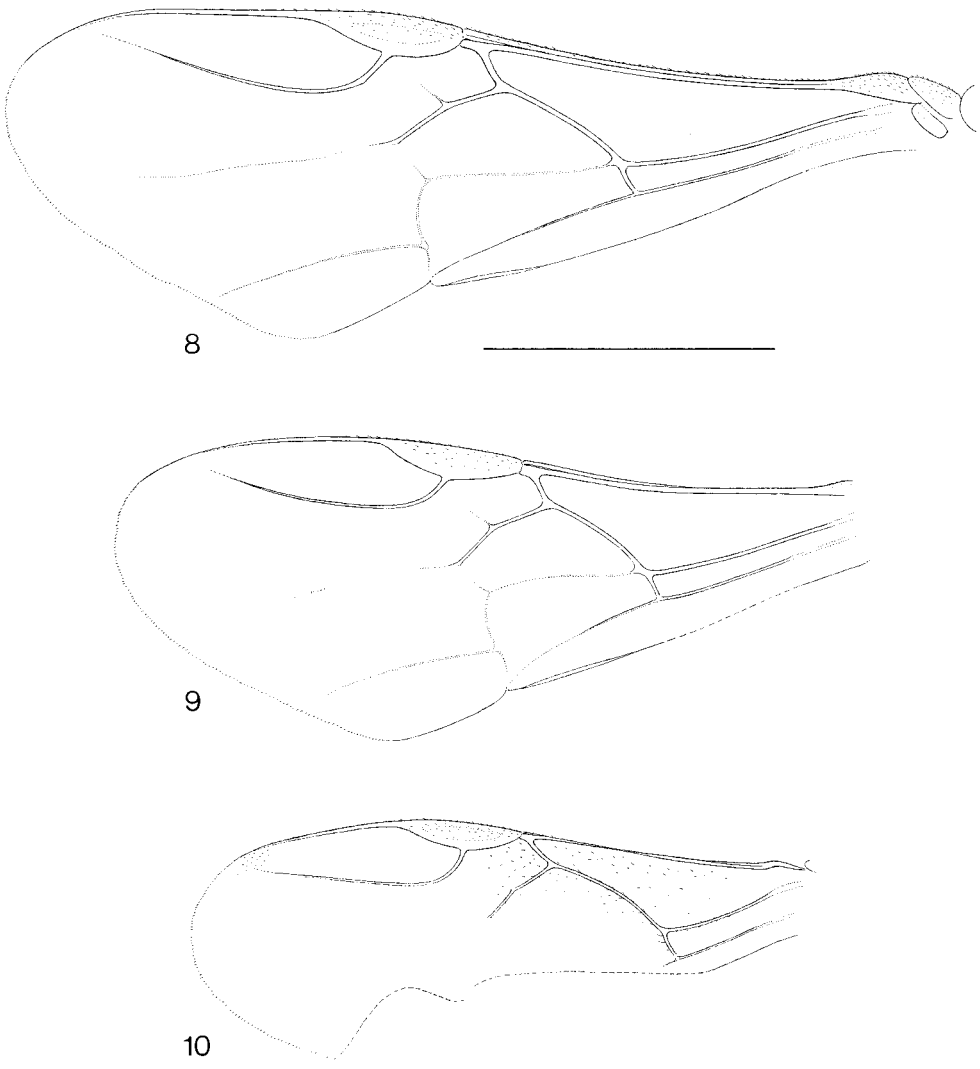
REMARKS: We tentatively interpreted the specimens listed above as males of *P. dominicana*. The males are very similar to the workers in size, conformation of the wing veins, and the yellow markings on the base of scutellum. The wings are the only structures that usually do not exhibit sexual dimorphism in Meliponini. Even for most extant species, it is only possible to associate sexes with confidence when they are collected together in the nest.

The main autapomorphies of male *P. dominicana* are: very long flagellomeres, ca. 1.7× longer than wide (Michener and Poinar, 1996, mentioned 3× longer than wide, which does not correspond to their figure 8, p. 357, where the proportion is ca. 2:1), S6 with median projection very long and broad, and apically bifid, and S7 with a row of long hairs along the distal margin [superficially similar to *Austroplebeia symei* (Rayment, 1932)]. Other comments are given under *P. tantilla* Remarks, and under Discussion below.





Figs. 6, 7. *Proplebeia dominicana*, genitalia of male, posterior view and profile, specimen AMNH-DR-14-954; S5–S7 = 5th–7th metasomal sterna, respectively. Scale = 1.0 mm.



Figs. 8–10. Forewing, worker; **8.** *Proplebeia vetusta*, sp.n., holotype, specimen, AMNH-DR-14-854; **9.** *Proplebeia dominicana*, specimen AMNH-DR-14-1175; **10.** *Proplebeia tantilla*, sp. n., paratype, specimen AMNH-DR-14-911. Scale = 1.0 mm.

Proplebeia vetusta, new species
Figures 8, 11–14, 22

Plebeia sp.; Poinar, 1994b: 73, fig 2 (fossil review).

DIAGNOSIS: **Worker.** Differs from *P. dominicana* by the large body size (3.80–4.40 mm; *P. dominicana*, 3.0 mm), forewing length (2.88–3.16; *P. dominicana*, 2.50–2.75 mm); malar area a little longer than diameter of scape; clypeus yellowish on distal third; parocular areas with a yellow stripe, slightly truncate above the tentorial pits (in holotype); and mandible with only a slight emargination separating the two denticles (in *P. dominicana* the emargination between denticles is deep).

DESCRIPTION: **Worker** (AMNH-DR-14-1481). **Dimensions:** Approximate body length 3.80 mm (metasoma quite compressed; in paratypes AMNH-DR-14-854 and DR-14-1440 approximate body length 4.40 and 4.32 mm, respectively); forewing length 2.88 mm from apex of costal sclerite

to wing tip (including tegula, 3.24 mm), in the paratype DR-14-854, 3.16 mm (including tegula, 3.72 mm), and in DR-14-1440, 3.00 mm (including tegula, 3.44 mm); maximum head width 1.55 mm. **Color of integument:** Black, including antennal scapes, except tarsomeres, chestnut and trochanters discolored, translucent; head with following parts diffuse yellowish: distal third of clypeus, lower parocular area to tentorial pit, supraclypeal area between antennal alveolus, and labrum; mandibles dark chestnut. Mesonotum black, devoid of yellow markings. Forewing C and R veins and tegulae dark chestnut; pterostigma with translucent spot in middle; wing membrane hyaline. **Pilosity:** Pale yellow over entire body. Decumbent, pale, minute plumose hairs covering entire face. Erect, unbranched hairs sparse on upper half of frons and increasing in number and length toward vertex; longest hairs on vertex ca. 0.17 mm; ones on scape 0.04 mm. Labial palpi with 3–4 long hairs (0.17–0.18 mm). Longest hairs on labrum 0.22 mm. Mesoscutum with fine, decumbent, unbranched micropilosity a little sparser than on head; erect hairs sparser on discal area and more abundant and longer (0.14 mm) on anterior corners; longest hairs on scutellum 0.18 mm on ventral part of mesepisterna 0.12–0.16 mm. Basal area of propodeum glabrous. Posterior border of tibia III with unbranched hairs, the longest ones ca. 0.18 mm. Only basal half of inner surface of tibia III visible (fig. 14); in wider visible part, corresponding approximately to middle of tibia, keirotrichiate area ca. 0.20 mm wide, posterior rim glabrous (clearly depressed, forming a step), ca. 0.08 mm wide. Externally tibiae partially covered by amorphous substance (pollen?) and air bubbles, but it is possible to verify that the penicillum is normal, as in *Plebeia* (s.s.); posterior parapenicillum with long, slender hairs and anterior parapenicillum well differentiated with a row of at least eight stiff hairs; rastellum apex visible with at least seven stiff, spinelike hairs. Microtrichia on wing membrane ferruginous and as long as hair interspaces (ca. 0.02 mm). T1 practically glabrous, only some minute hairs on sides; other terga and sterna covered by wings, legs, bubbles, and a whitish substance. **Integument:** Smooth and shiny as in *Proplebeia dominicana*; only piligerous punctures present. **Form and proportions:** Head 1.2× wider than long (1.55: 1.28, length measured from the apex of clypeus to upper tangent of median ocellus), a little narrower than mesosoma (1.66, measured across mesepisterna). Eyes 2.38× longer than wide (1.00:0.42), slightly convergent below; upper interorbital distance 1.01, maximum distance 1.10 and lower distance 0.89. Malar area a little longer than diameter of scape (0.12:0.10). Clypeus 2.23× wider than long (0.80:0.36), slightly convex. Labrum normal. Distance between clypeus and median ocellus 0.81. Interalveolar distance a little longer than diameter of antennal alveolus (0.19: 0.16), but shorter than alveolorbital distance (0.22). Frons slightly depressed along median line. Distance between lateral ocelli ca. 3.0× diameter of median ocellus and 1.5× ocellorbital distance (0.36:0.12: 0.24). Vertex rounded behind ocelli; preoccipital ridge slightly rounded (as in *Plebeia*, s.s.). Scape length 5.4× its diameter (0.54: 0.10), and ca. $\frac{5}{6}$ distance between antennal alveolus and lateral ocellus (0.64). Flagellum plus pedicel (1.08) ca. 2.0× length of scape; flagellomeres shorter than wide (the second one, 0.08:0.12). Scutellum with distal border semicircular, slightly projecting over metanotum, 2.06× wider than long (0.70: 0.34), basal pit normal (as in *Plebeia*, s.s.). Forewing 2.32× longer than wide (2.88:1.24), pterostigma 3.43× longer than wide (0.48: 0.14); marginal cell 3.76× longer than wide (0.94:0.25), slightly open at apex, Rs slightly sinuate toward apex; right angle between Rs and Rs + M (ca. 90°); first abscissa of M ca. $\frac{2}{3}$ length of first abscissa of Cu (0.42: 0.62) and slightly shorter than Rs + M + second M (0.46). First submarginal cell with limits relatively clear; second submarginal cell completely absent. Hamuli, 5. Tibia III subtriangular (as *P. dominicana* and *Plebeia*, s.s.), with posterodistal corner approximately right angled (position of tibiae, and presence of residues and bubbles do not permit reliable measures and details of shape); depressed rim on posterior border of inner surface $\frac{2}{5}$ width of elevated keirotrichiate area. Basitarsus III 1.93× longer than wide (0.56: 0.29), slightly broadened toward apex, posterodistal corner right angled.

TYPES: Holotype, worker, specimen

AMNH-DR-14-1481, paratypes, workers AMNH-DR-14-854 and DR-14-1440, in amber from Miocene of Dominican Republic. Specific mine of origin unknown.

ETYMOLOGY: From the Latin, *vetustus*, old, ancient.

REMARKS: Poinar (1994b: 73, fig. 2) referred to specimen AMNH-DR-14-1440 (here designated as a paratype) as *Plebeia* sp. Michener and Poinar (1996: 354) examined this same specimen and considered it a species distinct from *P. dominicana*, however these authors disagreed about its placement in the genus *Plebeia*. *Proplebeia vestusta* is placed in the genus tentatively, based on the form of the forewing medial cell, the surrounding veins, integument structure, and general body form (which is as robust as in *P. dominicana* and *Plebeia*, s.s.) and, mainly, by the depression of the posterior rim of the inner surface of tibia III, with ca. $\frac{2}{5}$ the width of the keirotrichiate area. The rastellum and penicillum apparently do not differ from what is seen in the species of *Plebeia* (s.s.).

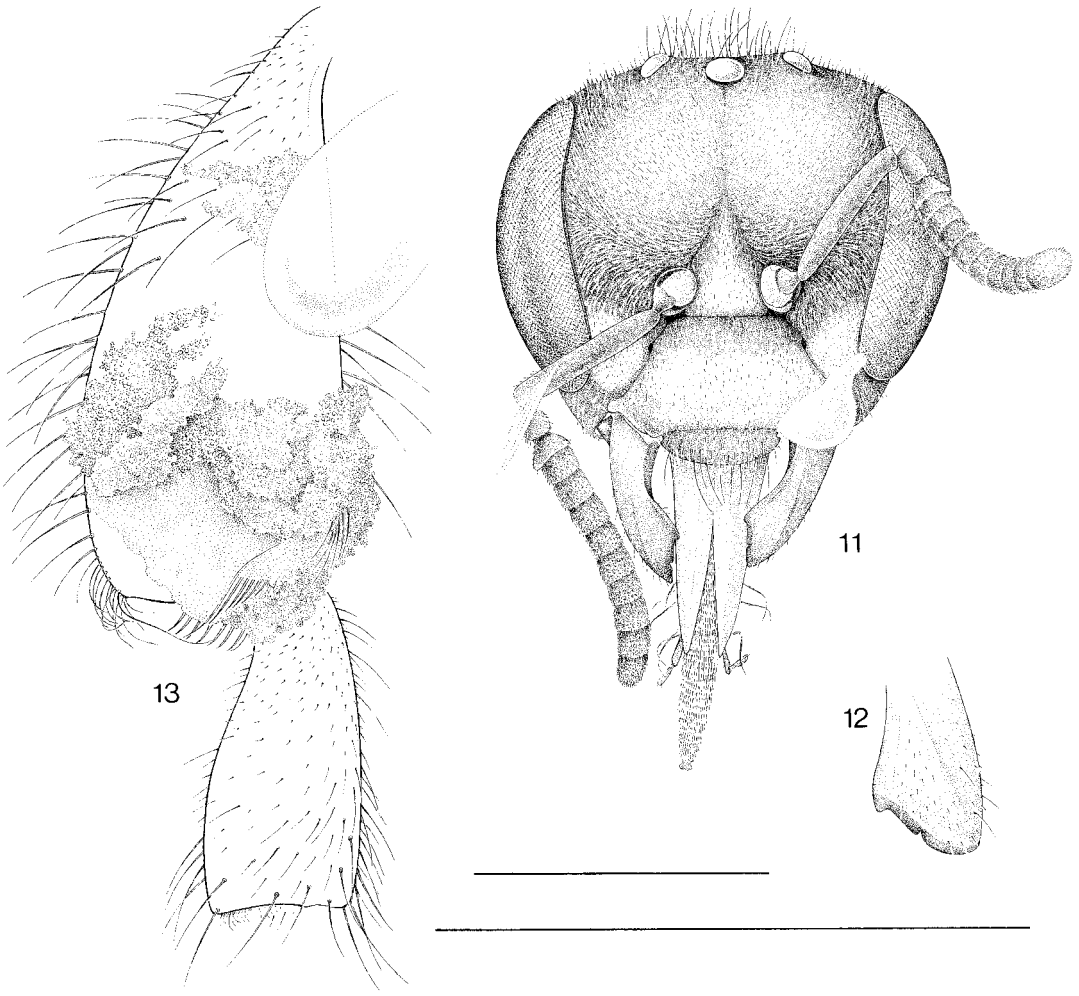
In the paratype AMNH-DR-14-854 the clypeus has only a pale yellow stripe along the distal border, a little narrower than the diameter of the scape, and the supraclypeal area is also pale yellow, but the parocular areas are black. In the paratype AMNH-DR-14-1440 only one premarginal, fine, yellow stripe is visible in the clypeus; the other areas are blackish. On both paratypes (extensively surrounded by air bubbles and the legs tangled in such a way that is impossible to examine important characters), the vertex is arched and well elevated above the lateral ocelli, but this condition can be due to the lenticular deformation of the amber. In the remaining characters (e.g., size and proportions of structures), these specimens do not differ from the holotype.

Proplebeia tantilla, new species

Figures 10, 15–21

DIAGNOSIS: The male is distinguished from that of *P. dominicana*, mainly by flagellomeres wider than long, median projection of S6 without apical emargination, and gonostyli swollen and with a hairy, solelike area at apex. Worker is easily distinguished from *P. dominicana* and *P. vestusta* by small body size (2.1, 3.0–3.2, 4.4 mm, respectively), presence of relatively long, straight hairs on sterna, and long microtrichia over veins M + Cu and first abscissa of M. *Proplebeia tantilla* is very similar to *P. dominicana* and the small *Plebeia* (s.s.) in the general form of the head, mesosoma, and metasoma.

DESCRIPTION: **Male**(AMNH-DR-14-1439). **Dimensions:** Approximate body length 2.52 mm, forewing length from apex of costal sclerite to wing tip 1.90 mm (including tegula 2.24 mm; wing seems slightly shortened due to striations in the amber); maximum head width 1.04 mm. **Color of integument:** Predominantly black, lacking yellow marks; chestnut on ventral part of metasoma, legs, tarsomeres, labrum, mandibles except condyles, maxillar galeae and tegulae; wing veins honey-colored, membrane hyaline. **Pilosity:** Pale yellow over entire body. Decumbent, plumose, pale, minute hairs relatively sparse on face; some erect hairs on clypeus (0.06 mm long); vertex with unbranched erect hairs up to 0.14 mm long. Mesoscutum practically devoid of micropilosity, only some sparse erect hairs, the longest ones on anterior corners ca. 0.08 mm on scutellum ca. 0.16 mm long; on ventral part of mesepisterna up to 0.12 mm long. Basal area of propodeum glabrous. Posterior edge of tibia III with unbranched hairs (ca. 0.14 mm long). T1-3 glabrous; T4-6 with some hairs on sides, T7 with some unbranched hairs up to 0.20 mm long. S2-4 with only one hairy band, S5 with a row of short hairs on median portion of apical margin (0.04 mm), S6-7 apparently lacking hairs. **Integument:** Smooth and shiny, except for some sparse piligerous punctures; slightly rugose on superior part of head. **Form and proportions**: Head 1.24× wider than long (1.04: 0.84, length measured from apex of clypeus to upper tangent of median ocellus). Eyes 1.9× longer than wide (0.72: 0.38) and convergent below; upper interorbital distance 0.56, maximum distance 0.58, lower distance 0.38. Malar area linear. Clypeus trapezoidal, 1.7× wider than long (0.34: 0.20), slightly convex; labrum normal, slightly convex. Distance between clypeus and median ocellus (0.54) practically equal to the upper interorbital distance. Interalveolar distance nearly equal to the diameter of antennal alveolus and ca. 2× longer than the



Figs. 11–13. *Proplebeia vetusta*, sp. n., holotype, AMNH-DR-14-1481, head, detail of mandible, tibia and tarsus III, detail of penicillum and rastellum. Minor scale bar = 1.0 mm (fig. 11), large scale bar = 1.0 mm (figs. 12–13).

alveolorbital distance (0.11: 0.12: 0.06). Frons with median line impressed well. Distance between lateral ocelli 2.0× diameter of median ocellus and 2.4× ocellorbital distance (0.22: 0.11: 0.09). Vertex very narrow, with abrupt slope behind lateral ocelli; preoccipital ridge slightly rounded. Scape length ca. 3.5× its diameter (0.28: 0.08), and ca. $^{2}/_{3}$ distance between antennal alveolus and lateral ocellus (0.42 mm). Flagellum plus pedicel (1.04) ca. 3.7× length of scape; flagellomeres shorter than wide (the second one, 0.08: 0.10). Scutellum not visible in dorsal view, in profile slightly projected beyond metanotum. Forewing 2.04× longer than wide (1.90: 0.93; the wing may be slightly shortened due to striations in the amber; this distortion could not be corrected by application of glycerin and a coverslip); pterostigma 4× longer than wide (0.40: 0.10); marginal cell 4.37× longer than wide (0.70: 0.16), slightly open at apex; Rs slightly sinuate toward apex; angle between Rs and Rs + M slightly open; first abscissa of M ca. $^{5}/_{7}$ length of first abscissa of Cu (0.30: 0.42), and a little shorter than Rs + M + second M (0.32). First submarginal cell without clear limits, entirely open. Hamuli, 5. Tibia

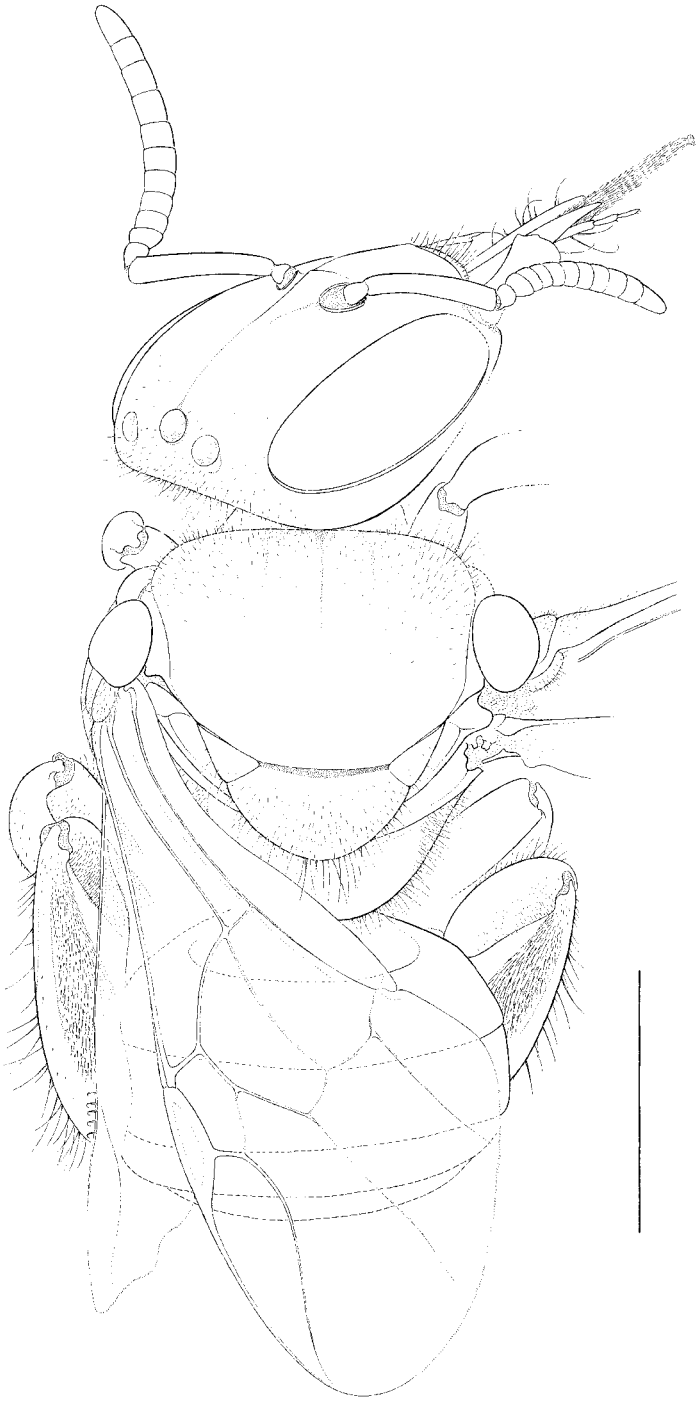
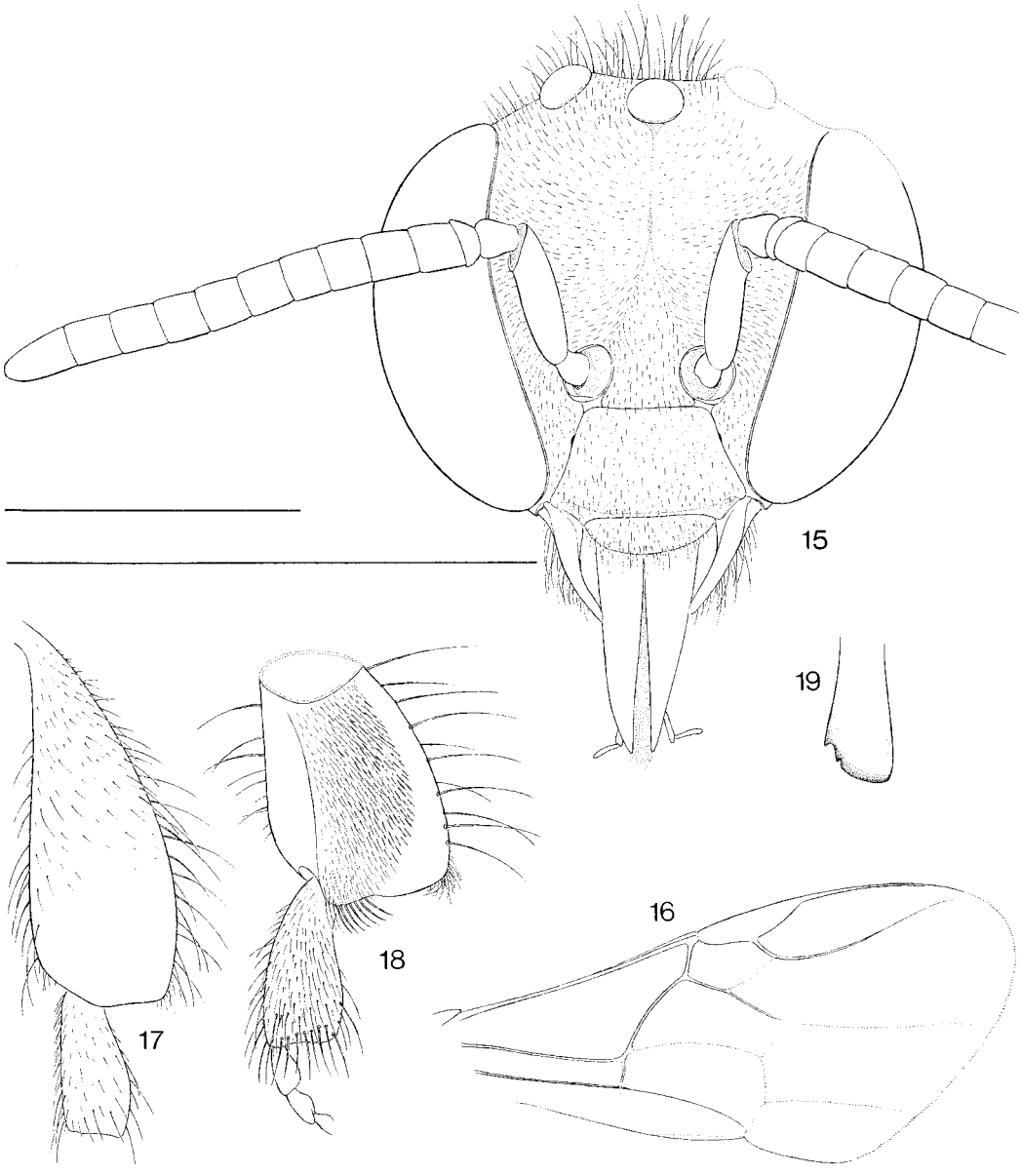


Fig. 14. *Proplebeia vetusta*, sp. n., holotype, AMNH-DR-14-1481. Scale bar = 1.0 mm.



Figs. 15–19. *Proplebeia tantilla*, sp. n. **15–17.** holotype, male, AMNH-DR-14-1439, head, forewing, and tibia and tarsus III. **18, 19.** paratype, worker, same amber piece, fragments of tibia and tarsus III, detail of rastellum, and mandible, detail of denticles.

III subtriangular, 3.08× longer than wide (0.80: 0.26); posterodistal corner angled slightly open. Basitarsus III 2.15× longer than wide (0.28: 0.13), with anterior margin practically straight and posterior margin slightly sinuate; posterodistal corner right angled. S2-4 unmodified; S5 invaginated, but apparently with slight emargination on each side of median distal border; S6 with one long, median, spatulate projection turned downward, and deeply emarginate on each side; S7 very wide and strongly sclerotized. Genitalia triggered, with penis covering part of the structures; penis valves short, about

half of the length of gonostyli and strongly arched; gosnostyli relatively short and swollen at apex, forming a hairy, solelike area on inner surface; no structure visible that can be interpreted as a spatha (details of genitalia and pregenital sterna in fig. 20).

Worker (AMNH-DR-14-911). Specimen very deformed due to dehydration in amber (e.g., antennae completely flattened, ocelli pedunculate), so measurements provided here do not reveal real size of body structure; only wings are apparently unaltered. **Dimensions:** Approximate body length 2.1 mm; forewing length from apex of costal sclerite to wing tip 1.96 mm (including tegula 2.26 mm); maximum head width 0.96 mm. **Color of integument:** Predominantly black, with several parts of the body discolored and translucent. There are no perceptible yellow markings on head; clypeus and supraclypeal area chestnut (discolored?); lower parocular areas lighter; scape yellowish, discolored; flagellum dark chestnut; mandibles discolored (translucent). Mesosoma black, lacking yellow markings, only anterior corners of mesoscutum discolored. Legs strongly discolored and translucent; only posterior distal border of tibia III and whole basitarsus III blackish. Forewing C and R veins distinctly black; pterostigma largely translucent in middle; wings membrane hyaline; microtrichia dusky. Metasomal terga blackish; sterna discolored. **Pilosity:** Fine, decumbent, minute hairs covering whole face as in *Plebeia* (s.s.), clearly plumose on lower parocular areas; less perceptible on clypeus. Vertex with some erect, unbranched, pale hairs, longest ones ca. 0.12 mm. A fine layer of bubbles on integument hinders observation of micropilosity on mesoscutum; however, pale and sparsely distributed erect hairs are quite visible; on anterior corners they are denser and as long as ones on vertex. Distal border of scutellum with some very long unbranched hairs, ca. 0.18 mm. Microtrichia sparse, clearly visible in radial and cubital cells and in area corresponding to first submarginal cell of forewing (fig. 10), longest ones ca. 0.02 mm; denser and shorter toward wing apex; veins M + Cu and first abscissa of M with some long hairs (ca. 0.03 mm), black, clearly visible. Sterna, mainly S3, with very long, erect hairs, T1–2 apparently glabrous dorsally, T3–4 with some erect hairs; T5 and especially T6 with erect very long, unbranched hairs, the longest ones ca. 0.16 mm. Posterior border of tibia III, with unbranched hairs ca. 0.16 mm long; one corbicular hair 0.20 mm long; basal third of tibia with some erect hairs 0.10 mm long, all pale yellow. Penicillum with very long (ca. 0.20 mm) hairs; posterior parapenicillum with two visible hairs, largely bent, ca. 0.20 mm long. Positions of legs preclude observation of details of the keirotrichiate area and presence of a rastellum; only right tibia III observable with two long hairs (ca. 0.07), which might belong to rastellum. Left leg measurements possible for only the length of some hairs of keirotrichiate area (ca. 0.03 mm). **Integument:** Smooth and shiny, as in *P. dominicana*. **Form and proportions**: Although measurements do not correspond to exact size of structures (except for wings), some are given below which might provide useful proportions: maximum head width 0.98; upper, maximum, and lower distances 0.65, 0.67, 0.52, respectively; eye length 0.68; clypeus width 0.36; length of pedicel plus flagellum 0.76; scape 0.32; malar area length 0.08; mandible 0.80, with two denticles on inner corner of apical cutting edge, space between them semicircular. General form of head as in the small species of *Plebeia* (s.s.). Labium ca. 1.20 mm long (glossa only 0.48), completely translucent. Mesosoma very deformed, but apparently similar to those of *P. dominicana* and *Plebeia* (s.s.); scutellum normal, in an approximately equilateral arch with round apex, without basal fovea. Tibia III subtriangular (as in *P. dominicana* and *Plebeia*, s.s.), elongate, with posterodistal corner acutely angled, strongly projected (tibia is very compressed, approximately 0.20 wide). Forewings folded and cannot be measured; pterostigma 3.6× longer than wide (0.36: 0.10); marginal cell a little more bulging at base than in *P. dominicana* (0.64: 0.20), and more open apically; angle between Rs and Rs + M slightly acute, ca. 85°; first abscissa of M 1.35× longer than Rs + M + second M (0.38: 0.28); free portion of Cu vein imperceptible; submarginal cell entirely open, lacking any trace of vein that delimits it. Hamuli, 5. Metasoma short, triangular; last tergum pointed apically.

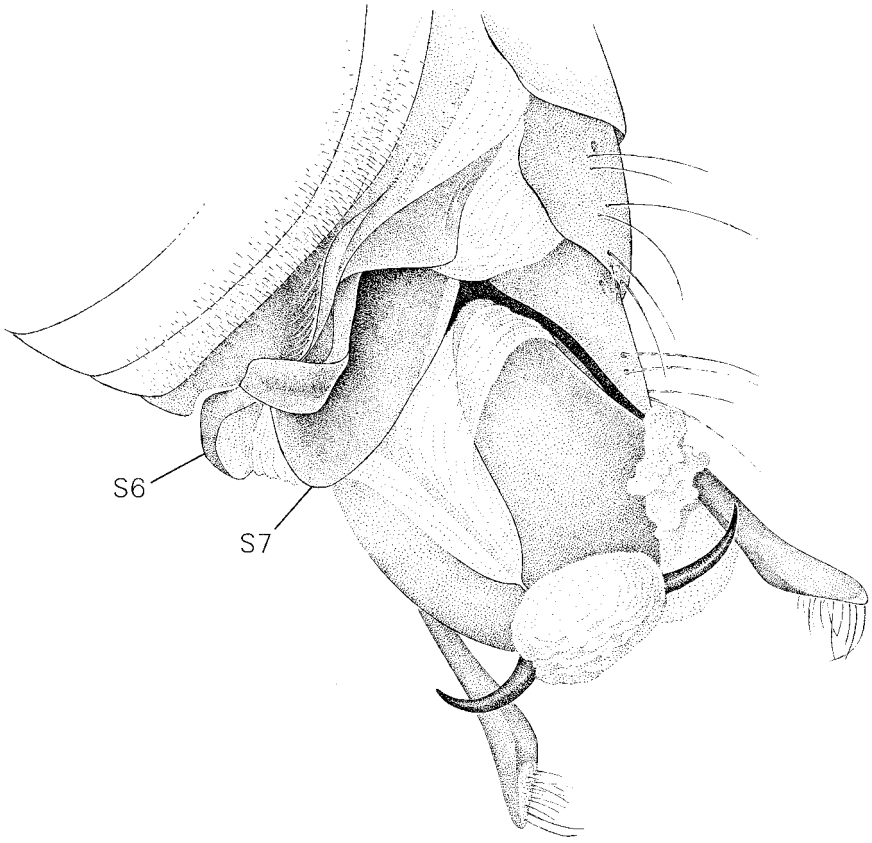


Fig. 20. *Proplebeia tantilla*, sp. n., holotype, male, AMNH-DR-14-1439, detail of pregenital sterna and genitalia, ventral view.

TYPES: Holotype, male, AMNH-DR-14-1439, in Miocene amber of the Dominican Republic. Fragments of one male and fragments of one worker in the same amber piece are paratypes. One worker in an additional piece, AMNH-DR-14-911, with same origin, is also a paratype. Exact mine where amber was found is unknown.

ETYMOLOGY: From the Latin, *tantillus*, little, small.

REMARKS: Another male of the same species, sectioned longitudinally during polishing of the piece by Dominican dealers is included in the same piece of amber with the holotype (AMNH-DR-14-1439). What remains are the ventral portion of the mesosoma, part of the metasoma, genitalia and legs; there are also fragments of the maxillae, labium, mandible and legs of one worker, supposedly of the same species. In the fragment of tibia III, which corresponds to the distal half, it is possible to see the rastellum with at least seven long (cylindrical?) hairs (fig. 18), as in *P. dominicana*; the penicillum and anterior parapenicillum are well developed but it is not possible to see details; in the distal half of the inner surface, the posterior glabrous rim, about $^{2}/_{7}$ the keirotrichiate area width, is apparently not depressed. In *Nogueirapis silacea* the depressed area is limited to the basal half of the tibia (Wille, 1959), and in *P. dominicana* the step does not follow the contour of the keirotrichiate area and is gentler toward the apex of the

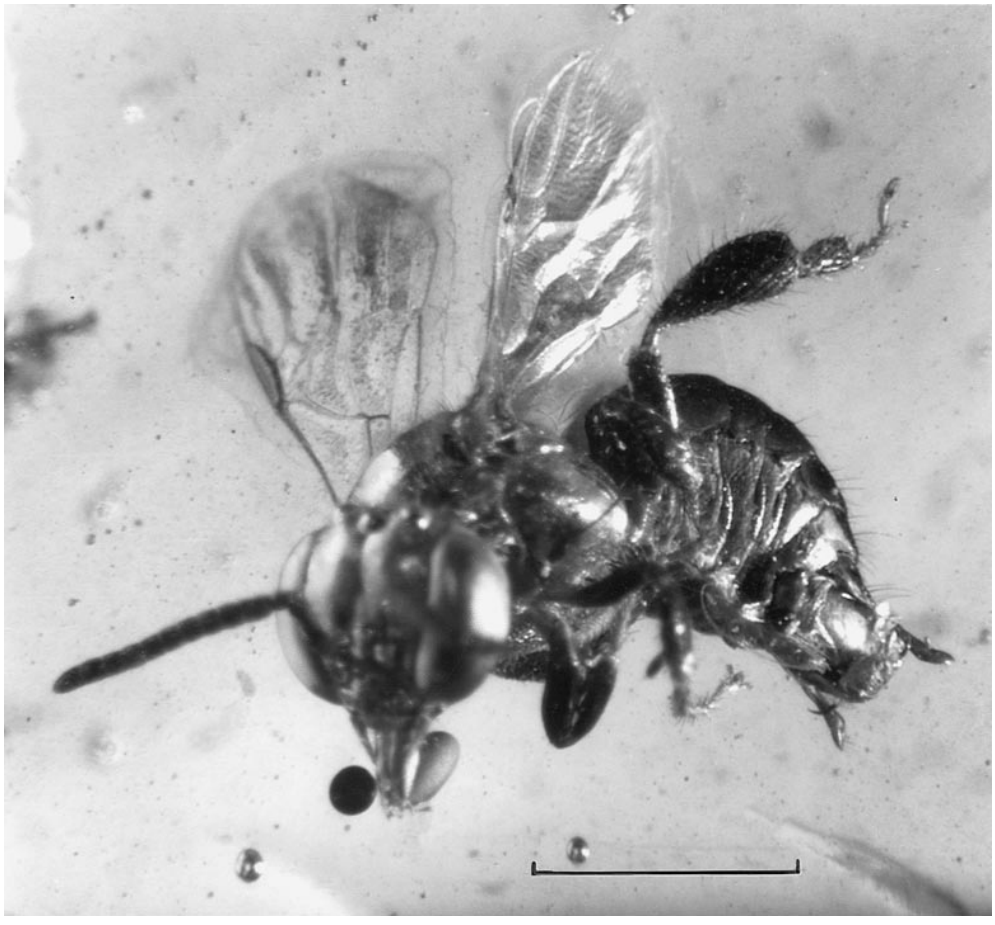


Fig. 21. Photomicrograph of *Proplebeia tantilla*, sp. n., male, holotype, AMNH-DR-14-1439. Scale = 1.0 mm.

tibia (fig. 4). The worker (AMNH-DR-14-911) was interpreted as *P. tantilla* based on the body size, and the shape and size of the wing veins; it was not possible, however, to verify if the male has long microtrichia on veins M + Cu and the first abscissa of M, as in the worker.

The male of *P. tantilla* differs from that of *P. dominicana* mainly by having flagellomeres wider than long, the median projection of S6 not apically emarginate, penis valvae short and slender, and gonostyli swollen at the apex, forming a hairy, solelike area (an autapomorphic condition). There are no shared apomorphies among male characters, only S7 is well developed and sclerotized in both species (but this can be a plesiomorphic condition; in modern genera S7 is usually reduced and weakly sclerotized). The decision to include this species in the genus *Proplebeia* was based on characters of the worker: rastellum with 7–8 long, spinelike hairs, and glabrous posterior rim of inner surface of tibia III very wide, ca. $\frac{2}{7}$ the width of keirotrichiate area, although it is not clear if the rim is depressed and forms a step.

DISCUSSION

Phylogenetic and biogeographic relationships of the fauna of Meliponini from the Dominican Republic cannot be fully appreciated without study of the fauna preserved in amber from Chiapas, Mexico, since there are indications that these faunas are closely related (Roubik et al., 1997). Both deposits

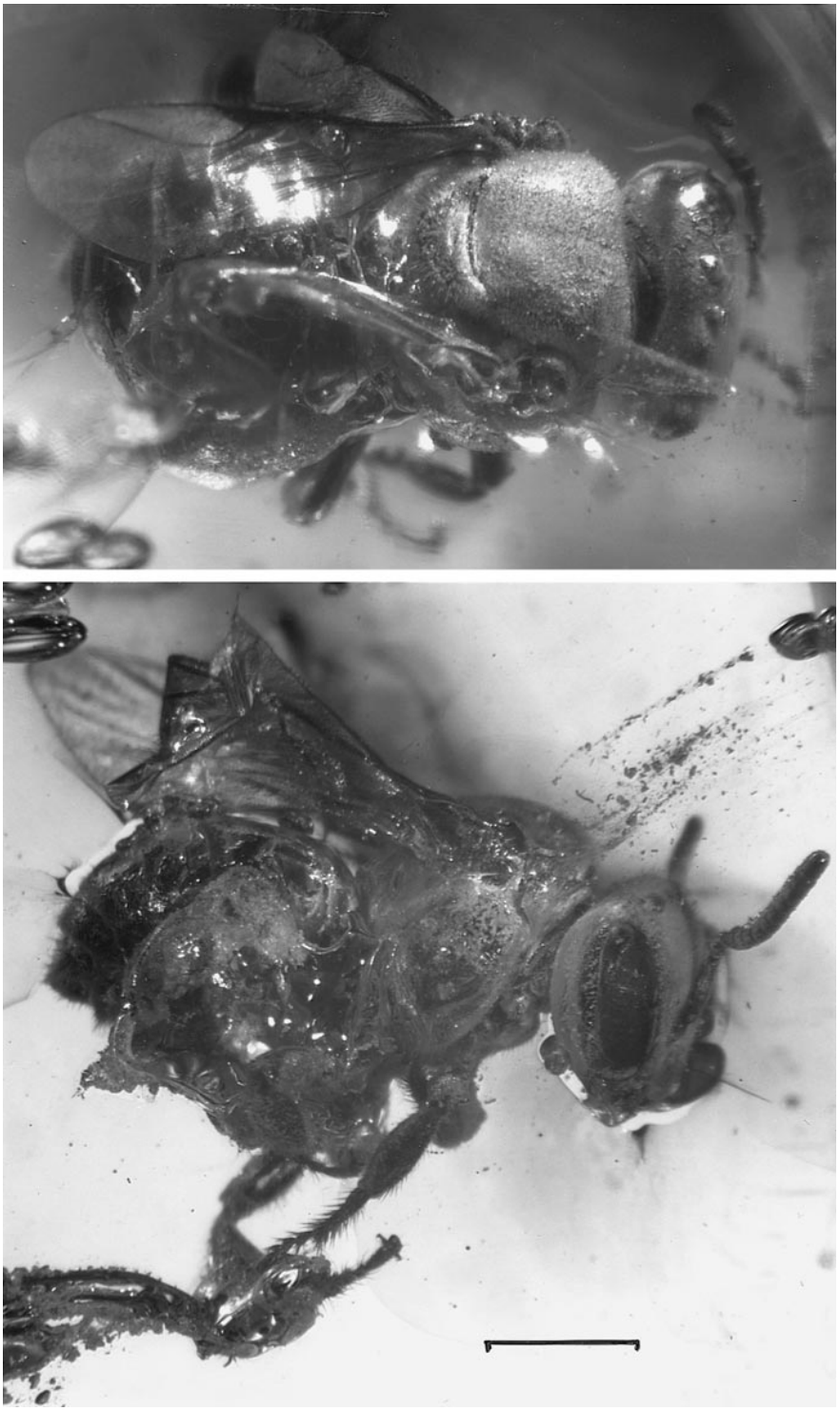


Fig. 22. Photomicrographs of *Proplebeia vetusta*, sp. n., worker, paratype, AMNH-DR-14-1440. Scale = 1.0 mm.

are similar in age, botanical origin, and were in closer proximity during the Oligo-Miocene.

Wille (1959) described *Nogueirapis silacea*, from the amber of Chiapas. It shares with *Proplebeia* some derived, presumably homologous characters, such as: tibia III subtriangular with the inner posterior rim depressed, glabrous and very wide (ca. $^4/_9$ the width of keirotrichiate area, 5:11, Wille, 1959: 850, 851) and the rastellum composed of long, slender hairs concentrated on the anterior corner of the inner distal edge of the tibia (ca. 14 hairs according to Wille, 1959: 850, fig. 3, 851). These two taxa also share similarities in the pattern of wing venation, size and shape of the body, long malar area, and yellow markings on the head. Although Wille has placed this species in the modern genus *Nogueirapis*, he admitted that there are differences between the two in the wing veins and inner surface of tibia III. In all extant species of *Nogueirapis* the inner posterior margin of tibia III is very narrow and in the same plane of the keirotrichiate area (about $^1/_{10}$ as wide as the keirotrichiate area; in some specimens the glabrous margin is slightly depressed on the basal third), and the first abscissa of M on the forewing is very long, ca. 1.6× the length of Rs + M + second M. In *Proplebeia* these veins have approximately the same length and in *N. silacea* the first abscissa of M is about 1.2× longer than Rs + M + second M.

Considering the worker characters mentioned above and those described by Wille, *N. silacea* is probably not part of the *Nogueirapis* clade; these characters are, rather, more indicative of relationship with *Proplebeia*. If this interpretation is correct, only one phylogenetic lineage, now extinct, inhabited the northern terrains of Central America–southern Mexico and Hispaniola (so-called ''nuclear'' America). This lineage probably originated no earlier than the Oligocene,[4] and descendents evolved in isolation as the Greater Antilles fragmented and drifted from the Central American mainland during the Miocene.

[4] Actually, Mexican amber may be Miocene in age, according to the published data of Frost and Langenheim (1974) (M. Iturralde-Vinent, personal commun. to D.G.).

The hypothesis that *Proplebeia* was an exclusive meliponine lineage in nuclear America is corroborated by the fact that among thousands of meliponine specimens in Dominican amber and hundreds from Chiapas, there are no specimens belonging to other lineages (here considering *N. silacea* to likely be a *Proplebeia* or a sister group). Except for the cleptobiotic species, all known Meliponini are resin collectors, including *Proplebeia dominicana* and *P. vetusta* (see description of specimen AMNH-DR-14-1440, here, and photos of *Proplebeia* with resin-filled corbicula, e.g., Poinar, 1992: 467; Grimaldi, 1996b: 118). The corbicula is a structure that evolved associated with transport of resin as well as pollen and other materials in meliponines. Indirect evidence that *Proplebeia* routinely and actively gathered resin from the extinct *Hymenaea* are several Dominican amber pieces in the AMNH that contain hundreds of *Proplebeia* workers. Thus, we consider entrapment in resin an efficient method for surveying meliponines, even rare ones.

With reference to the extant taxa, the study of *P. dominicana* and *P. tantilla* males indicates that *Proplebeia* comprised a lineage differentiated from *Plebeia* (s.s.), its prime sister-group candidate (Michener, 1982, 1990). In *Proplebeia*, S6 has a long, broad median projection (different states of this character are present in most Meliponini), while in *Plebeia* (s.s.) this sternum is largely emarginate and the median projection is reduced or absent (Camargo and Moure, 1988; Ayala, 1992), the latter condition is clearly apomorphic. Another important character is the form of S5: in *Proplebeia* it is unmodified, whereas males of *Plebeia* (s.s.) have a large hairy protuberance on either side (Camargo and Moure, 1988; Ayala, 1992)—this is possibly the most significant apomorphy for the genus *Plebeia*.

Concerning workers, little can be added to the discussion by Michener (1982, 1990); the main autapomorphy of *Proplebeia* refers to the form of the rastellum, which is comprised of seven to nine long, cylindrical, spinelike hairs concentrated on the anterior corner of the distal edge of tibia III. The hairs of the rastellum are shorter, flattened, and extend toward the posterior distal margin of the tibia

in modern forms of *Plebeia* (s.s.), which range today from the lowlands of Mexico to northwestern Argentina, and *Plebeia*-like genera *(Friesella, Mourella, Schwarziana, Schwarzula,* and *Scaura* from the Neotropical region; *Plebeina* from Africa; *Austroplebeia* from Australia and New Guinea; and the Indo-Malayan *Pariotrigona* and *Lisotrigona*). Another character is the posterior margin of the internal surface of tibia III being depressed in a step or sulcus (Camargo and Pedro, 1992a), with the width of the sulcus in *Proplebeia* ca. $\frac{2}{7}$ to $\frac{1}{3}$ of the keirotrichiate area (measured in the middle of the tibia). In the modern forms of *Plebeia* (*s. s.*) and *Plebeia*-like groups, the depressed region is ca. $\frac{1}{6}$–$\frac{1}{5}$ as wide as the keirotrichiate area (except in *Austroplebeia,* in which the depression does not form a step or discrete sulcus).

Unambiguous synapomorphies indicative of a sister-group relationship between *Proplebeia* and *Plebeia* (s.s.), as suggested by Michener (1982, 1990), are unclear. However, besides the general body form, these genera share an exclusive combination of character states, such as: clypeus short (slightly more than twice as wide as long), trapezoidal, and very wide at the base (the distance between the subantennal sutures approximately as large as the length of the clypeus); shape of yellow markings on the clypeus, supraclypeal, and parocular areas; triangular shape of the forewing medial cell and the length of surrounding veins—first abscissa of M approximately as long as Rs + M + second M, such that the vertex of the triangle is in the middle of the cell (figs. 8, 9); tibia III subtriangular with the posterodistal corner angled; and basitarsus III nearly subparallel, with the posterior margin only slightly convex with the basal quarter; and the inner surface of tibia III with the keirotrichiate area broadened and the glabrous posterior rim depressed in a step or sulcus (Camargo and Pedro, 1992a). The congruence of these characters could indicate that they evolved in concert only once, corroborating the hypothesis that *Proplebeia* and *Plebeia* (s.s.) shared a common ancestor. In support of the hypothesis that *Proplebeia* was derived from a Neotropical lineage, is the fact that the worker of *P. dominicana* has cylindrical gonostyli convergent toward the apex and covered with setaceous hairs, as described by Michener (1990). These sting features are only known in the Neotropical–Indo-Malayan meliponines. The African genera possess distinct combinations of sting characters, suggesting a monophyletic lineage independent from the modern American and Indo-Malayan Meliponini (Michener, 1990, Camargo and Pedro, 1992a, 1992b).

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