



## Taxonomic revision of the genus *Probolomyrmex* Mayr, 1901 (Hymenoptera: Formicidae: Proceratiinae) for the Neotropical Region

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### Table of contents

Abstract	61
Introduction	61
Material and methods	62
Results	64
<i>Probolomyrmex</i> Mayr, 1901	64
Taxonomic synopsis for the Neotropical species	65
Key to the identification of Neotropical workers and queens of <i>Probolomyrmex</i>	65
Species accounts	68
<i>Probolomyrmex boliviensis</i> Mann, 1923	68
<i>Probolomyrmex brujitae</i> Agosti, 1995	72
<i>Probolomyrmex cegua</i> New species	75
<i>Probolomyrmex dentinodis</i> New species	78
<i>Probolomyrmex guanacastensis</i> O’Keefe & Agosti, 1998	80
<i>Probolomyrmex kelleri</i> New species	81
<i>Probolomyrmex lamellatus</i> New species	86
<i>Probolomyrmex petiolatus</i> Weber, 1940	90
Acknowledgments	92
Literature Cited	92

### Abstract

We revise the taxonomy of the ant genus *Probolomyrmex* for the Neotropical region. Eight species are recognized, four of them already known: *P. boliviensis*, *P. brujitae*, *P. guanacastensis*, and *P. petiolatus*. Four new species are described: *P. cegua* **sp. n.**, *P. dentinodis* **sp. n.**, *P. kelleri* **sp. n.** and *P. lamellatus* **sp. n.** We present complete descriptions and redescriptions for all the species, including diagnoses, comments on the taxonomic history and biology, high-quality images, and scanning electron microscope micrographs for diagnostic anatomic structures. In addition, distribution maps and an illustrated identification key are provided.

**Key words:** Neotropics, taxonomy, review, ants, Probolomyrmecini

### Introduction

*Probolomyrmex* is a rarely collected ant genus with a circumtropical distribution. It is the only genus of the Proceratiinae tribe Probolomyrmecini (Bolton, 2019), and has 26 known species. Taylor (1965) was the first to revise the genus for the world, based on the study of 57 specimens, 17 of which were from the Neotropics, recognizing three species for this region. In 1994, Agosti revised *Probolomyrmex* from South America using 27 specimens and provided a key for the four known species at the time. After the synonymy of *P. angusticeps* under *P. boliviensis* by Brown (1975) and the description of *P. guanacastensis* (O’Keefe & Agosti, 1997), four species are now recognized

for the New World: *P. boliviensis* Mann, *P. brujitae* Agosti, *P. guanacastensis* O’Keefe & Agosti, and *P. petiolatus* Weber.

Morphologically, the genus is recognized by the diagnostic characteristics of proceratiine ants and the combination of eyes generally absent, antennal insertions exposed and located on a frontal shelf-like platform which extends over the mandibles, and the second segment of gaster never bent anteroventrally towards the mesosoma.

Traditional collection techniques for ants have shown little efficiency in finding *Probolomyrmex* specimens. This is due, in part, to the cryptic habit of the species, the low population densities of the colonies, and the solitary foraging of workers (Kikuchi & Tsuji, 2005; Ito, 1998). O’Keefe & Agosti (1997) collected only two specimens of *Probolomyrmex* in more than 2000 pitfall samplings between 1995 and 1996 in Barro Colorado, Panama. Hita Garcia & Fisher (2014) examined only 41 specimens from more than 6000 leaf-litter samples, 4000 pitfall traps and 9000 additional hand collecting events between 1992 and 2011, in Madagascar. Shattuck *et al.* (2012), in the revision of the Australian and Melanesian species of the genus, observed only 39 specimens available in collections for those regions. Given the difficulty of collecting specimens, *Probolomyrmex* is relatively under-represented in entomological collections.

Nests of *Probolomyrmex* have been observed for at least three species in the Neotropics and Asia. They can be established in rotten logs, empty snail shells, and natural cavities in soil and leaf-litter, comprising about 20 workers (Taylor, 1965; Ito, 1998; Kikuchi & Tsuji, 2005). Colonies can be found in a wide diversity of environments including xeric habitats, dry forests, grasslands, lowland and montane rainforests, occurring from 180m to 2150m (Shattuck *et al.* 2012; Fisher, 2007). Little is known about the feeding habits of *Probolomyrmex*, but some observations suggest that they may be specialist predators of polyxenid millipedes as observed for the ponerine ant *Thaumatomyrmex* (Ito, 1998).

Most species for which the reproductive caste is known have winged queens and males, suggesting that mating occurs in a nuptial flight. However, an ergatoid queen is reported for at least one species, *P. guanacastensis* (O’Keefe & Agosti, 1997).

This paper revises the taxonomy and natural history of the Neotropical species of *Probolomyrmex* based on the largest number of specimens yet studied for this biogeographical region. Four new species are described, and we provide an updated identification key, distribution maps, and high-resolution light and scanning electron microscopy images for all the species.

## Material and methods

Approximately 180 *Probolomyrmex* specimens known to exist in museum collections were examined for this work. Entomological collections are referred to by the following acronyms:

<b>AMNH</b>	American Museum of Natural History, New York, New York, USA.
<b>BMNH</b>	The Natural History Museum, London, England.
<b>CASC</b>	California Academy of Sciences, San Francisco, California, USA.
<b>CPDC</b>	Centro de Pesquisas do Cacau, Comissão Executiva do Plano da Lavoura Cacaueira, Itabuna, Bahia, Brazil.
<b>DZUP</b>	Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil.
<b>INBC</b>	Instituto Nacional de Biodiversidad, Heredia, Heredia, Costa Rica.
<b>MIZA</b>	Museo de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Aragua, Venezuela.
<b>JTLC</b>	John T. Longino Collection, University of Utah, Salt Lake City, Utah, USA.
<b>MCZC</b>	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
<b>MHNG</b>	Musée d’Histoire Naturelle, Geneva, Switzerland.
<b>MPEG</b>	Museu Paraense Emilio Goeldi, Belém, Pará, Brazil.
<b>MUSM</b>	Museo de Historia Natural “Javier Prado”, Lima, Provincia de Lima, Peru.
<b>MZSP</b>	Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil.
<b>NMNH</b>	Smithsonian Institution, United States National Museum of Natural History, Washington DC, USA.

Measurements are in mm and were taken using a Wild Heerbrugg stereomicroscope at 60× magnifications. All measurements are presented as ranges, except for unique specimens. For each species, we measured workers from different localities (listed in the “Additional Material Examined” sections) to better describe geographical variation. The abbreviations used are:

**HL:** head length—the maximum measurable length of head capsule excluding mandibles, measured in full-face view, in a straight line from the mid-point of the anterior clypeal margin to the midpoint of the vertexal margin;

**HW:** head width—the maximum width of the head capsule measured in full-face view;

**SL:** antennal scape length—the length of the antennal scape, excluding the basal condyle and its peduncle;

**WL:** mesosomal length (Weber’s length)—the diagonal length of mesosoma in profile, from the midpoint of the anterior pronotal declivity to the posterior margin of the propodeal lobes;

**PL:** petiole length—in lateral view, the maximum length of the petiole;

**PW:** petiole width—in dorsal view, the maximum width of the petiole;

**PH:** petiole height—in lateral view, the maximum height of the petiole including the subpetiolar process;

**GL:** gaster length—the length of first and second gaster segments (the remaining gastral segments were not measured because they are not visible in all specimens);

**TL:** total length—the summed length of HL, WL, PL, and GL;

**CI:** cephalic index— $HW \times 100/HL$ ;

**SI:** scape index— $SL \times 100/HW$ ;

**PI:** petiole index— $PH \times 100/PL$ .

Terms for the external morphology of adult forms follow Bolton (1994, 1995), and for surface sculpture we applied terms from Harris (1979). Alate forms were described following Boudinot (2015) and Yoshimura & Fisher (2009) (for wing venation). Superficial foveae and punctulae in the integument of *Probolomyrmex* specimens are always associated with hairs; however, in the name of clarity, sculpture and pilosity patterns are presented separately in the species descriptions, which are based on scanning electron micrographs, where these characteristics are clearer. Thus, at the description sections we separate sculpture, pilosity and morphology in distinct paragraphs, always following the ant body orientation (from mandibles to gaster).

High-resolution images were obtained with a Leica M205C stereomicroscope attached to a Leica DFC 295 video camera in the *Laboratório de Sistemática, Evolução e Biologia de Hymenoptera* - MZSP and a Zeiss Stereo DiscoveryV20 stereomicroscope attached to a Zeiss AxioCam 305 color video camera in the *Laboratório de Sistemática e Biologia de Formigas* - UFPR. Photos were then combined by the multiple-image overlay system Zerene Stacker (Zerene Systems LLC). The photographed specimens are indicated in the captions.

Scanning electron micrographs (SEM) were made in low and high vacuum microscopy systems. For the high vacuum system, a specimen was dehydrated sequentially through a series of ethanol concentrations to 100%, and then critical-point dried in a Bal-Tec CPD-030 using liquid CO<sub>2</sub>. Once the ethanol was replaced with CO<sub>2</sub>, the samples were slowly heated to the critical point, then slowly depressurized back to atmospheric pressure, dried, and mounted on aluminum stubs. The specimens were then sputter-coated with 60:40 wt% gold in a Balzers Union FL 9496 SCD-030 metallizer. Six additional specimens were submitted to low vacuum microscopy. The scanning electron micrographs were prepared in a JEOL JSM 6360 - LV Scanning Electron Microscope. SEM micrographs were obtained at the *Centro de Microscopia Eletrônica* of the Universidade Federal do Paraná (CME – UFPR). All images were edited in Photoshop CS6 (Adobe) only to enhance parameters of brightness and contrast. The specimens used for SEM are indicated in the captions. Illustrations for the identification key were made with Adobe Illustrator CS6 (Adobe).

Distribution maps were generated by QGIS (Version 2.18) with coordinates obtained from specimen labels and imported from Google Earth (Google).

## Results

### *Probolomyrmex* Mayr, 1901

Type-species: *Probolomyrmex filiformis*, by monotypy. Mayr, 1901: 2.

*Probolomyrmex* in Dorylinae, Dorylini: Ashmead, 1905: 381; Ashmead, 1906: 27.

*Probolomyrmex* in Ponerinae, Cerapachyini: Wheeler, 1910: 137.

*Probolomyrmex* in Ponerinae, Proceratiini: Emery, 1911: 52; Arnold, 1915: 33; Forel, 1917: 236; Wheeler, 1922: 645; Donisthorpe, 1943: 686; Chapman & Capco, 1951: 77.

*Probolomyrmex* in Ponerinae, Platythyreini: Brown, 1952: 1; Brown, 1975: 7; Dlussky & Fedoseeva, 1988: 79; Hölldobler & Wilson, 1990: 10; Jaffe, 1993: 7; Bolton, 1994: 164.

*Probolomyrmex* in Probolomyrmecinae: Perrault, 2000: 271.

*Probolomyrmex* in Proceratiinae, Probolomyrmecini: Bolton, 2003: 49, 180.

**Genus diagnosis. Worker** (after Taylor, 1965; Agosti, 1994; Eguchi *et al.* 2006; Keller, 2011; and this study): Small monomorphic ants. Body color from pale yellow to reddish brown. Integument opaque and covered by extremely fine pubescence, small punctures or foveae; foveae generally deeper and more visible on first segment of gaster. Head foveated, interval between foveae covered by micropunctures. Antennal scapes densely punctate, with sparse small foveae. Dorsum of mesosoma and metasoma with incomplete (open posteriorly) foveae; latero-dorsal region of pronotum with micropunctures and sparse foveae.

Outer surface of mandibles with thick and short setae. Antennal funiculi with abundant pubescence and relatively long appressed hairs set in longitudinal grooves, space between hairs filled by short hairs.

Head longer than wide, with broadly convex sides. Sclerites of the anterior frons and the clypeus are highly fused and extend anteromedially beyond the clypeo-labral articulation, forming a shelflike platform that projects anteriorly covering mandibles in full-face view. Antennae with 12 segments; antennal insertions fully exposed, positioned on frontoclypeal shelflike projection and separated by narrow vertically raised carina, which is formed by the fusion of the frontal carinae. Mandibles small and triangular, hidden in frontal view by frontoclypeal shelflike projection; each mandible has a well-developed apical tooth followed by series of denticles; palpal formula 4,2; three basal maxillary palpomeres equal in size, and apical one longer; labial palpomeres equal in size. Eyes absent, except for holotype of *P. brevirostris* Forel, one worker of *P. dentinodis* **sp. n.**, and two workers of *P. kelleri* **sp. n.**

Mesosoma slender and long in profile, with dorsum flat to weakly convex, without visible promesonotal and metanotal sutures, which are represented only by weak ventro-lateral superficial lines. Propleuron inflated, projecting ventrally. Propodeal declivity usually posteriorly emarginated on each side by low and obtuse carina, which can present an apical tooth. All tibiae with single pectinate spur; tarsal claws simple, without internal teeth.

Petiole node narrow and strongly elevated, with uniform antero-dorsal curve in profile; posterior face high and usually concave in lateral view. Subpetiole process present. First and second segments of gaster separated by constriction. First segment of gaster with tergite and sternite fused laterally forming tubular structure. Sting well-developed.

**Queen** (after Taylor, 1965; Agosti, 1994; Eguchi, *et al.* 2006; and this study): Size, color, sculpturing, structure of head, appendages, and metasoma as in workers. Additionally, queens present well-developed eyes, three ocelli similar in size and associated to dark spots. Pronotum subtriangular in lateral view. Mesoscutum and scutellum shield-shaped; transcutal suture straight; notauli absent; parapsidal lines vestigial. Mesopleural sulcus diagonal, rendering katepisternum triangular. Metanotum convex. Flight sclerites developed in most species. Wings long and narrow, venation greatly reduced. Forewings with Sc+R and M+Cu forming submedian cell; veins 2r-rs, Cu, cu-a e A not extending to external border of wing. Posterior wings with short R-Rs and A veins; three submedian hamuli present.

**Male** (after Eguchi *et al.* 2006; Yoshimura & Fisher, 2009; and this study): Head subglobose, frontoclypeal shelflike projection not as strongly projecting as in workers and queens. Antennae with 13 segments; scapes relatively long. Eyes well developed, occupying half of head lateral margins; three ocelli present. Metepisternum separated from propodeum by a strong suture. Wings as in female.

**Comments.** *Probolomyrmex* can be easily recognized from the other genera of Proceratiinae mainly by the shape of the gaster. The second gastral sternite is not reduced, so the gaster is tubular and not bent antero-ventrally as in *Discothyrea* and *Proceratium*.

In the Neotropical region it is found from northern Argentina to southern Mexico, mainly in the leaf-litter of rainforests. In the Indo-Pacific Region *Probolomyrmex* is divided into two species-groups (Eguchi *et al.* 2006), *P. greavesi* group and *P. longinodus* group. Both species-groups occur from India east to Australia, with the *greavesi* group extending on to the Solomon Islands. In Australia, species can be found in habitats ranging from rainforests, *Eucalyptus* woodlands to spinifex grasslands (Shattuck *et al.* 2012). In the Afrotropical region the genus is well distributed in sub-Saharan forests (Hita Garcia *et al.* 2013). In Madagascar, species can be found in several environments, such as tropical dry forest, littoral rainforest, lowland rainforest, and montane rainforest (Hita Garcia & Fisher, 2014).

Some species of *Probolomyrmex* present the postero-ventral lobe of the petiole subquadrate and lack a prora. On the other hand, species with a rounded postero-ventral lobe of the petiole often possess a prora. This could suggest a relationship between these structures, possibly involving a distinct bending mechanism of the gaster when ants are capturing (stinging) or transporting prey. The presence of a fitting mechanism between the prora and subpetiolar process could improve precision and better allow the sting to reach the mandibular region where the prey would be grasped.

Thus, when bending the gaster forwards, and engaging the prora in the subpetiolar process, the postero-ventral lobe of the petiole could serve as a support, when they are rounded; in species with a subquadrate subpetiolar process, it would be an obstacle for that fitting to occur, therefore the prora is absent. In addition, if this fitting mechanism really occurs, it is possible that it causes friction between these two structures, which could explain the small differences in the degree of development of the prora and the subpetiolar process observed in individuals of the same species, such as in *P. kelleri* **sp. n.**

This fitting mechanism between prora and subpetiolar process may occur in other genera in which these structures are present, as in *Gnamptogenys*, *Prionopelta*, *Pseudoponera*, and *Thaumatomyrmex*. In these groups, and even in the remaining proceratiine genera, the morphology of the abdomen seems to be closely related to alimentary habits (Hölldobler & Wilson, 1990). However, more detailed observations should be made to confirm this condition.

Little is known about the feeding habits of *Probolomyrmex*, except for observations by Ito (1998) on the Oriental species *P. dammermani* Wheeler feeding on polyxenid millipedes. Different kinds of potential prey were offered to colonies of *P. boliviensis* kept in artificial conditions, but none were accepted (Taylor, 1965).

### Taxonomic synopsis for the Neotropical species

*Probolomyrmex boliviensis* Mann, 1923. Bolivia, Brazil (AC and RO), Colombia, Costa Rica, Honduras, Panama, and Peru.

*Probolomyrmex brujitae* Agosti, 1995. Argentina and Brazil (GO, MS, MT, RO, and TO).

*Probolomyrmex cegua* **new species**. Nicaragua.

*Probolomyrmex dentinodis* **new species**. Brazil (PA, RO, and TO).

*Probolomyrmex guanacastensis* O'Keefe & Agosti, 1998. Costa Rica.

*Probolomyrmex kelleri* **new species**. Guyana, Peru, and Venezuela.

*Probolomyrmex lamellatus* **new species**. Brazil (PA).

*Probolomyrmex petiolatus* Weber, 1940. Guatemala, Mexico, and Panama.

### Key to the identification of Neotropical workers and queens of *Probolomyrmex*

- |   |                                    |   |
|---|------------------------------------|---|
| 1 | Prora absent (Fig. 1A) .....       | 2 |
| - | Prora present (Fig. 1B - pr) ..... | 3 |

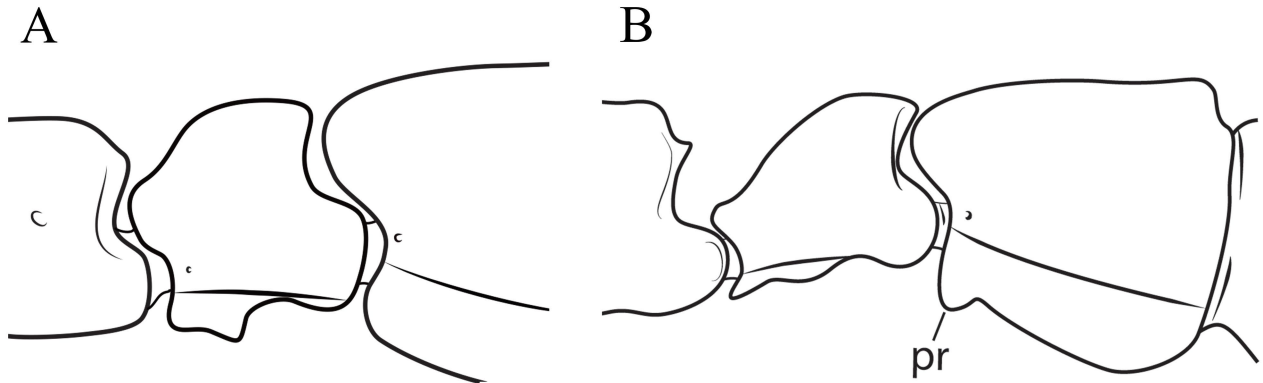


FIGURE 1. Lateral view of gaster. A: prora absent. B: prora present. pr = prora.

- 2 Ventral profile of the petiole with a subrectangular anterior projection. Guatemala, Mexico, and Panama (Fig. 2A - sp) . . . . . *P. petiolatus*
- Ventral profile of the petiole without a subrectangular anterior projection. Argentina and Brazil (GO, MS, MT, RO, and TO) (Fig. 2B - sp). . . . . *P. brujitae*

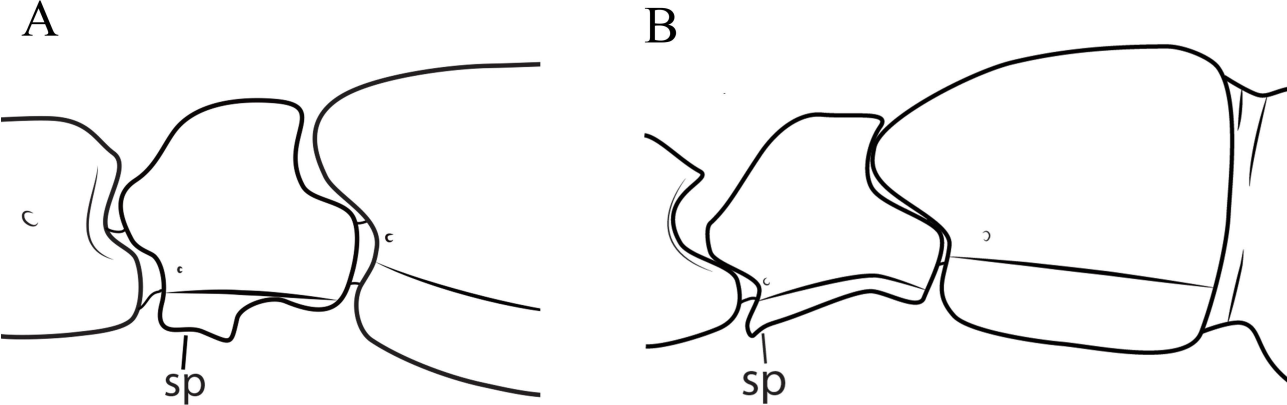


FIGURE 2. Lateral view of petiole. A: subpetiolar process subrectangular. B: subpetiolar process not subrectangular. sp = subpetiolar process.

- 3 In lateral view, dorsal and posterior margins of propodeum meeting in a rounded angle, without any acute projection. Brazil (PA) (Fig. 3A - pd) . . . . . *P. lamellatus* sp. n.
- In lateral view, dorsal and posterior margins of propodeum meeting in an acute angle, forming distinct teeth. (Fig. 3B - pd) . . . . . 4

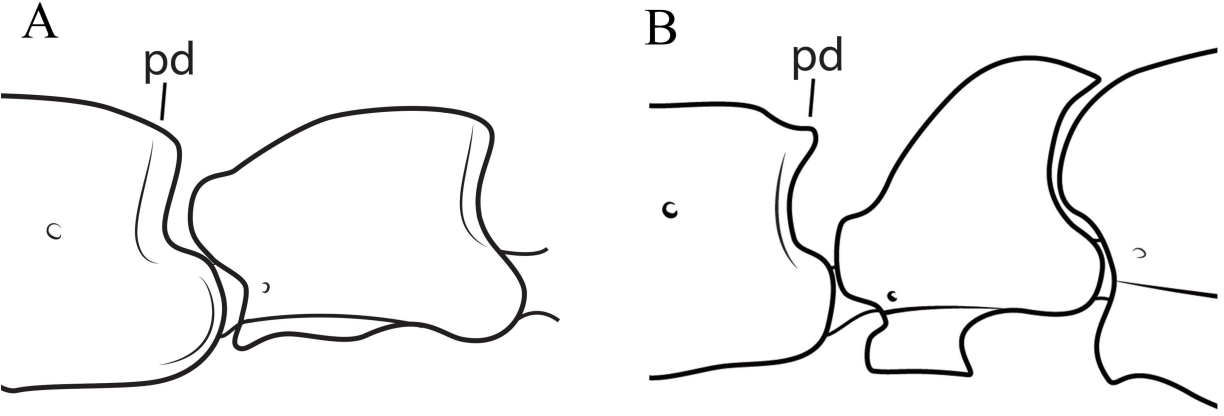


FIGURE 3. Lateral view of propodeum. A: propodeum margins rounded. B: propodeum margins angled. pd = propodeum.

- 4 In lateral view petiole higher than long (Fig. 4A). In dorsal view petiolar teeth well developed. Brazil (PA, RO and TO) (Fig. 17C) ..... *P. dentinodis* sp. n.
- In lateral view petiole longer than high (Fig. 4B). In dorsal view petiolar teeth absent or weakly developed (Fig. 21C) ..... 5

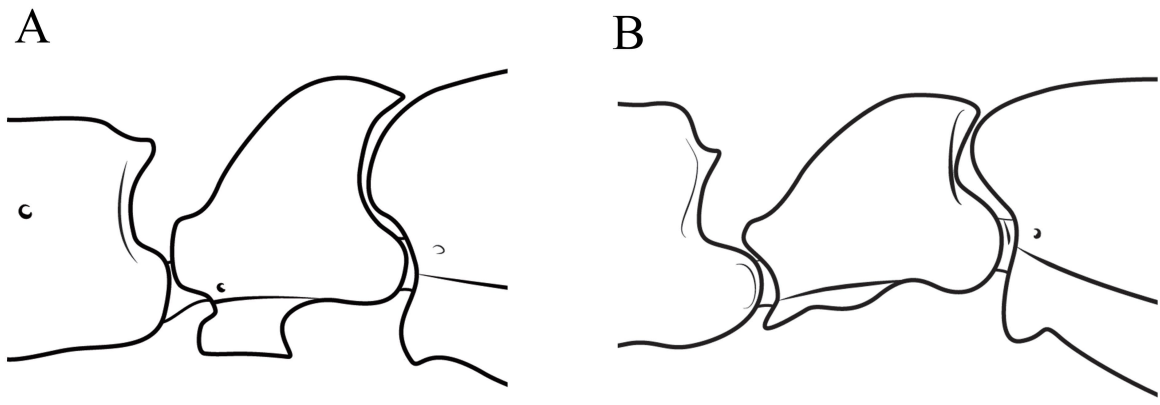


FIGURE 4. Lateral view of petiole. A: petiole higher than long. B: petiole longer than high.

- 5 In lateral view, the highest point of the dorsal profile of the first gastral tergite is at the posterior limit of the tergite. Nicaragua (Fig. 5A) ..... *P. cegua* sp. n.
- In lateral view, the highest point of the dorsal profile of the first gastral tergite is anterior to the posterior limit of the tergite. (Fig. 5B - ppd) ..... 6

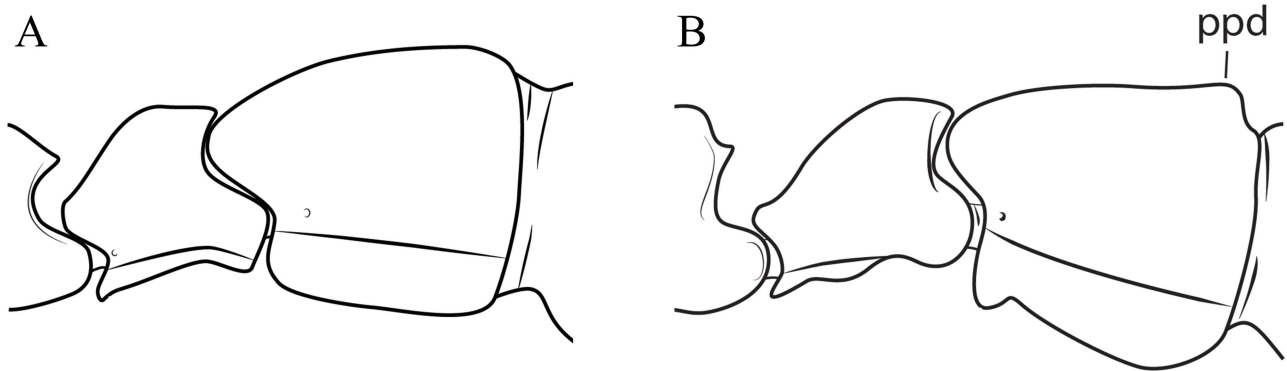


FIGURE 5. Lateral view of gaster. A: dorsal protuberance in the gaster absent. B: dorsal protuberance in the gaster present. ppd = dorsal protuberance in the posterior region of the first gastral tergite.

- 6 Antennal scapes relatively longer, distance from scape apex to posterior margin of head less than or equal to two times the pedicel length. Brazil (AC and RO); Bolivia, Colombia, Costa Rica, Honduras, Panama, and Peru (Fig. 6A) .... *P. boliviensis*
- Antennal scapes relatively shorter, distance of scape apex to posterior margin greater than two times the pedicel length (Fig. 6B) ..... 7

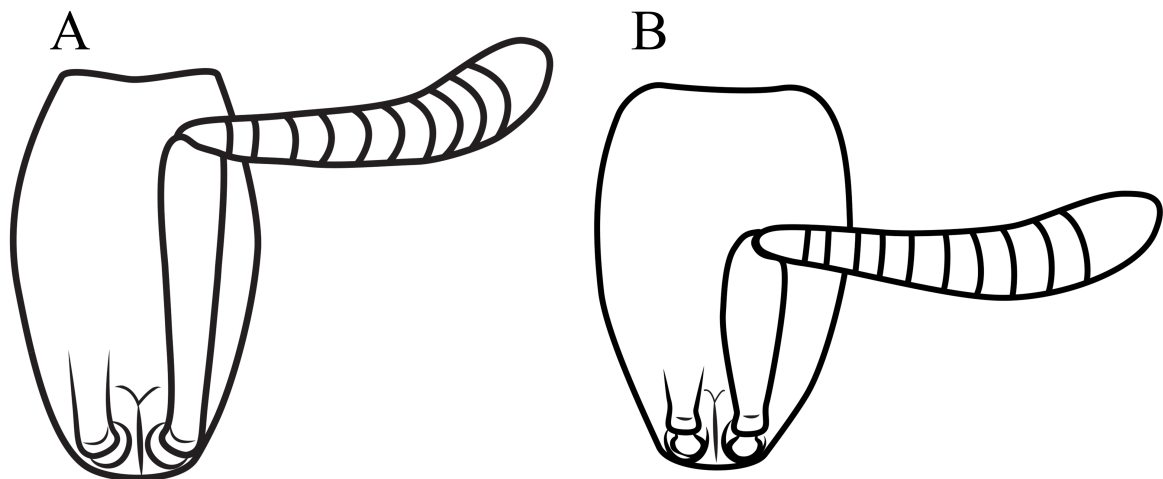
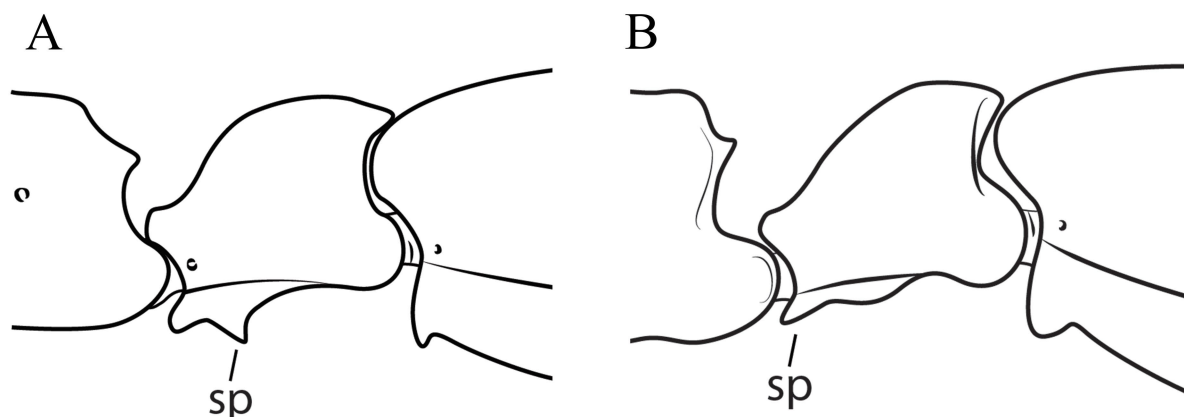


FIGURE 6. Frontal view of head. A. Antennal scapes long. B. Antennal scapes short.

- 7 Subpetiolar process well developed, medially concave ventrally to subrectangular, with an acute postero-ventral corner. Guyana, Peru, and Venezuela (Fig. 7A - sp) ..... *P. kelleri* sp.n.  
 - Subpetiolar process weakly developed. Costa Rica (Figs. 7B - sp) ..... *P. guanacastensis*



**FIGURE 7.** Lateral view of petiole. A: subpetiolar process well developed. B: subpetiolar process weakly developed. sp = subpetiolar process.

### Species accounts

#### *Probolomyrmex boliviensis* Mann, 1923

(Figs. 8, 9, 10)

**Holotype: Bolivia, Beni:** Rurrenabaque, W.M. Mann. USNM, type 25906 (queen) [NMNH] [examined].

**Diagnosis:** Antennal scape extends to posterior third of cephalic capsule, distance from scape apex to posterior margin of head less than or equal to two times pedicel length. Postero-ventral lobe of petiole short and rounded. Subpetiolar process weakly developed. Prora and dorsal protuberance on posterior region of first gastral tergite present.

**Worker measurements:** (n=35) HL 0.63–0.72; HW 0.37–0.42; SL 0.43–0.56; WL 0.85–1.02; PL 0.31–0.41; PW 0.31–0.36; PH 0.27–0.36; TL 2.78–3.27; CI 56.5–61.5; SI 67.5–77.5; PI 76.5–94.5.

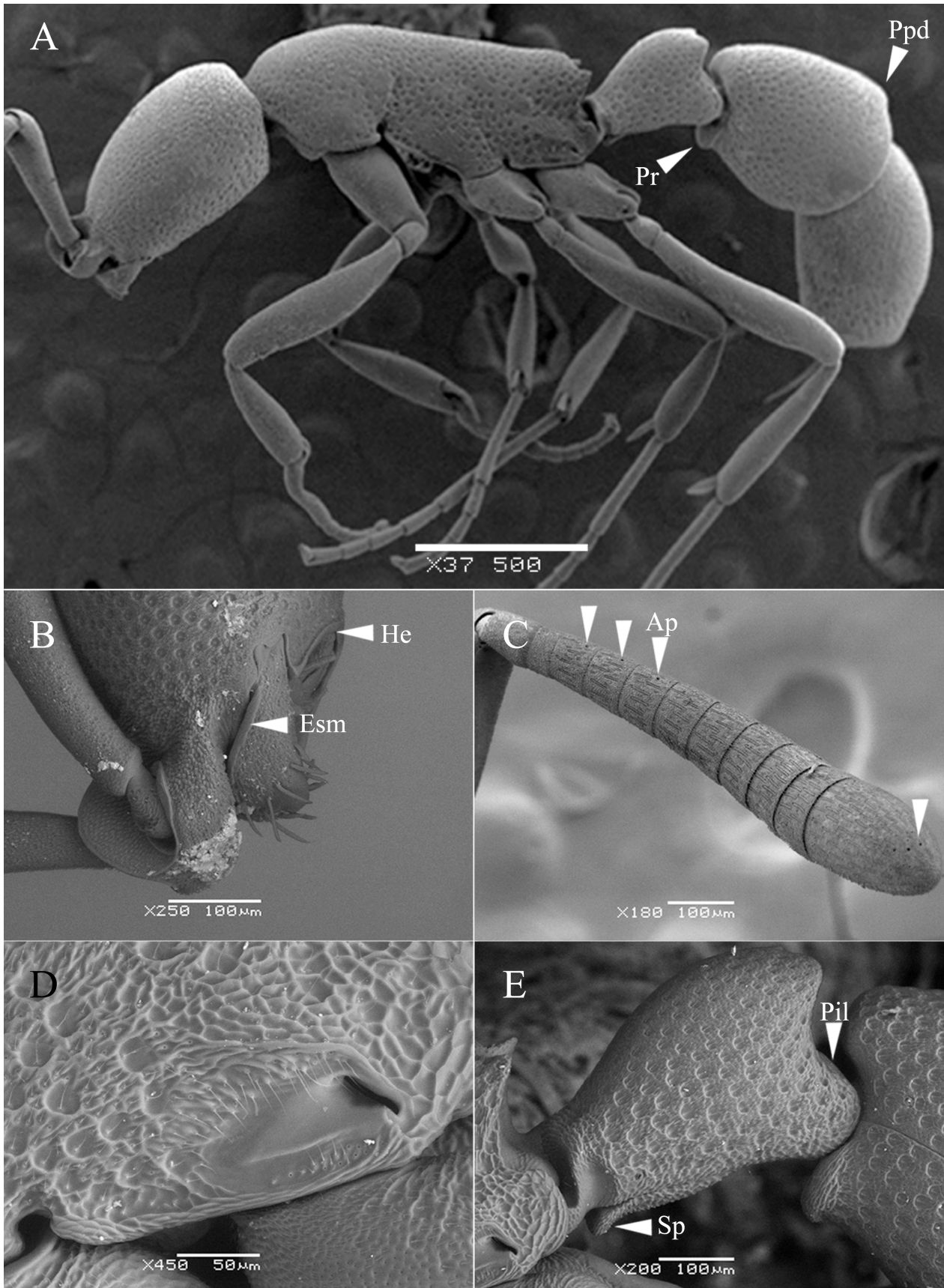
**Worker description:** Frontoclypeal shelflike projection with hair-bearing tubercles or cylindrical micro-pegs. Mandibles densely punctate; external surface of mandibular basal margin smooth (Fig. 8B – esm). Antennal funiculi with pits in each segment, tip of apical segment bearing pits of different sizes (Fig. 8C – ap). Mesopleuron, metapleuron and lateral faces of propodeum alveolate; alveoli denser just above metapleural gland orifice; opening of metapleural gland narrow, with smooth anterior region surrounded by rows of hairs (Fig. 8D). Petiolar node with incomplete foveae, intercalated by micropunctures; latero-ventral region of petiole imbricate; subpetiolar process alveolate (Fig. 8E). Posterior region of second gastral tergite with transversal rows of deep rounded pits.

Space between mesosomal foveae covered by dense pubescence. Pygidium with dense pubescence and few long and thick hairs.

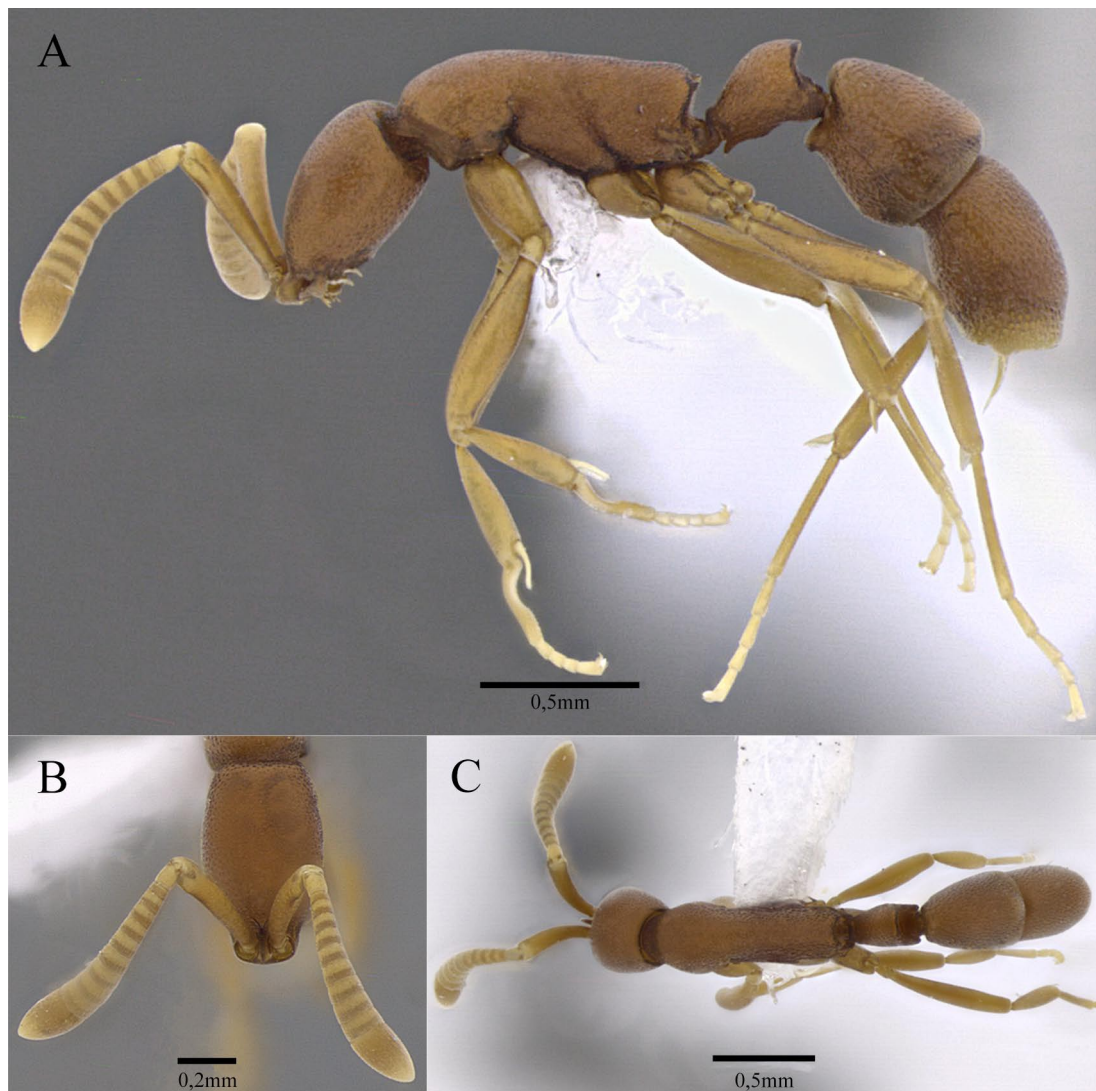
Head 1.7 times longer than wide (Fig. 9B). Hypostomal margin flattened (Fig. 8B – he). Antennal scapes extend beyond head midlength, distance from scape apex to of head less than or equal to two times pedicel length (SI 67.5–77.5). Propodeal declivity emarginated laterally by narrow and dark carina, with teeth at their apices. Petiole in lateral view at least 1.2 times longer than high (PI 76.5–94.5), posterodorsally with two weakly developed, round, projections; node posterior face short, concave, and smooth; postero-ventral lobe short and rounded; subpetiolar process weakly developed, many times forming acute anterior projection (Fig. 8E). First gastral segment with prora and dorsal protuberance on posterior region of tergite, characterized by a gentle elevation of the integument (Figs. 8A – ppd, 9A).

**Queen:** (n=3) HL 0.63–0.70; HW 0.40–0.50; SL 0.44–0.61; WL 0.89–0.93; PL 0.32–0.33; PH 0.29–0.31; TL 2.96–3.08; CI 61.5–69; SI 76.5–77.5; PI 86.5–94.5. With the morphological modifications described for *Probolomyrmex* queens and the diagnostic characters of the workers (Fig. 10).





**FIGURE 8.** SEM micrography of *Probolomyrmex boliviensis* (worker - DZUP 549761). A. Habitus (pr = prora; ppd = dorsal protuberance in the posterior region of the first gastral tergite). B. Mandibles (he = hypostomal margin; esm = external surface of basal region of mandible). C. Antenna (ap = antennal pit). D. Metapleural gland. E. Petiole (pil = postero-inferior lobe of petiole; sp = subpetiolar process).



**FIGURE 9.** *Probolomyrmex boliviensis* (worker - DZUP 549761). A. Habitus. B. head in frontal view. C. dorsal view.

**Larva** (see Taylor, 1965).

**Distribution** (Fig. 28): Northern Brazil (AC and RO), Bolivia, Colombia, Costa Rica, Panama, and Peru.

**Comments:** *P. boliviensis* is similar to *P. guanacastensis*, but the latter is smaller and has distinctly shorter scapes. Both species are found in Costa Rica but differ in habitat. *Probolomyrmex guanacastensis* is restricted to the Guanacaste region, in tropical dry forest with average rainfall below 1700 mm/year. Costa Rican *P. boliviensis* are known from Limón and southern Puntarenas provinces, in tropical submontane rainforests up to 1000m and average rainfall between 3500–5000 mm/year (Janzen, 1991; IMN, 2019).

Taylor (1965) found a nest of *P. boliviensis* in an old beetle gallery in a fairly sound, dry portion of a rotting branch on the floor of primary rainforest in Panama, with 22 workers, seven queens (four of them alate) and 19 immatures. It was taken to the laboratory for observation where various small soil arthropods and eggs were placed in the nest from time to time, but none of these organisms was attacked or accepted as food. This species was also recorded in termite nests and leaf-litter samples (Taylor, 1965).

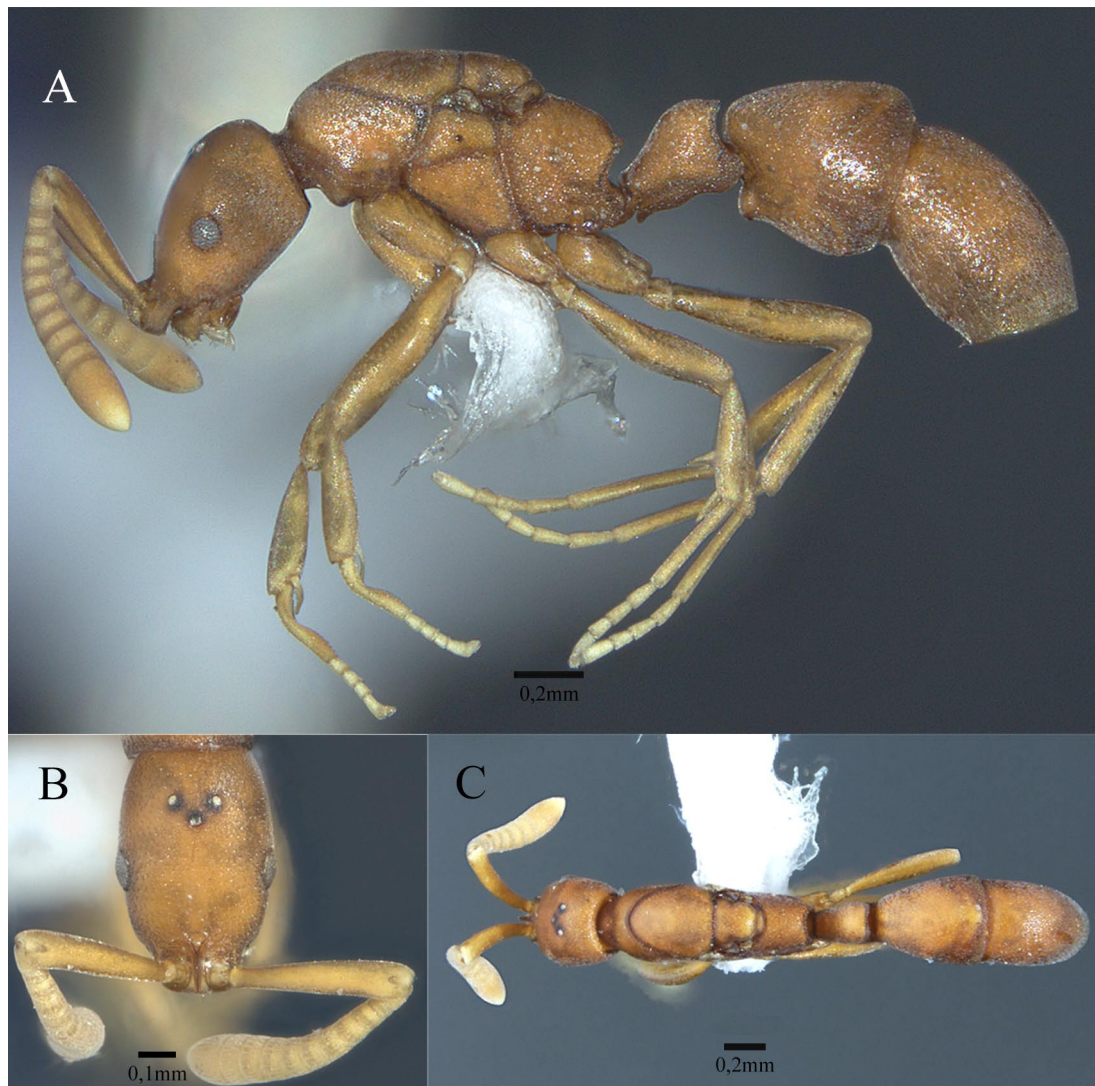
**Additional material examined (n=87): BRAZIL: Acre:** Senador Guiomard, Faz. Exp. Catuaba, 10°4'48.13"S 67°37'37.87"W, 220m, 07.ix.2016, A.C. Ferreira, R.M. Feitosa & T.S. Silva col. (1 worker) [DZUP]; Mâncio Lima, P.N. da Serra do Divisor, Mirante, 7°26'56.65"S 73°40'13.94"W, 360m, 15–18.ix.2016, A.C. Ferreira, R.M. Feitosa & T.S. Silva col. (2 workers) [DZUP]; **Rondônia:** Porto Velho, Área Abunã, 09°35'53.1"S 65°22'00.1"W, 04–18.ix.2012, Vicente R.E. & Oliveira J. cols, A10P1 DZUP 549760 (1 queen) [DZUP]; 09°35'48"S 65°21'56"W, 17–30.vi.2012, Sanhudo C.E.D. & Andrioli F.S. cols, A10P1 (2 workers) [DZUP]; (2 workers) [MZSP]; 09°36'36"S 65°22'44"W, A12P1 (5 workers – 1 queen) [MZSP]; 09°35'53.1"S 65°49'58.2"W, 4–18.ix.2012, Vicente R.E. &

Oliveira J. cols C3P1 (1 worker) [DZUP]; 09°36'36"S 65°22'44"W, 17–30.vi.2011, Albuquerque EZ & LF Silva cols, A12P1 (4 workers – 1 queen) [MZSP]; 70°6'3,1"W 12°34'8,4"S, 08–11.iii.2010, R. Feitosa & R. Silva cols, A12P1 (3 workers) [MZSP]; Área Caiçara, 09°26'41"S 64°49'39"W, 29.iii–05.iv.2012, Silva R.R. & Albuquerque E.Z. cols, C3P1 (5 workers) [MPEG]; (3 workers) [MZSP]; 09°26'46.8"S 64°49'31.1"W, 04–18.ix.2012, Vicente R.E. & Oliveira J. cols, C3P1 (1 worker) [DZUP]; 09°26'41"S 64°49'39"W, 27.iii–09.iv.2011, RR Silva & RM Feitosa cols, C3P1 (1 queen) [MZSP]; 09°26'52"S 64°50'05"W, C3P2 (5 workers) [MZSP]; 09°26'18"S 64°50'36"W, 04–17.i.2011, RR Silva & R Probst cols, C1P2 (1 queen) [MZSP]; Área Mutum, 09°35'29.5"S 65°02'57.6"W, 28.iv–12.v.2013, Mazão G.R. & Mendonça R.T.T. cols, M5P3 (1 worker) [MZSP]; 09°36'06"S 65°03'35"W, 29.iii–05.iv.2012, Silva RR & Albuquerque EZ cols, M8P1 (3 workers) [MZSP]; 09°35'44"S 65°04'00"W, M7P1 (1 worker – 1 queen) [DZUP]; DZUP 549761 (1 worker) [DZUP]; (2 workers) [MZSP]; 09°35'26"S 65°02'52"W, M5P1 (1 worker - 1 queen) [MZSP]; 09°34'49"S 65°03'13"W, 08–20.ix.2011, FS Andriolli & WF Datilo cols, M5P3 (1 queen) [MZSP]; 09°36'06"S. 65°03'35"W, 08–21.ix.2010, RR Silva & RM Feitosa cols, M8P1 (1 worker) [MZSP].

**COLOMBIA: Antioquia:** Amalfi, Cañon del rio Porce, 6°47'6.25"N 75°8'29.08"W, ix.2006, M.A. Vanegas, 1015, 1 msnm, (1 worker) [DZUP]; **Valle del Cauca:** Zarzal, Bosque El Medio, 4° 20'N 76° 4'W 950m, 12.iii.1999, L. Osorio Leg, PON47/271 Tronco descomp., Det. G. Zabala. 2013, PON 47 (1 worker) [MZSP]; **Magdalena:** Tayrona PK, Pueblito, 1.x.1976, C. Kugler, Berlese (1 worker) [MCZ].

**COSTA RICA: Province Limon:** Guapiles, 10°13'N 83°47'W, 28.iv.1996, R. Matlock col (1 worker) [INBIO]; **Puntarenas:** 15km SSW Pto. Jimenez, 8.40798 - 83.32791, 170m, 7.v.2010, J. Longino, #JTLC6901.29 CASENT 0612004 (1 queen) [JTLC]; +30m 170m, 7.iii.2010, J. Longino #JTL6901.21 CASENT0611998 (1 worker) [DZUP].

**HONDURAS: Gr. a Dios:** Las Marias, 15.66442° -84.85764°, 60m, 8.vi.2010, LLAMA, #Wa-C-07-1-25 CASENT0612324 (1 worker) [JTLC];



**FIGURE 10.** *Probolomyrmex boliviensis* (queen - DZUP 549760). A. Habitus. B. head in frontal view. C. dorsal view.

15.66538 -84.85738 +20m 60m, 8.vi.2010, LLAMA#Wa-C-07-1-47 CASENT0612331 (1 queen) [DZUP]. **PANAMA: Canal Zone:** Barro Colorado Island: 21.vi.1961, R.W & W. Taylor, Rotten branch 3" diameter forest floor (3 workers) [MCZ]; Det. Taylor, 1964 CASENT0101757 (1 worker) [MHNG]; Mekou 064007, Det. R. W. Taylor, 1965 (1 worker) [NMNH]; Rdep, 5.v.1983, D. Wheeler, Berlese (1 worker) [MCZ]; LN 9°9' LW 079°51' 20–50m, v–viii.2007, J.Z.Shik (2 workers) [DZUP]; Mekou 064008 (1 worker) [MZSP]; Mekou 064414 (1 worker) [MZSP]; **Panamá Prov.:** Gamboa/Pipeline. Rd - 2km past Rio Frijoles, 72m, 25.v.2002, C.J. Marshall, CJM020525-01-LS02 Litter sample, Det. J. Sosa 2003 00411652USNM (2 workers) [NMNH]; **Colón Province:** San Lorenzo Forest, 9°17'N 79°58'W, 30.xi.2004, Dejean, Orivel, Corbara, Aberlac, Leponce, W12634 Winkler (1 worker) [CPDC]; W12634 (1 worker) [MPEG]; W12348 (1 worker) [CPDC]; W12351 (1 worker) [CPDC]. **PERU: Madre de Dios:** Reserva Nacional Tambopata/ Centro Sachavacayoc, 12°51'21"S 69°21'43"W 210 m, 19–31.vii.2012, J. Lattke col, Curso hormigas, (1 worker) [DZUP]; Los Amigos Field Station, 70°6'3.1"W 12°34'8.4"S 277m, 6.x.2004, T.R. Schultz, C. Marshall, J. Sosa-Calvo, JSC041006-16, TRS041006-01-LS-16 Trail 6 - 1° forest litter sample, USNM 00446594 (2 workers) [NMNH]; Cuzco Amazonico: 15 km NE of Puerto Maldonado - Tambopata Prov., 200m, 22.vi.1989, S.P. Cover & J. Tobim, CA - 386/MUSM-ENT0200711 Terra firme forest, plot1U15, rotten chunk of wood 1/2 buried in soil, (1 worker) [MUSM]; 100m, (4 workers) [MCZ]; CA 892 (1 worker) [MCZ]; 220m, CASENT0102223 (1 worker) [BMNH].

### ***Probolomyrmex brujitae* Agosti, 1995**

(Figs. 11, 12, 13)

**Holotype: ARGENTINA: Salta:** Aguas Blancas - Yaculica, 22°43'44"S 64°22'25"W, 25.x.1994, D. Agosti & J. M. Carpenter, Winkler Yungas forest, leaf-litter, 35469 (worker) [MCZ] [examined].

**Paratype:** same data as holotype, except: ATNC6044 (1 queen) [AMNH] [examined by images in [www.antweb.org](http://www.antweb.org); specimen CASENT0104672].

**Diagnosis:** Postero-ventral lobe of petiole long and subquadrate. Subpetiolar process weakly developed and anteriorly directed. Prora and protuberance on posterior region of first gastral tergite absent.

**Worker measurements:** (n=12) HL 0.48–0.56; HW 0.30–0.33; SL 0.28–0.33; WL 0.61–0.70; PL 0.22–0.34; PW 0.24–0.26; PH 0.20–0.24; TL 2.17–2.41; CI 56.5–64; SI 56.5–64.5; PI 75.5–92.5.

**Worker description:** Frontoclypeal shelflike projection and mandibles foveolate, with hair-bearing tubercles or cylindrical micro-pegs; external surface of mandibular basal margin transversely striolate (Fig. 11B – esm). Tip of apical antennal segment bearing minute pits (Fig. 11C – Ap). Mesopleuron, metapleuron and lateral faces of propodeum alveolate and foveate; alveoli denser just above metapleural gland orifice; opening of metapleural gland narrow, with smooth anterior region, surrounded by rows of hairs (Fig. 11D). Petiolar node foveate, interval between foveae covered by micropunctures (punctulae); postero-ventral lobe and latero-ventral region of petiole alveolate, with short hair projecting from each alveolus; subpetiolar process alveolate (Fig. 11E). Posterior region of second gastral segment with foveae.

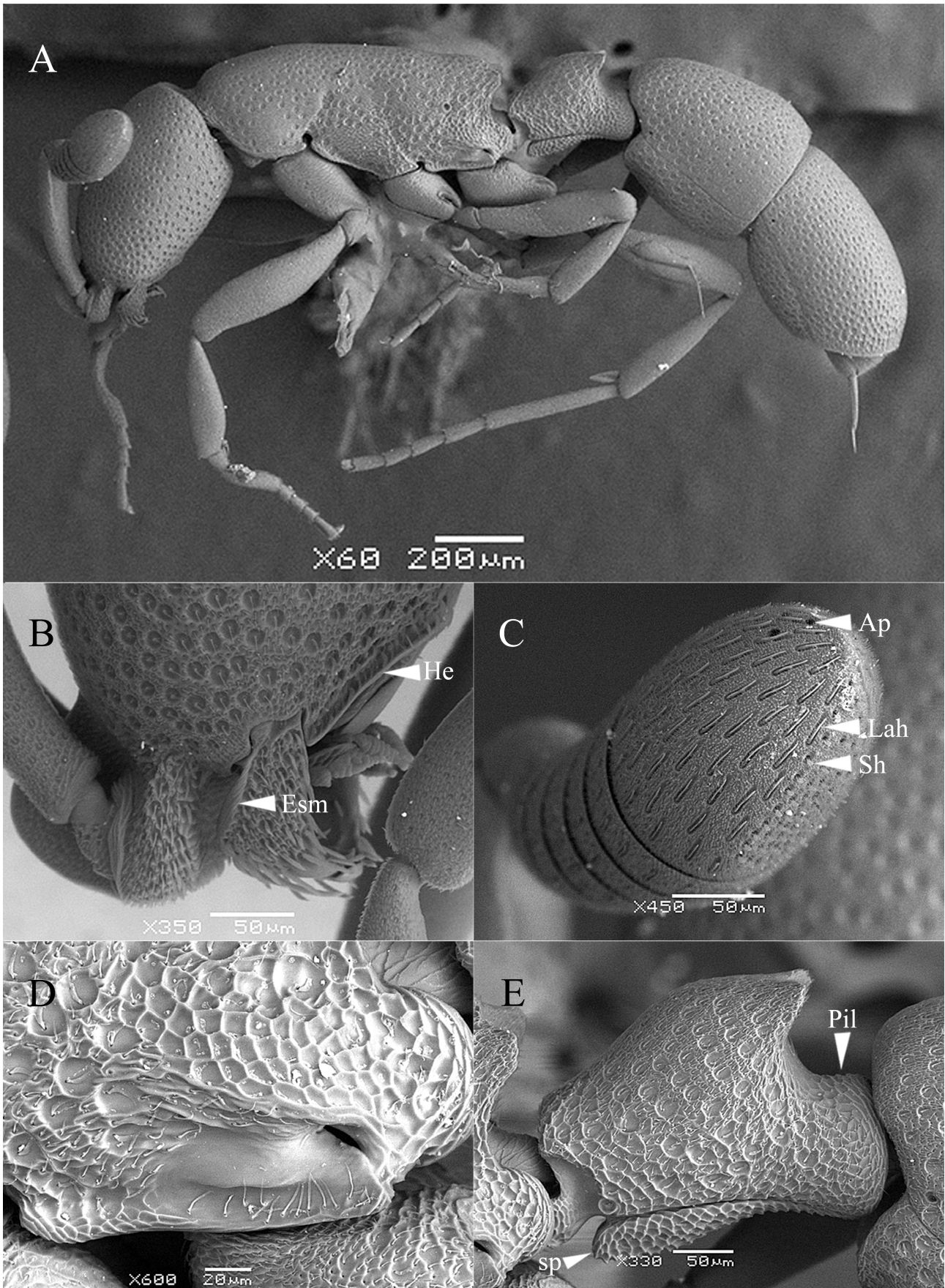
Space between mesosomal foveae covered by dense pubescence. Pygidium with hair-bearing tubercles or cylindrical micro-pegs.

Head 1.6 times longer than wide (Fig. 12B). Hypostomal margin curved (Fig. 11B – he). Antennal scapes extend to head mid length, distance from scape apex to of head more than two times pedicel length (SI 56.5–64.5). Propodeal declivity with lateral carina, laterodorsal teeth present. Petiole in lateral view at least 1.2 times longer than high (PI 75.5–92.5), apex with two weakly developed posterior teeth; posterior face short, concave and smooth; postero-ventral lobe long and subquadrate; subpetiolar process weakly developed and directed anteriorly (Fig. 11E). First gastral segment without prora or dorsal protuberance on posterior region of tergite (Fig. 12A).

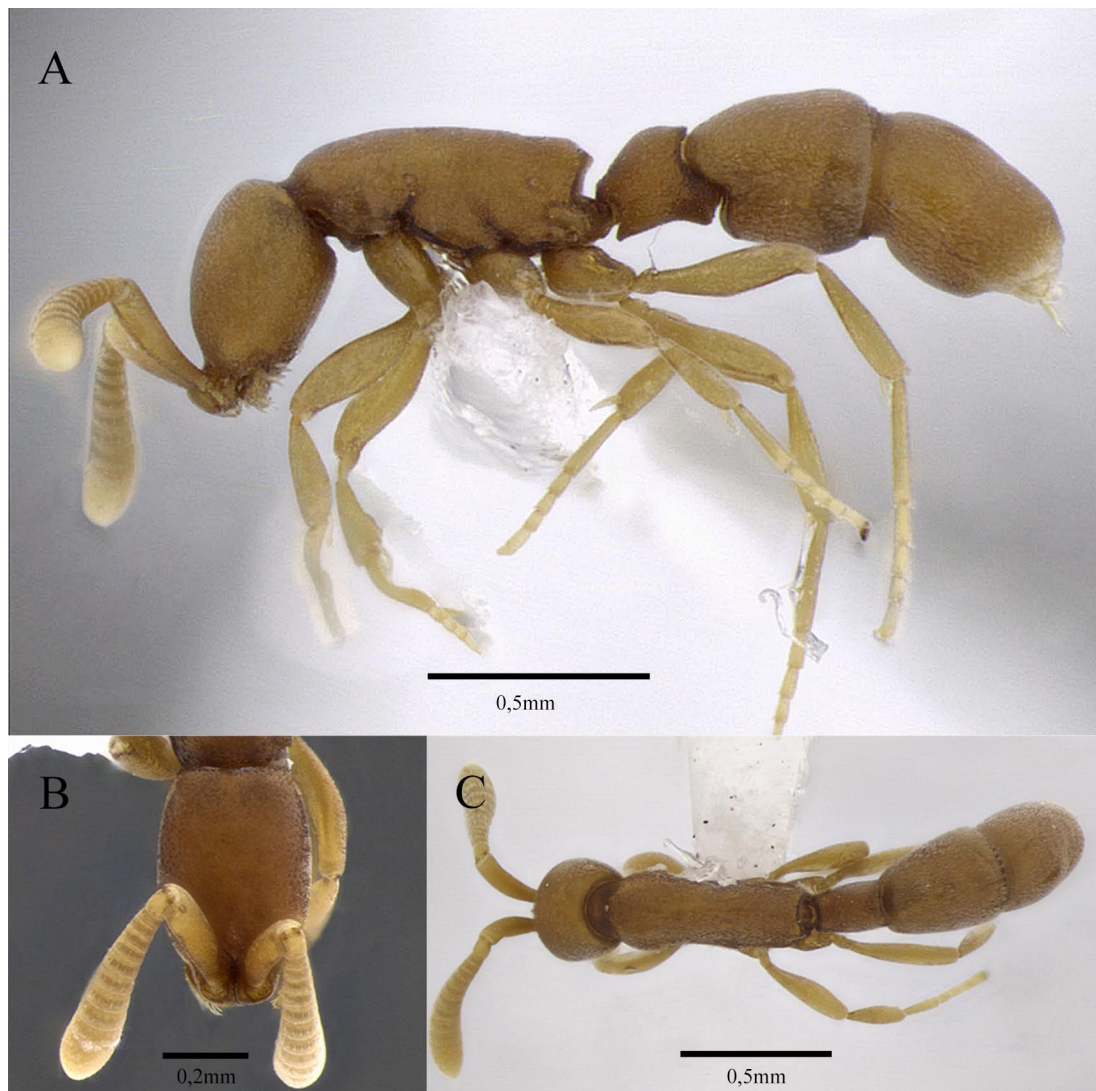
**Queen** (n=3) HL 0.50–0.52; HW 0.32–0.33; SL 0.31–0.33; WL 0.67; PL 0.23–0.25; PH 0.21–0.22; TL 2.21–2.28. CI 64.5; SI 62.5–64.5; PI 85.5–92. Queen presents the characters already described in the genus description and the diagnostic characters of the workers (Fig. 13).

**Distribution** (Fig. 29): Northwest Argentina (Salta), North and Midwest Brazil (GO, MA, MS, MT, RO, and TO).

**Comments:** This species differs from all others by the weak, anteriorly directed subpetiolar process. All specimens were obtained from leaf-litter samples. There is a record of a single individual of *P. brujitae* in Bahia, Brazil



**FIGURE 11.** SEM micrography of *Probolomyrmex brujitae* (worker - DZUP 549768). A. Habitus. B. Mandibles (he = hypostomal margin; esm = external surface of basal region of mandible). C. Antenna (ap = antennal pit; lah = long appressed hair; sh = short basicnonic hair). D. Metapleural gland. E. Petiole (pil = postero-inferior lobe of petiole; sp = subpetiolar process).

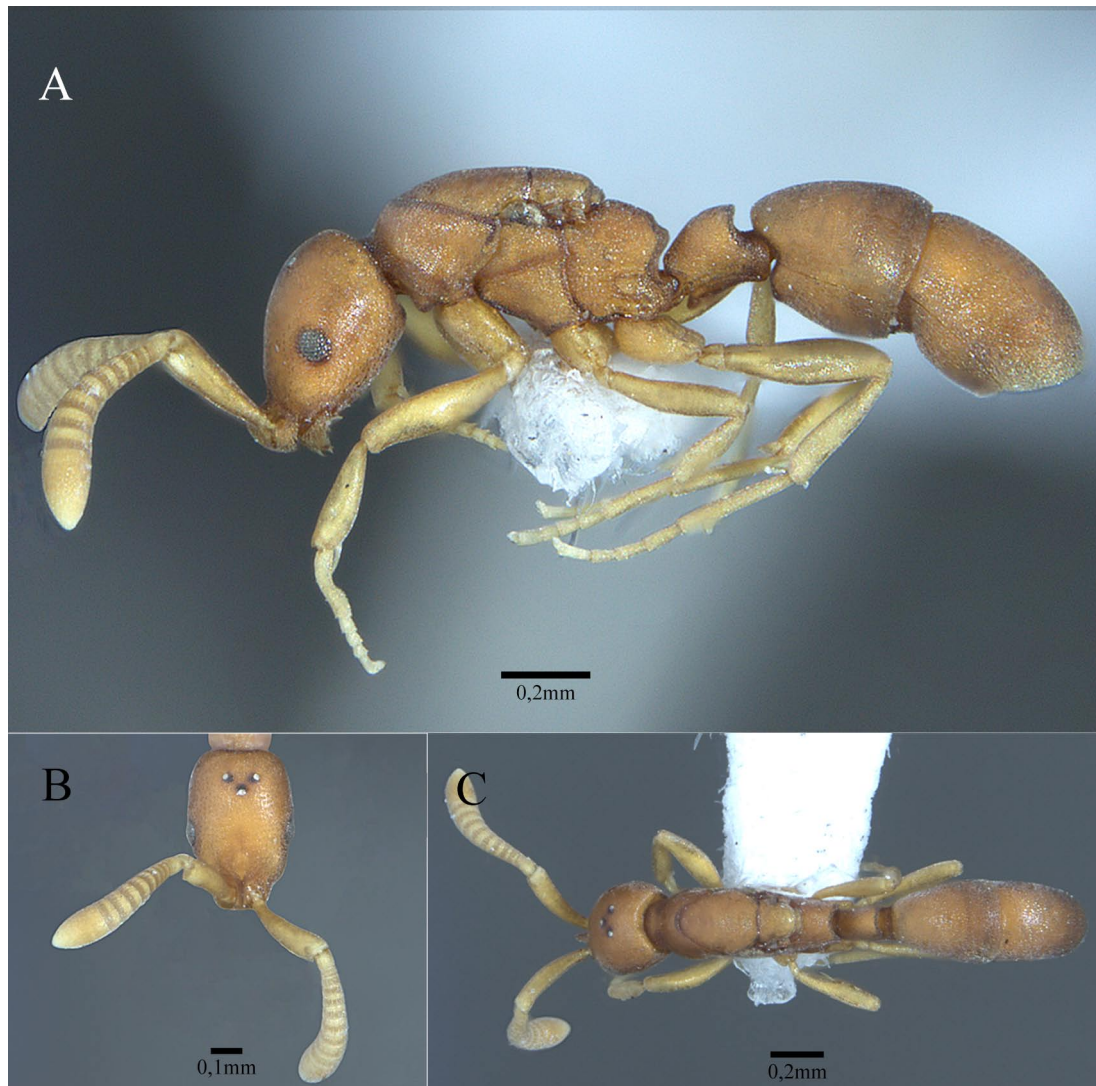


**FIGURE 12.** *Probolomyrmex brujitae* (worker - DZUP 549768). A. Habitus. B. head in frontal view. C. dorsal view.

(Nascimento *et al.* 2004). However, after careful examination of the specimen, we concluded it actually corresponds to a different and undescribed species. We refrain from describing it here, since the only known specimen is in very poor condition.

**Additional material examined (n=40): BRAZIL: Goiás:** Jataí, Faz. Ariranha, 17°57'34"S 51°51'34"W, 797m, 11.ii.2009, G.G. Santos col, Frag. 02, M. W. Ponto 23 (1 queen) [MZSP]; Faz. Leão, 17°48'24"S 51°41'41"W, 21.ii.2009, G. Santos & S. Barbosa cols, Mini-winkler Pto2 (1 worker) [MZSP]; (1 worker) [DZUP]; **Maranhão:** Estreito, Faz. Planalto, 06°35'59.3"S 47°24'50.4"W, 12–22.ii.2006, Silva R.R. & Feitosa R.M. cols, Winkler 5 (1 worker) [DZUP]; (2 workers) [MZSP]; Winkler 1 (3 workers) [MZSP]; (2 workers) [MPEG]; Winkler 2 (1 worker) [MZSP]; 12–22.vi.2006, Winkler 7 (1 worker) [DZUP]; **Mato Grosso:** Alta Floresta, 09°53'S, 56°28'W, iii–vii.2008, Castuera de Oliveira L., Winkler (1 worker - 1 queen) [MZSP]; **Mato Grosso do Sul:** Bodoquena, Fazenda Santa Laura da Vicunha I Farm, 20°47'59.94" S 56°44'54.05"W, 2010, Silvestre, R. & Demétrio, M.F. cols. (1 worker) [UFGD]; II Farm, 20°45'53.60"S 56°44'53.10" W (1 worker) [UFGD]; Campo Grande, RPPN, UFMS, 20°30'39"S 54°36'54"W, 13–19.x.2017, Tibcherani M. eq. Cols, Winkler P41 (1 worker) [MPEG]; 20–26.vii.2017, Tibcherani M. eq. Cols, Winkler P12 (1 worker) [MPEG]; Jardim, Fazenda Santa Maria da Serra, 21°25'39.24" S 56°45'48.90" W, 2010, Silvestre, R. & Demétrio, M.F. cols. (1 worker) [UFGD]; **Rondônia:** Porto Velho, Área Abunã, 09°37'33"S 65°26'38"W, 17–30.vi.2011, Albuquerque E.Z. & L.F. Silva cols, A9P2 (2 workers) [MPEG]; DZUP 549768 (1 worker– 1 queen) [DZUP]; (1 worker) [DZUP]; (3 workers) [MZSP]; 09°37'40"S 65°27'30"W, 27.iii–09.iv.2011, RR. Silva & EZ Albuquerque cols, A11P3 (1 queen) [MZSP]; Área Caiçara, 09°26'46.8"S 64°49'31.1"W, 04–18.ix.2012, Vicente R.E. & Oliveira J. cols, C3P2 (1 queen) [DZUP]; Área Mu-

tum, 09°35'07"S 65°04'15"W, 29.iii–05.iv.2012, Silva RR & Albuquerque EZ cols, M7P3, (3 workers) [MZSP]; 09°35'44"S 65°04'00"W, 27.iii–09.iv.2011, RR. Silva & EZ Albuquerque cols, M7P1 (4 workers) [MZSP]; **Tocantins:** Palmeirante, 07°52'25.3"S 47°57'07.4"W, 15–19.xii.2001, Albuquerque & Silva cols, Transecto 1, Winkler 8 - Mata ciliar-Cerradão (1 worker) [MZSP].



**FIGURE 13.** *Probolomyrmex brujitae* (queen - DZUP 549768). A. Habitus. B. head in frontal view. C. dorsal view.

***Probolomyrmex cegua* New species**

(Figs. 14, 15)

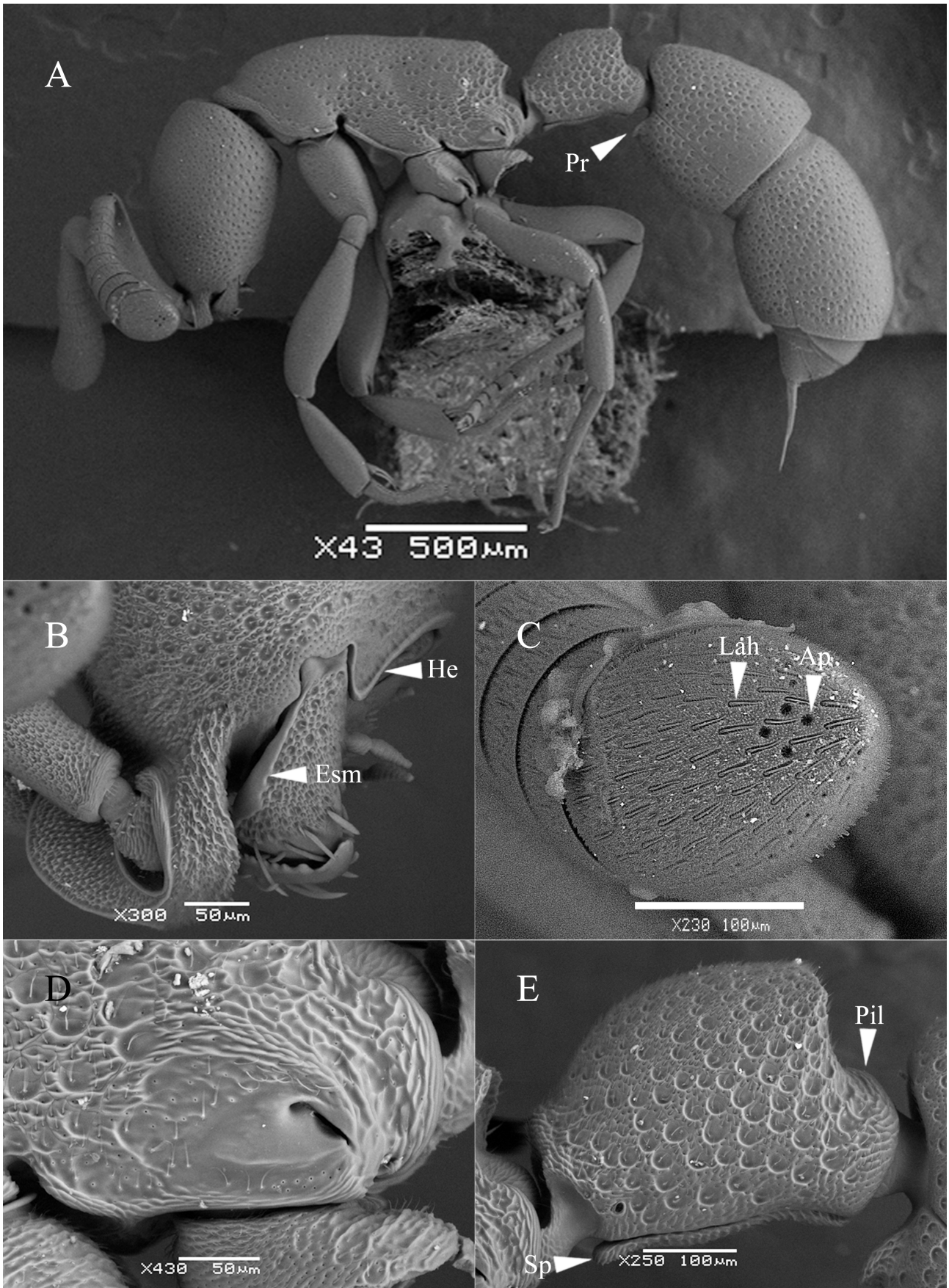
**Holotype:** NICARAGUA: **Jinotega:** RN Datanlí El Diablo, 13.09543, -85.85804, 1310m, 20.v.2011, LLAMA, #Wm-D-04-2-03, (worker) [CASC, unique specimen identifier CASENT0629220].

**Paratype:** same data as holotype, except: 13.10974, -85.86772, 1440m, 18.v.2011, LLAMA, #Wa-D-04-1-35 (1 worker) [DZUP, unique specimen identifier CASENT0629183].

**Diagnosis:** Petiole unarmed; postero-ventral lobe short and evenly rounded; subpetiolar process weakly developed. Prora present; dorsal protuberance on posterior region of first gastral tergite absent.

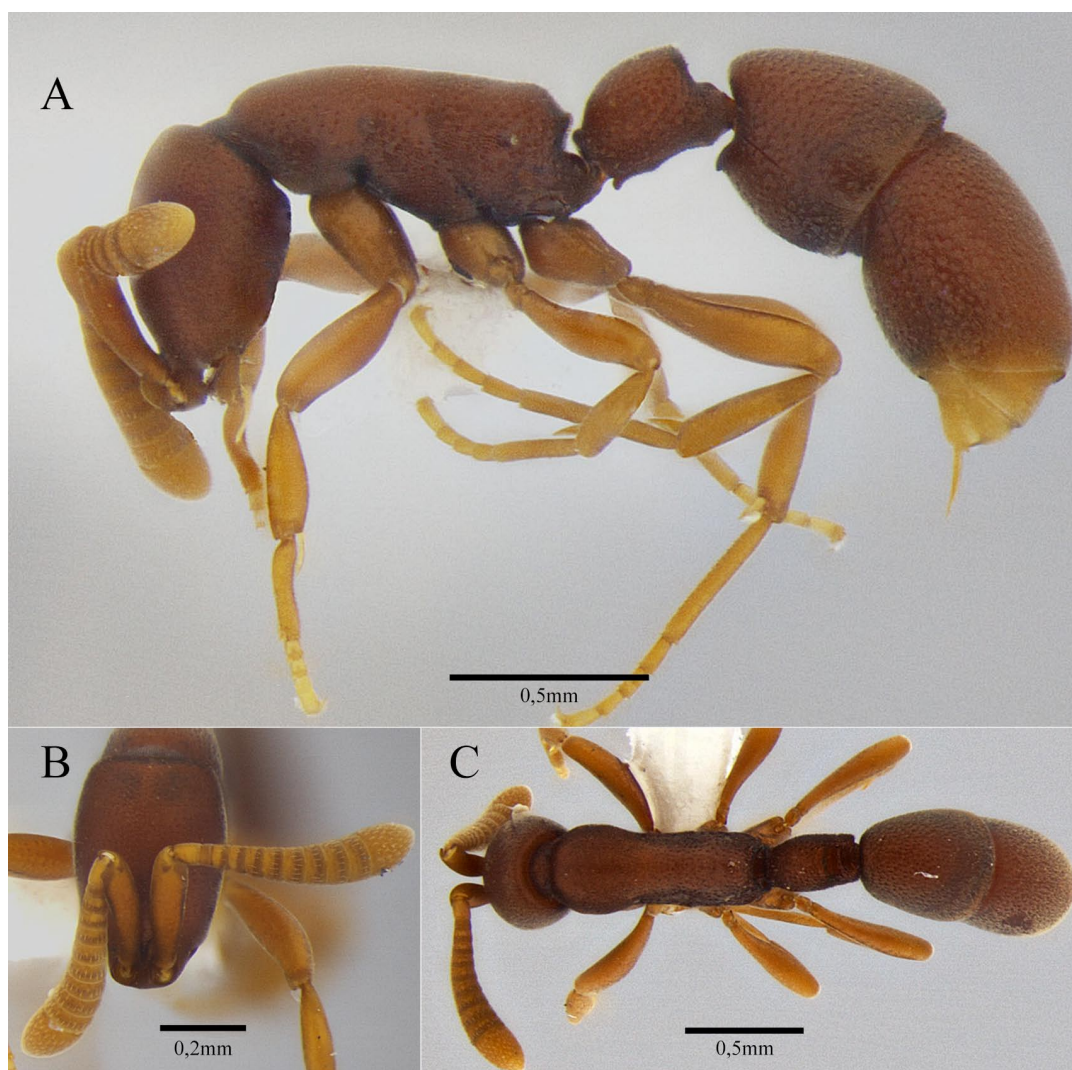
**Worker measurements:** (n=2) HL 0.67–0.69; HW 0.41–0.43; SL 0.41–0.43; WL 81–83; PL 0.35–0.37; PW 0.33–0.34; PH 0.28–0.29; TL 1.92–2.93; CI 61–62; SI 61–62; PI 77.5–78.9.

**Worker description:** Frontoclypeal shelflike projection micropunctate. Mandibles foveated, interval between the foveae covered by micropunctures; external surface of mandibular basal margin smooth (Fig. 14B – esm). Tip of apical segment of antennae bearing different sized pits (Fig. 14C – Ap). Mesopleuron, metapleuron and lateral faces of propodeum alveolate and foveated; alveoli denser just above metapleural gland orifice; opening of metapleural



**FIGURE 14.** SEM micrography of *Probolomyrmex cegua* sp. n. (holotype worker). A. Habitus (pr = prora). B. Mandibles (he = hypostomal margin; esm = external surface of basal region of mandible). C. Antenna (ap = antennal pit; lah = long appressed hair). D. Metapleural gland. E. Petiole (pil = postero-inferior lobe of petiole; sp = subpetiolar process).





**FIGURE 15.** *Probolomyrmex cegua* sp. n. (holotype worker). A. Habitus. B. head in frontal view. C. dorsal view.

gland narrow, with a smooth anterior region, surrounded rows of hairs (Fig. 14D). Petiolar node and postero-ventral lobe of petiole with incomplete foveae and micropunctures; subpetiolar process and latero-ventral region of petiole alveolate (Fig. 14E). Posterior region of second gastral segment with foveae.

Space between mesosomal foveae covered by dense pubescence. Pygidium with dense pubescence.

Head 1.6 times longer than wide (Fig. 15B). Hypostomal margin curved (Fig. 14B – he). Antennal scapes extend to head midlength, distance from scape apex to of head more than two times pedicel length (SI 61–62). Propodeum emarginated posteriorly on each side by a narrow carina, with teeth at their apices. Petiole 1.3 times longer than high (PI 77.5–78.9), without projections of any kind; posterior face short, straight, and smooth; postero-ventral lobe short, evenly rounded; subpetiolar process weakly developed (Fig 14E). First gastral segment with prora; dorsal protuberance on posterior region of tergite absent (Figs. 14A, 15A).

**Etymology:** The name refers to a folkloric figure from Nicaragua, known as *La Cegua*. She is a woman that walks through the woods and back roads, attracting drunk and unfaithful men and asking them for a ride. She poses as a beautiful lady so, men give her a ride, but when they turn around, instead of beholding the enchanting companion, they see a monster with the skull of a horse and fiery red eyes. The words she speaks to these men are so horrific that the victim goes insane instantaneously and never recovers (Janzen, 2012). The name is applied here as a noun in apposition.

**Distribution** (Fig. 28): Nicaragua (Jinotega).

**Comments:** *Probolomyrmex cegua* is similar to *P. lamellatus* sp. n., but has propodeal angles, absent in *P. lamellatus* sp. n., and the postero-ventral lobe of the petiole is rounded.

Specimens come from Reserva Natural Datanlí El Diablo, which is a patchy matrix of private coffee farms

and primary and secondary cloud forests. The holotype was obtained from a sifted leaf-litter sample collected in a primary cloud forest, with many large oak trees and abundant tree ferns. The paratype was also found in a leaf litter sample from a montane wet forest, near coffee and agricultural clearings. Both localities are above 1300 meters of altitude.

***Probolomyrmex dentinodis* New species**

(Figs. 16, 17, 18)

*Probolomyrmex petiolatus*: Delabie *et al.* 2001 (misidentification).

**Holotype:** BRAZIL: Rondônia: Porto Velho, Área Caiçara, 09°26'14.6"S 64°49'58.2"W, 04–18.ix.2012, Vicente R.E. & Oliveira J. cols, C1P2, (worker) [DZUP, unique specimen identifier DZUP 549762].

**Paratype:** same data as holotype, except: (1 worker) [MZSP, unique specimen identifier DZUP 549769].

**Diagnosis:** Petiole higher than long, with the petiolar teeth well developed and forming a conspicuous posterior bifurcation in dorsal view. Subpetiolar process well developed and subrectangular. Prora present. First gastral tergite with a dorsal protuberance on the posterior region.

**Worker measurements:** (n=8): HL 0.57–0.61; HW 0.35–0.39; SL 0.36–0.44; WL 0.74–0.89; PL 0.23–0.30; PW 0.15–0.19; PH 0.26–0.33; GL 0.94–0.96; TL 2.63–2.74; CI 61.5–64.5; SI 61.5–73.5; PI 106.5–128.5.

**Worker description:** Frontoclypeal shelflike projection and mandibles with hair-bearing tubercles or cylindrical micro-pegs; external surface of mandibular basal margin transversely micro-striate (Fig. 16B – esm). Tip of apical segment of antennae bearing minute pits (Fig. 16C – Ap). Mesopleuron, metapleuron and lateral faces of propodeum alveolate; alveoli denser just above metapleural gland orifice; opening of metapleural gland large, with smooth anterior region, surrounded by rows of hairs (Fig. 16D). Petiolar node with incomplete foveae, postero-ventral lobe of petiole and subpetiolar process alveolate, each alveolus with an inner decumbent hair; latero-ventral region of petiole imbricate (Fig. 16E). Posterior region of second gastral tergite with transversal rows of deep rounded pits (Fig. 16A).

Space between the foveae on the mesosoma covered by dense pubescence. Pygidium with hair-bearing tubercles or cylindrical micro-pegs and some long and thick hairs.

Head 1.6 times longer than wide (Fig. 17B). Hypostomal margin curved (Fig. 16B – he). Antennal scapes extend to head midlength, distance from scape apex of head more than two times pedicel length (SI 61.5–73.5). Propodeum emarginated posteriorly on each side by a low and obtuse carina, with teeth at their apices. Petiole at least 1.1 times higher than long (PI 106.5–128.5), with postero-dorsal teeth forming a conspicuous bifurcation in dorsal view; posterior face long, concave and smooth; postero-ventral lobe short and rounded; subpetiolar process well developed and subrectangular, with the postero-ventral angle acute and directed towards the gaster (Fig. 16E). First gastral segment with prora and a dorsal protuberance on posterior region of tergite, characterized by a gentle elevation of the integument (Figs. 16A, 17A).

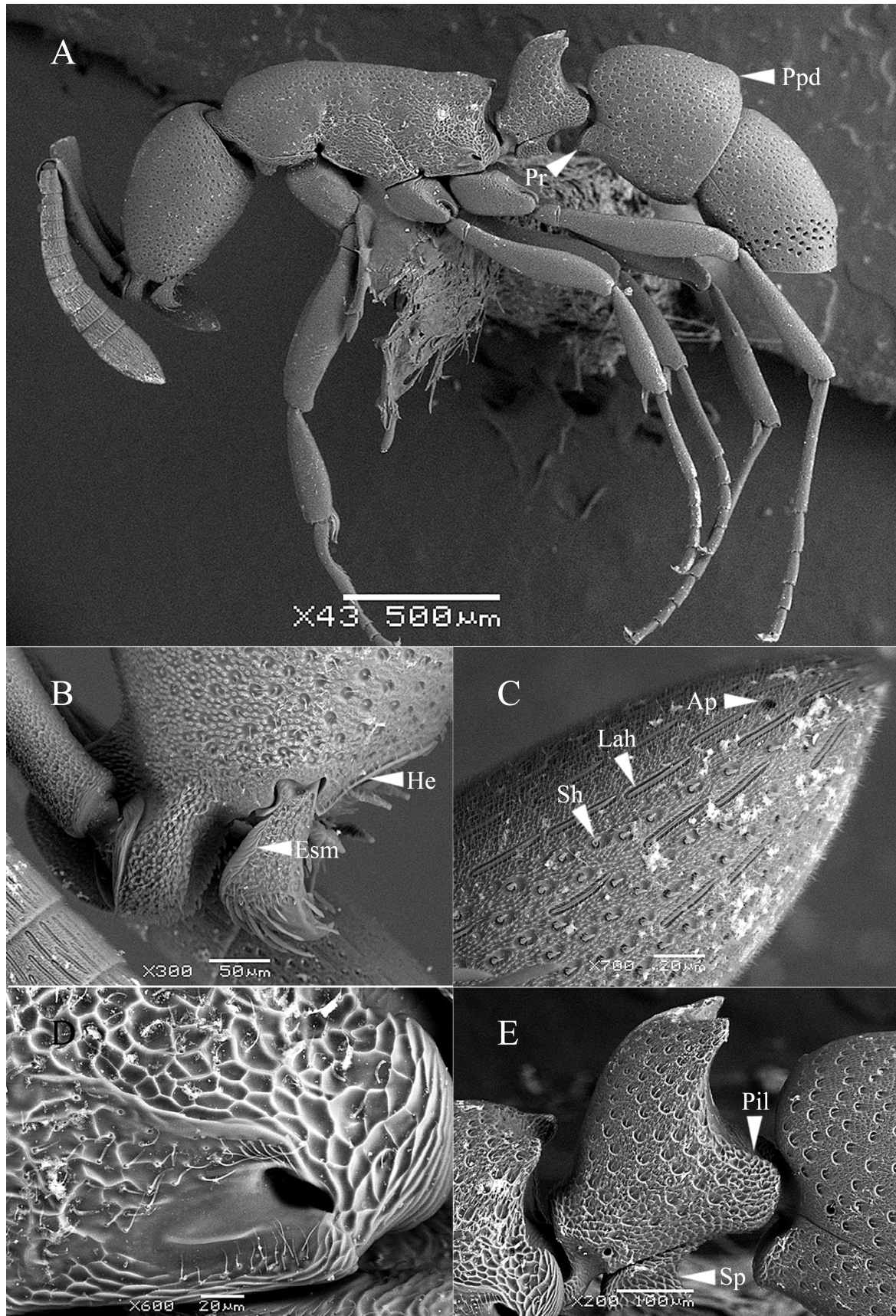
**Queen:** (n=2): HL 0.59–0.62; HW 0.39; SL 0.39–0.42. WL 0.80–0.87; PL 0.26–0.28; PH 0.30–0.32 GL 0.96–1.07; TL 2.61–2.84. CI 62–65; SI 65–67; PI 114–116. Queen presents the characters already described in the genus description and the diagnostic characters of the species (Fig. 18).

**Etymology:** The name is a reference to the presence of a pair of well developed postero-dorsal teeth on the petiolar node.

**Distribution** (Fig. 29): Northern Brazil (PA, RO, and TO).

**Comments:** The subrectangular shape of the subpetiolar process makes this species similar to *P. petiolatus*. However, *P. dentinodis* can be easily distinguished from the latter by the presence of a pair of propodeal and petiolar teeth and by the presence of the prora. All the specimens obtained came from leaf-litter samples collected in mature lowland Amazon forests (40m and 200m).

**Additional material examined (n=12): BRAZIL: Pará:** Alter do Chão, 2°30'S 54°57'W, 1.vii.1998, J.M. Vilhena, D. Agosti det. (1 worker) [CPDC]; Marituba, 1°22'S 48°20'W, 19.x.2004, Santos J.R.M., Winkler Cacau (2 workers) [CPDC]; (1 worker) [MPEG]; DZUP 549770 (queen) [DZUP]; **Tocantins:** Palmeiras do Tocantins, 06°40'12"S 47°31'48.6"W, 01–09.vi.2005, Silva R.R. & Feitosa R.M. cols (1 queen) [DZUP]; (1 worker) [MZSP]; 06°40'07"S 47°30'56" W, 12–22.vi.2006, Silva R.R. & Feitosa R.M. cols Winkler 12 (1 worker) [DZUP]; (1 worker) [MZSP].



**FIGURE 16.** SEM micrography of *Probolomyrmex dentinodis* sp. n. (holotype worker). A. Habitus (pr = prora; ppd = dorsal protuberance in the posterior region of the first gastral tergite). B. Mandibles (he = hypostomal margin; esm = external surface of basal region of mandible). C. Antenna (ap = antennal pit; Lah = long appressed hair; Sh = short hair). D. Metapleural gland. E. Petiole (pil = postero-inferior lobe of petiole; sp = subpetiolar process).

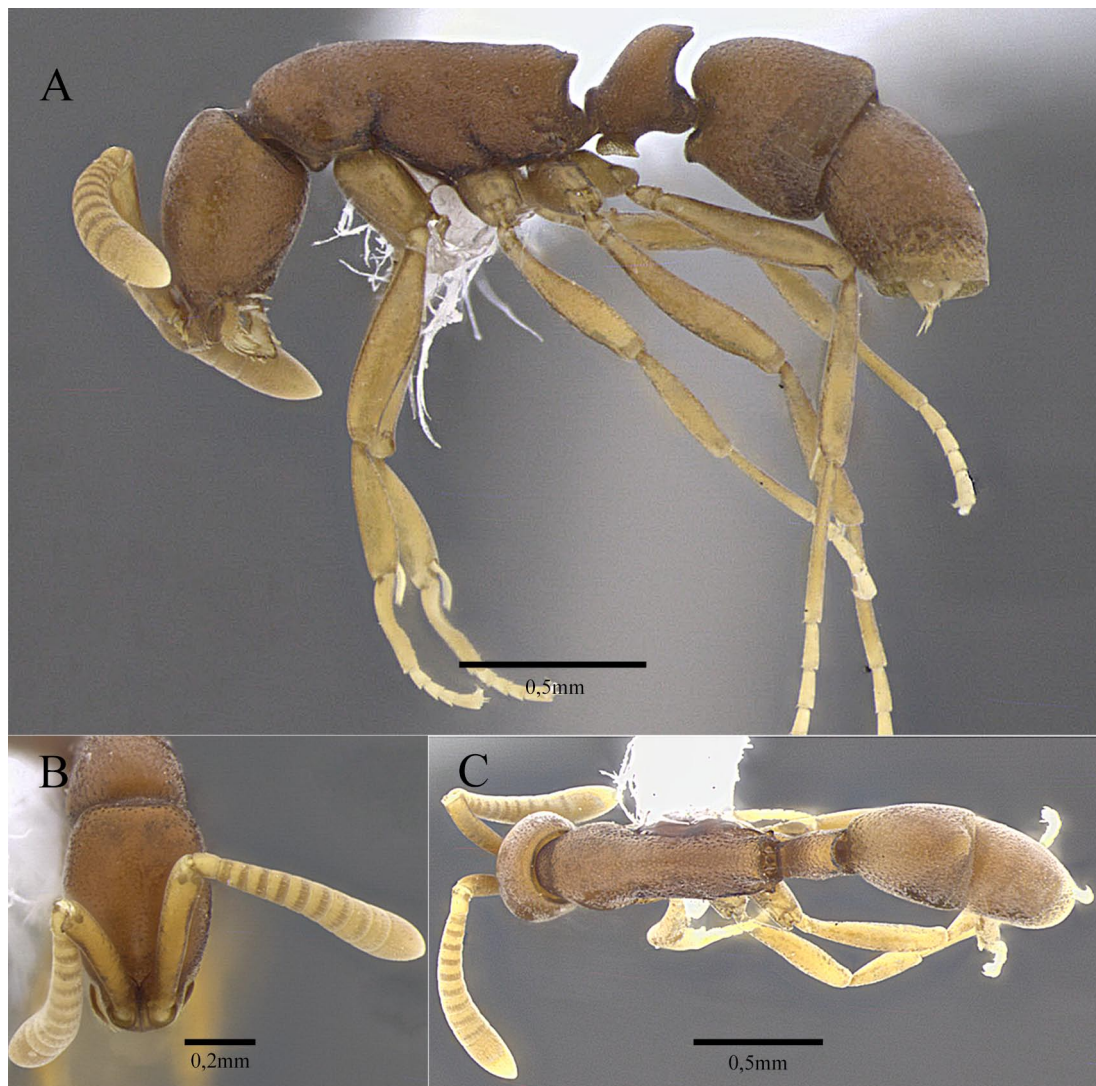


FIGURE 17. *Probolomyrmex dentinodis* sp. n. (paratype worker). A. Habitus. B. head in frontal view. C. dorsal view.

***Probolomyrmex guanacastensis* O’Keefe & Agosti, 1998**

(Fig. 19)

**Holotype:** COSTA RICA: Guanacaste, 8.5 km NW Bagaces: Plazuela Hacienda Monteverde, 31.viii.1996, S. O’Keefe, sift leaf debris (worker) [AMNH] [not examined].

**Paratype:** same data as holotype, except: (1 ergatoid queen) [examined by images in [www.antweb.org](http://www.antweb.org); specimen CASENT0104673].

**Diagnosis:** Postero-ventral lobe of petiole short and rounded. Subpetiolar process weakly developed. First gastral segment with prora and a dorsal protuberance on the posterior region of gaster.

**Worker measurements (from original description):** (n=1) HL 0.65; HW 0.39; SL 0.41; WL 0.79; CI 0.60; SI 106.

**Worker description:** similar to ergatoid queen (described below), except by the absence of eyes and ocelli.

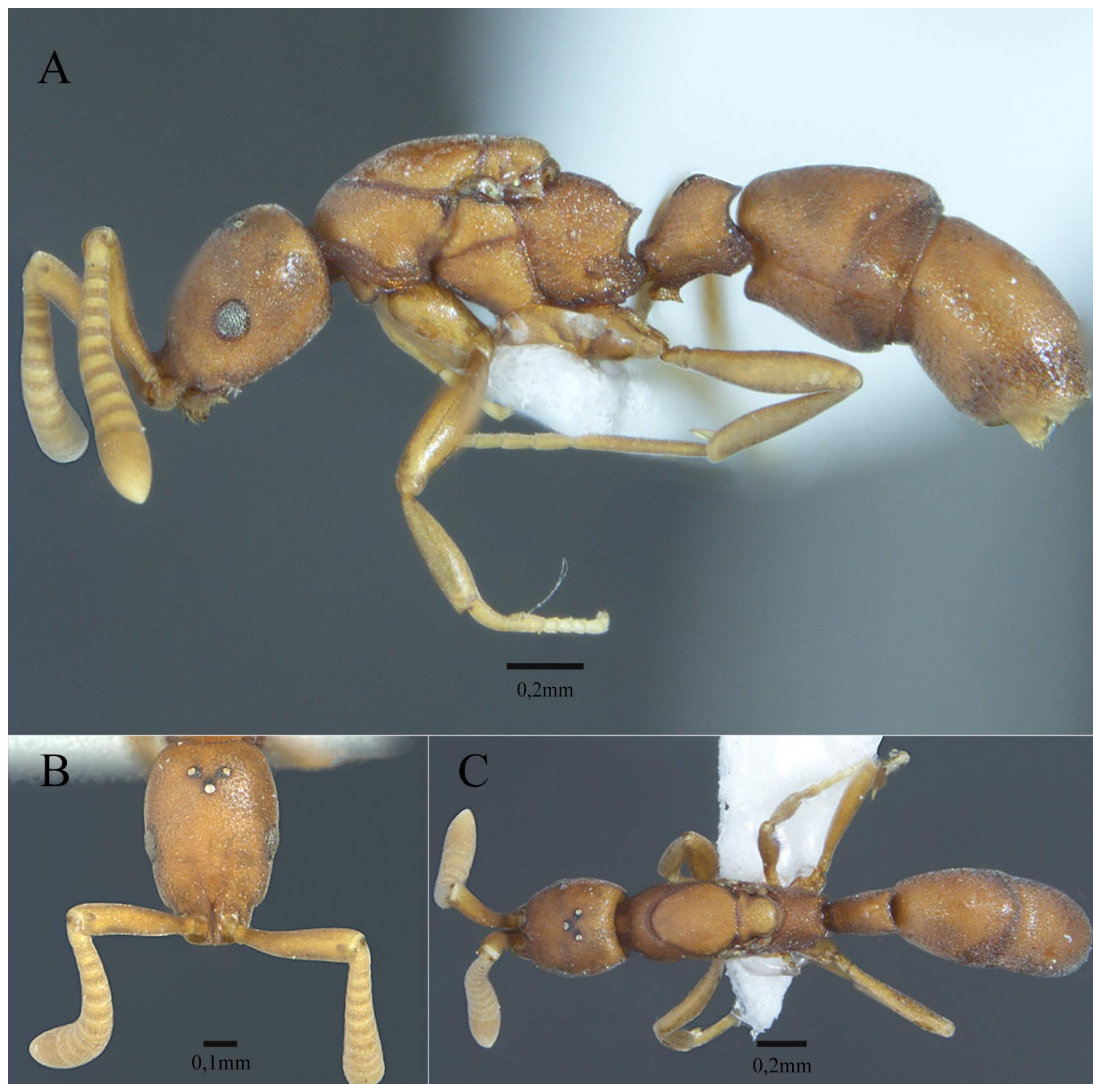
**Ergatoid queen measurements (from original description):** (n=1) HL 0.63; HW 0.41; SL 0.40; WL 0.81; CI 65; SI 63.5.

**Ergatoid queen description:** Head 1.6 times longer than wide (Fig. 19B). Antennal scapes extends beyond head midlength, distance from scape apex to of head more than two times pedicel length (SI 63.5). Compound eyes and three equally sized ocelli present. Propodeal declivity laterally with narrow carina, dorsolateral teeth present, almost in same plane as dorsal profile of the propodeum in lateral view. Petiole longer than high, without teeth;

anterior face of petiolar node long and inclined; posterior face short and concave; postero-ventral lobe short and rounded; subpetiolar process weakly developed (Fig. 19A). First gastral segment with prora and dorsal protuberance on posterior region of tergite, characterized by gentle elevation of the integument (Fig. 19A).

**Distribution** (Fig. 28): Costa Rica (Guanacaste).

**Comments:** *Probolomyrmex guanacastensis* is similar to *P. boliviensis* but is smaller and has shorter antennal scapes. This species has been collected in sifted debris processed through a modified Berlese-Tulgren funnel from riparian habitat in Costa Rica. This is the only record of an ergatoid queen in this genus. The presence of an ergatoid queen in *Probolomyrmex* is unexpected, because species with ergatoid queens normally have large colonies (Peeters, 1997). It is noteworthy that the term “ergatoid” was applied here by the authors of the species. It remains to be confirmed if the specimen was in fact a reproductive female.



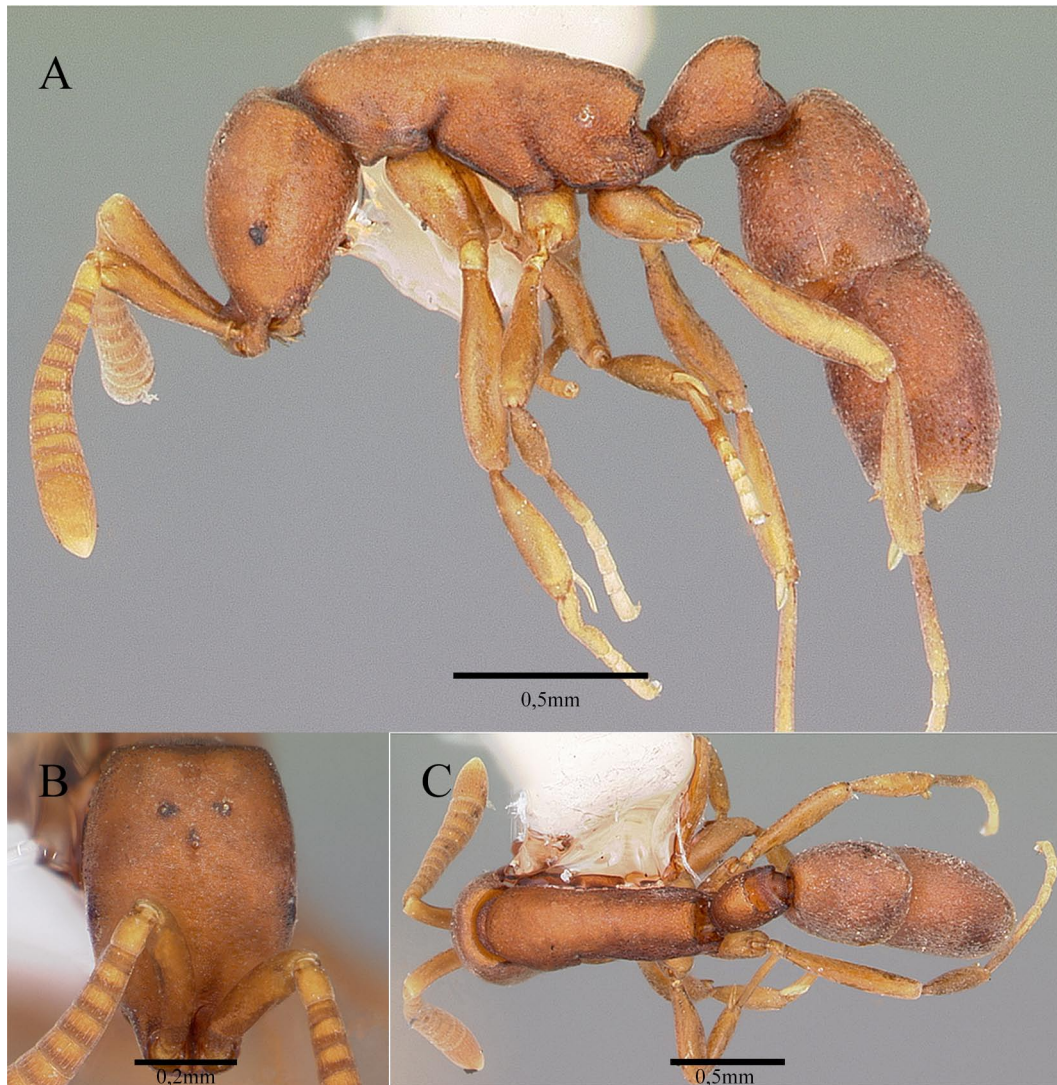
**FIGURE 18.** *Probolomyrmex dentinodis* sp. n. (queen - DZUP 549770). A. Habitus. B. head in frontal view. C. dorsal view.

### *Probolomyrmex kelleri* New species

(Figs. 20, 21, 22, 23)

**Holotype:** VENEZUELA: Lara: Finca Sta. Maria 3.8km, ESE Barbacoas, 9°49'N 70°2'W, 26.xii.2005, J. Latke col 2978 (worker) [DZUP, unique specimen identifier DZUP 549763].

**Paratype:** same data as holotype, except: (1 worker) [DZUP, unique specimen identifier DZUP 549764]; (1 queen) [DZUP, unique specimen identifier DZUP 549765]; (1 male) [DZUP, unique specimen identifier DZUP 549766]; 2978 (1 worker) [MZSP]; 2978 (1 worker) [MIZA].



**FIGURE 19.** *Probolomyrmex guanacastensis* (queen - CASENT0104673). A. Habitus. B. head in frontal view. C. dorsal view.

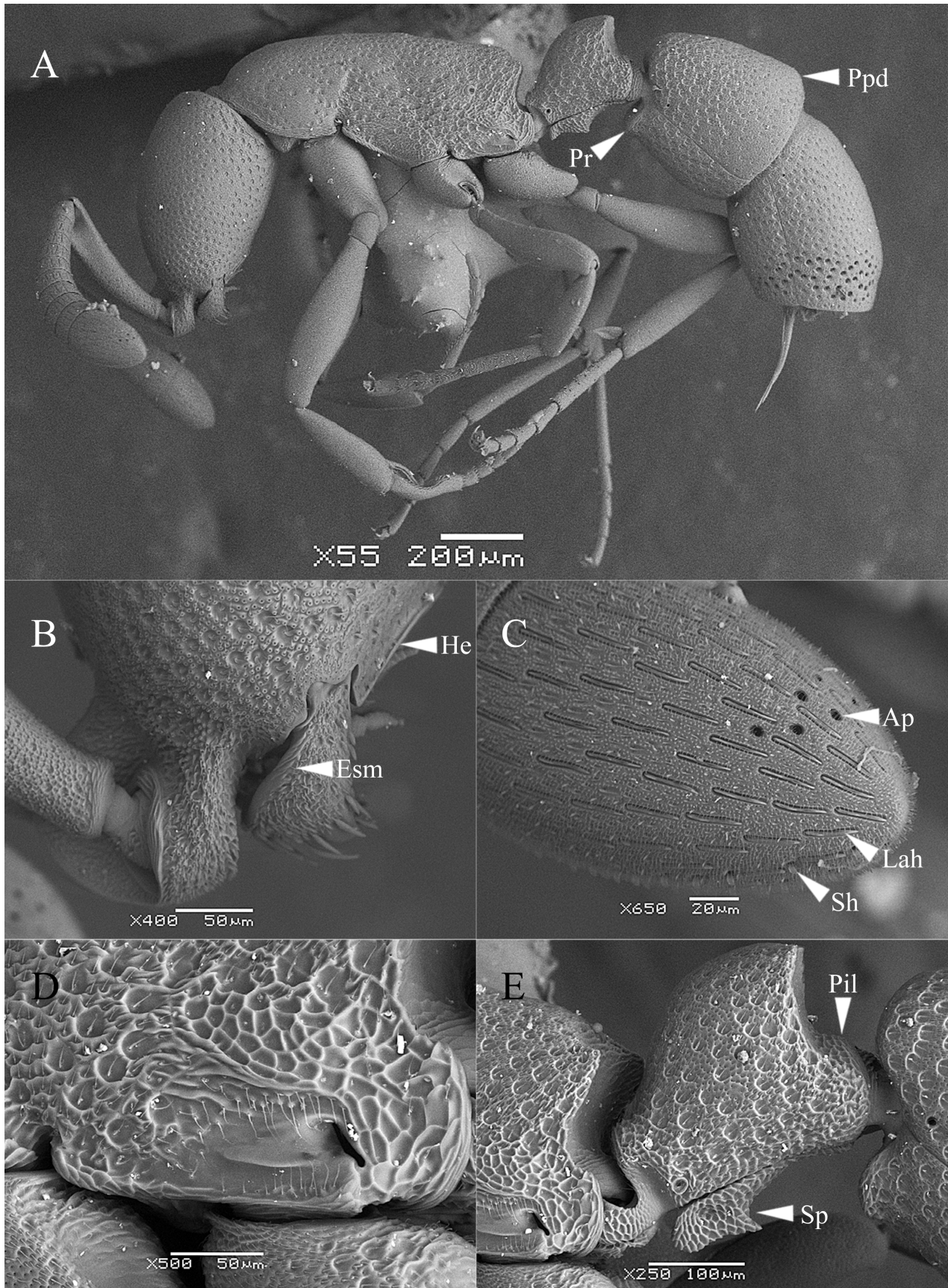
**Diagnosis:** Postero-ventral petiolar lobe short and rounded. Subpetiolar process well developed, ventrally concave to subrectangular, with the postero-ventral angle acute and directed towards the gaster. Prora and protuberance on the posterior region of the first gastral tergite present.

**Worker measurements:** (n=8) HL 0.57–0.64; HW 0.35–0.40; SL 0.35–0.41; WL 0.70–0.78; PL 0.25–.28; PW 0.28–0.34; PH 0.25–0.30; TL 1.96–2.62; CI 56.5–64.5; SI 59.5–64.5; PI 93.5–106.5.

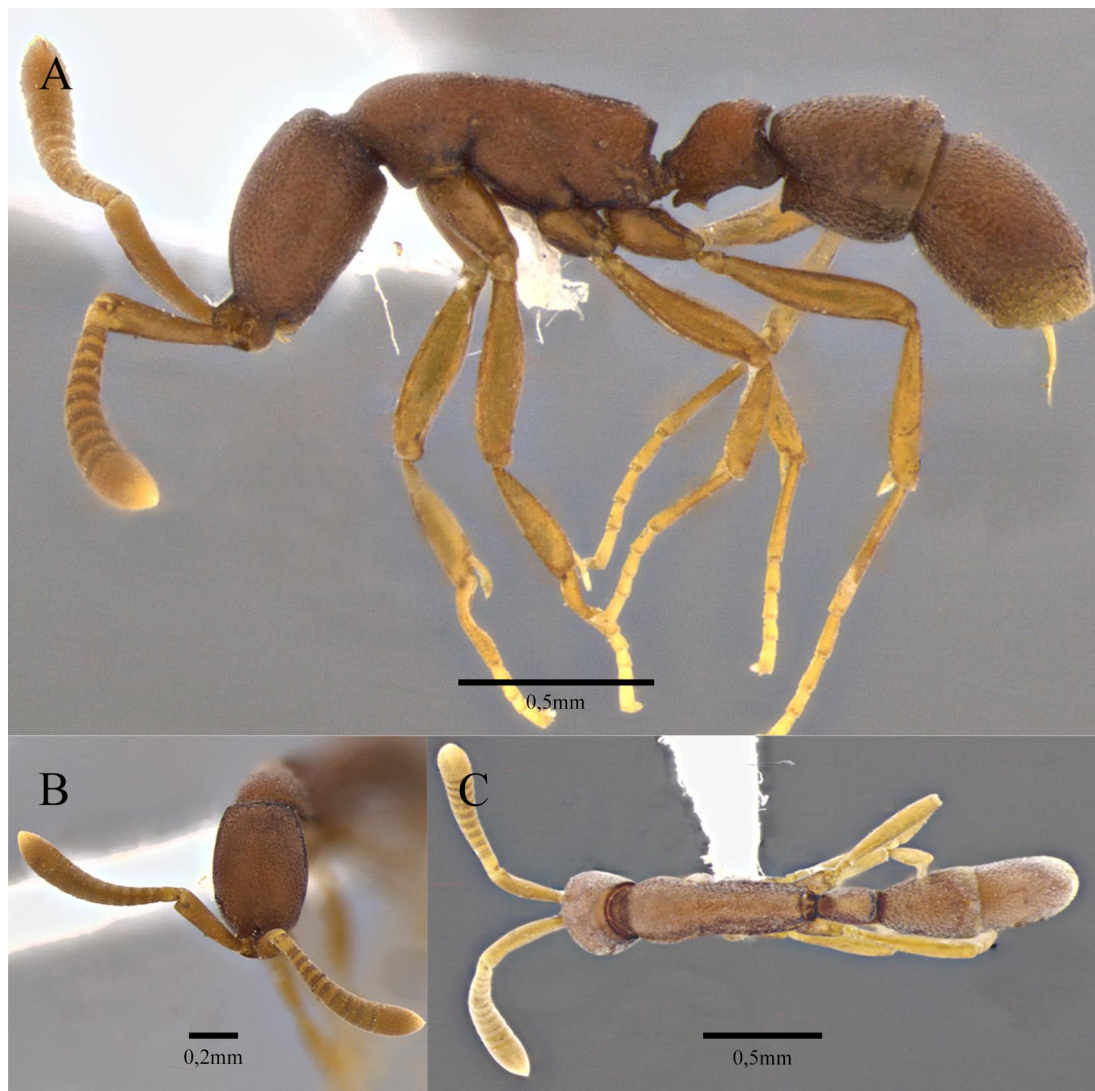
**Worker description:** Frontoclypeal shelflike projection and mandibles with hair-bearing tubercles or cylindrical micro-pegs; external surface of mandibular basal margin transversely micro-striate (Fig. 20B – esm). Tip of apical segment of antennae bearing minute pits (Fig. 20C – Ap). Mesopleuron foveated and micropunctate; metapleuron alveolate and foveated; lateral faces of propodeum foveated and micropunctate; alveoli denser just above metapleural gland orifice; opening of metapleural gland large, with a smooth anterior region, surrounded by rows of hairs (Fig. 20D). Petiolar node and postero-ventral lobe of petiole with incomplete foveae and micropunctures (Fig. 20E); subpetiolar process alveolate and latero-ventral region of petiole alveolate. Posterior region of second gastral tergite with transversal rows of deep rounded pits (Fig. 20A).

Space between mesosomal foveae covered by dense pubescence. Pygidium with dense pubescence and some long and thick hairs.

Head 1.6 times longer than wide (Fig. 21B). Hypostomal margin curved (Fig. 20B – he). Antennal scapes extend to head midlength, distance from scape apex to of head more than two times pedicel length (SI 59.5–64.5). Propodeum emarginated posteriorly on each side by a narrow carina, with teeth at their apices. Petiole as long as



**FIGURE 20.** SEM micrography of *Probolomyrmex kelleri* sp. n. (worker A, B, C, D: USNM 00412443; E: USNM 00446592.). A. Habitus (pr = prora; ppd = dorsal protuberance in the posterior region of the first gastral tergite). B. Mandibles (he = hypostomal margin; esm = external surface of basal region of mandible). C. Antenna (ap = antennal pit; lah = long appressed hair; sh = Short hair). D. Metapleural gland. E. Petiole (pil = postero-inferior lobe of petiole; sp = subpetiolar process).



**FIGURE 21.** *Probolomyrmex kelleri* sp. n. (worker - DZUP 549771). A. Habitus. B. head in frontal view. C. dorsal view.

high (PI 93.5–106.5), without teeth; posterior face long, slightly concave and smooth; postero-ventral lobe short and rounded; subpetiolar process with a projection ventrally concave (Fig. 20A) or subrectangular with the postero-ventral angle acute, directed downwards or towards the gaster (Fig. 20E). First gastral segment with prora and a dorsal protuberance on posterior region of tergite, characterized by a gentle elevation of the integument (Figs. 20A, 21A).

**Queen:** (n=4) HL 0.57–0.63; HW 0.37–0.40; SL 0.35–0.43; WL 0.78–0.85; PL 0.26–0.30; PH 0.26–0.28; TL 2.59–2.85; CI 62.5–67.5; SI 61–67; PI 93–100. With the morphological modifications described for *Probolomyrmex* queens and the diagnostic characters of the workers (Fig. 22).

**Male:** (n=1) HL 0.44; HW 0.44; SL 0.26; PL 0.19; PH 0.17; TL 1.98; CI 98; SI 58.3; PI 85.7. Scapes long, distance from scape apex to of anterior ocellus lesser than pedicel length (Fig. 23B). Propodeum without lateral carina, teeth absent, lateral surface smooth and shining (Fig. 23A). Petiole slightly longer than high, apical teeth absent. Anterior face longer than posterior face, apex rounded. Subpetiolar process weakly developed. First gastral segment with weakly developed prora and dorsal protuberance on posterior region of tergite.

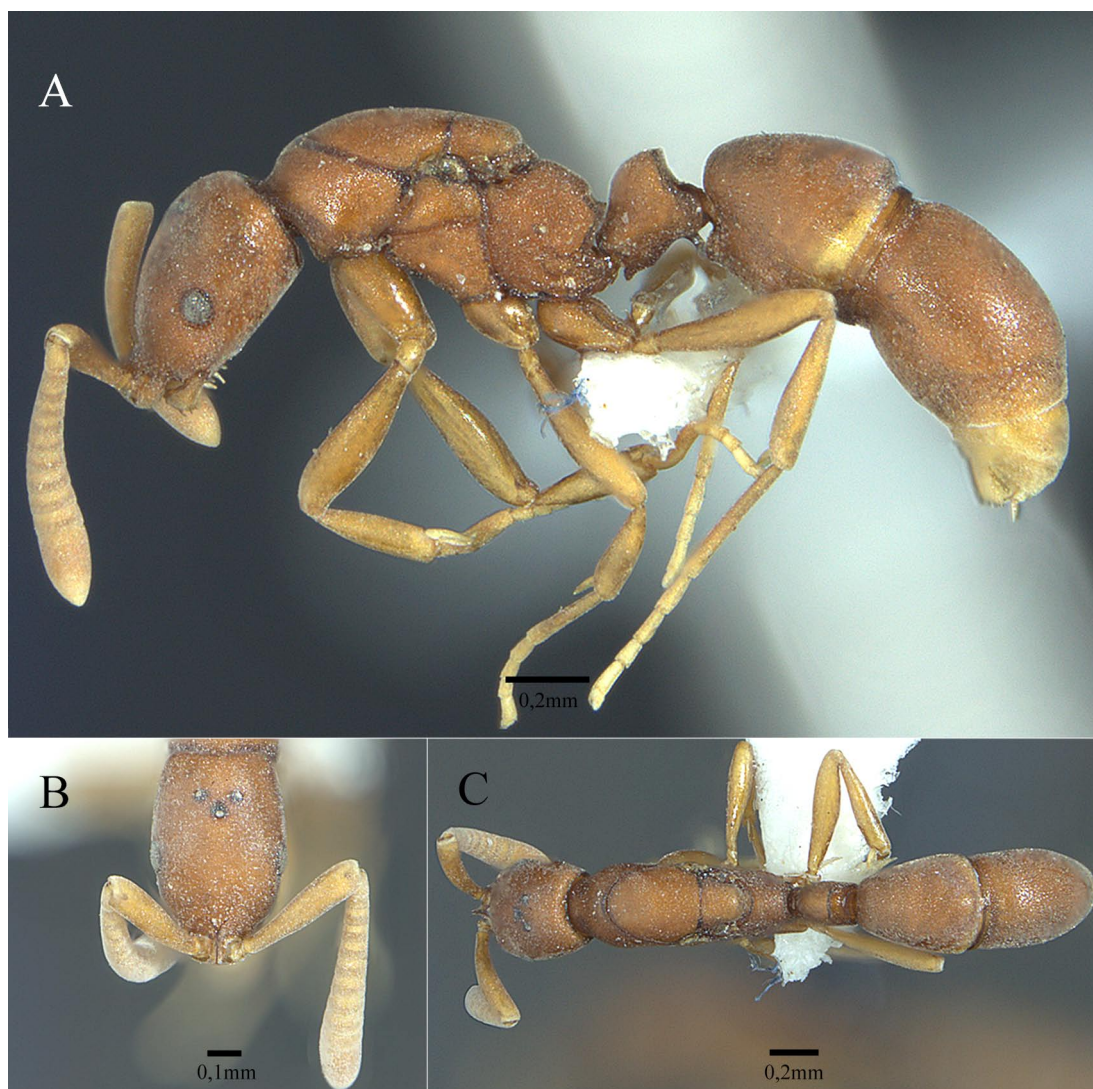
**Etymology:** This species is described in honor of Dr. Roberto Keller, prominent ant morphologist whose work has been inspiring old and new generations of myrmecologists.

**Distribution** (Fig. 28): Guyana, Peru, and Venezuela.

**Comments:** *Probolomyrmex kelleri* resembles *P. boliviensis*, but is smaller, with shorter antennal scapes and subpetiolar process well developed. An entire colony was found in an area of dry forest with much thorny scrub vegetation in Lara, Venezuela, under a stone, containing 16 workers, two queens, two males, three pupae, and 15 late



instar larvae. When uncovered, most of the ants were found clinging to the underside of the stone. They did not run away, presenting a sluggish and frozen behavior (John Lattke, unpublished data). One of these workers and another specimen from Aragua (Venezuela) have eyes formed by a unique omatite. Locality data suggests that it inhabits mesic as well as dry forests.



**FIGURE 22.** *Probolomyrmex kelleri* sp. n. (paratype queen). A. Habitus. B. head in frontal view. C. dorsal view.

**Additional material examined (n=27):** **GUYANA:** Iwokrama For. Res.: Whitewater Camp., 58°50.992'W 4°43.89N, 5.xi.2002, J.S. Lapolla *et al.*, 021105-1-LS10; JSL021105-01-LS10, 1° forest litter sample, Det. J. Sosa-Calvo USNM 00412443 (1 worker), USNM 00411949 (1 – queen) (1 worker) [NMNH]; 60m (1 worker) [DZUP]; 021105-1-LS2;JSL021105-01-LS02 (1 queen) [DZUP]; Kanuku Mountain: Moco-Moco Falls, 59°38'376''W 3°17'297''N 224m, 20.x.2002, T.R. Schultz, J. LaPolla, C. Marshall, R. Williams, JSL021020-01-LS20, Det. J. Sosa-Calvo (1 worker) [NMNH]. **PERU: Madre de Dios:** Los Amigos Field Station, 70°6'3.1''W 12°34'8.4''S 277m, 6.x.2004, T.R. Schultz, C. Marshall, J. Sosa-Calvo., JSC041006-08-TRS041006-01-LS-08 Trail 6 USNM 00446592 (1 worker) [NMNH]; 1° forest litter sample (1 queen); P. Maldonado, Sachavacayoc Centre, 12°51'15.4''S 49°22'15.9''W, 209m, 19–31.vii.2012, Feitosa R.M. & Probst R.S. cols, Winkler, folhiço (1 worker) [DZUP]. **VENEZUELA: Aragua:** Ocumare de la Costa, 10°46075'N 67°77194'W, 27m, 13.viii.2008, Ant Course, J. Lattke, Cacao plantation; (2 workers) [MIZA]; INIA (1 worker) [DZUP]; (1 worker) [MPEG]; (1 worker) [MIZA]; 10.49059 - 67.69369 10m, 20.ii.1971, S.B.Peck, #B-195 FMNH-INS 000 095 986 (1 worker) [JTLC]; P.N.H. Pittier. Valle Sta. Maria 3.8 km SSW Cumboto, Fila El viento. Bosque Seco, 10°22' N 67°49' W 615m, 31.viii.2003, E. Rodriguez, A. Grotto, J. Lattke (1 worker) [MIZA]; **Monagas:** Caripe, 10°10' N 63°30' O 1000m, 28.x.1986, J. Lattke & R. Brandão legs (1 worker) [MIZA]; **Bolívar:** Rio Cuyuni: 06°05'11.7''N 61°29'48.2''W 100m, 19.i.2008, L.E. Alonso col, Winkler 3 1° forest DZUP 549771 (1 worker) [MIZA]; **Sucre:** 30km W. Guirie, 10m, 23.vii.1987, S. & J Peck,

Floresta over cacao - litter at Sn. Antonio (1 worker) [MIZA]; T.F. Amaz.: Cerro de la Neblina Basecamp, 0°50'N 66°10'W 140m, 10-20.ii.1985, P.J. & P.M. Spangler. R.A. Faitoute. W.E. Steiner cols, Flight intercept pantrap in rainforest (1 queen) [DZUP]; D. Agosti, 1995 (1 queen) [NMNH].

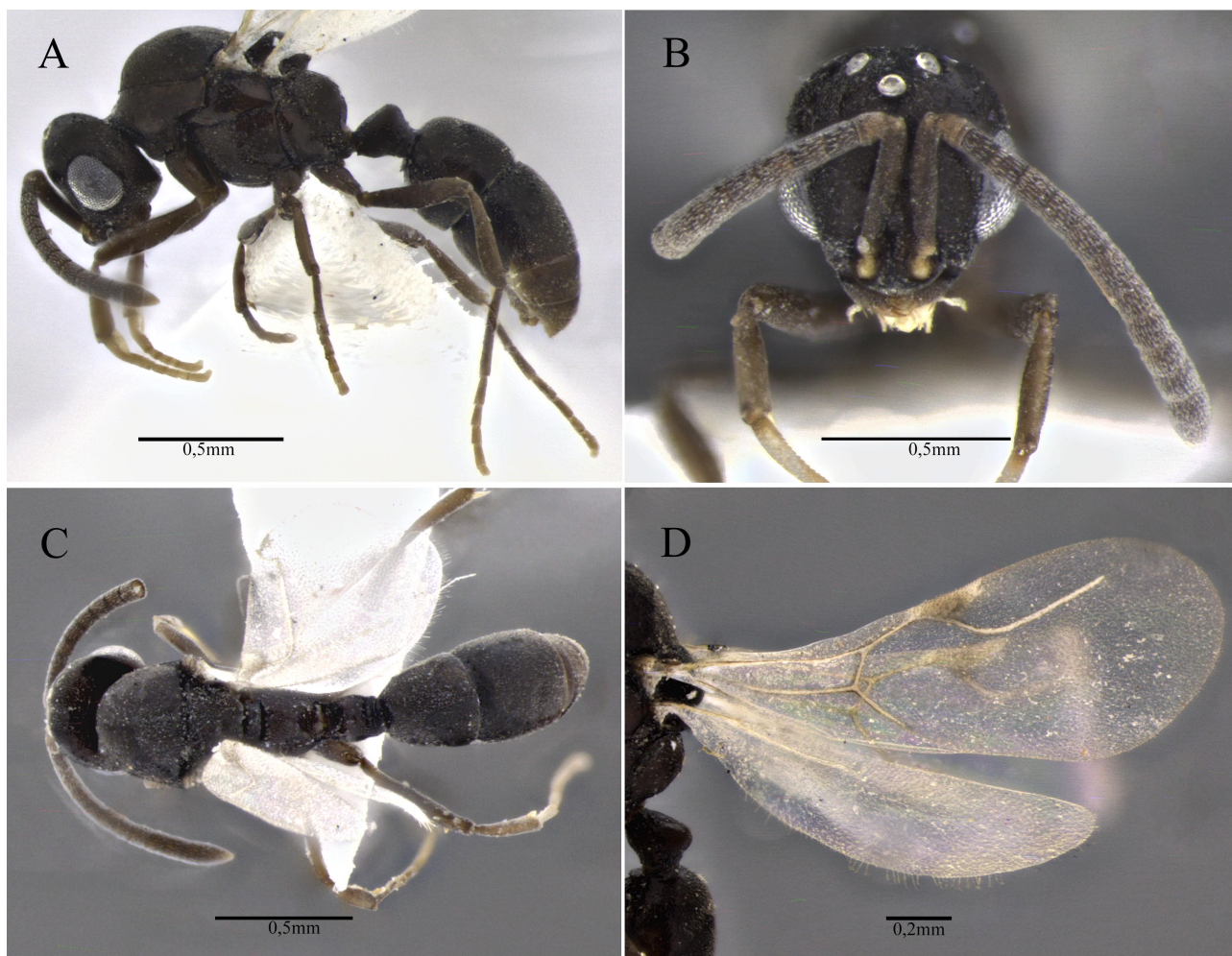


FIGURE 23. *Probolomyrmex kelleri* sp. n. (paratype male). A. Habitus. B. head in frontal view. C. dorsal view. D. Wings.

### *Probolomyrmex lamellatus* New species

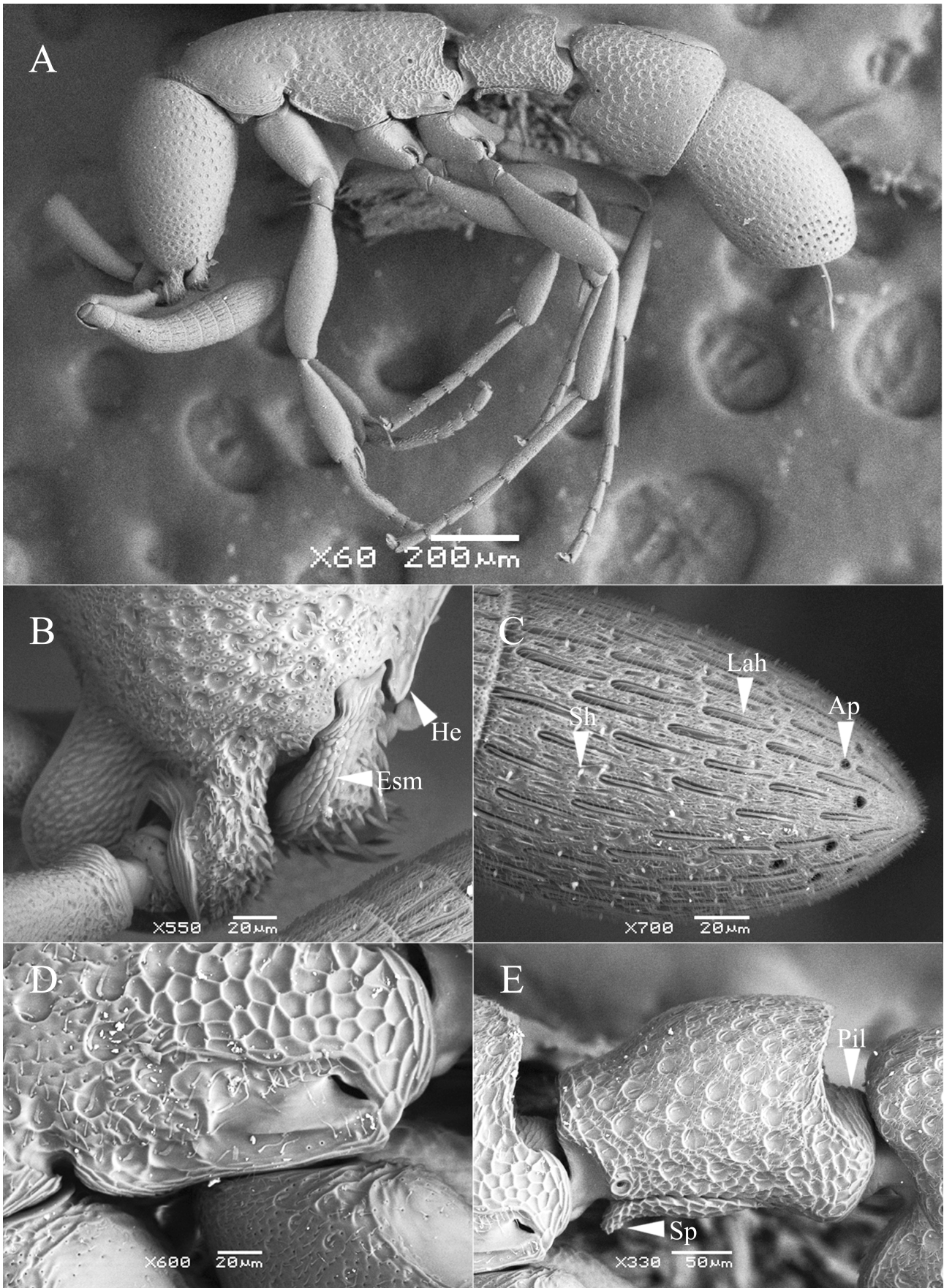
(Figs. 24, 25)

**Holotype:** BRAZIL: Pará: Terra Santa, FLONA, Saracá-Taquera, Base Patauá, 1°51'27.23"S 56°27'48.4"W, 70m, 25–29.viii.2016, R.M. Feitosa, E.Z. Albuquerque, R. Silva col, Winkler (worker) [DZUP, unique specimen identifier DZUP 549767].

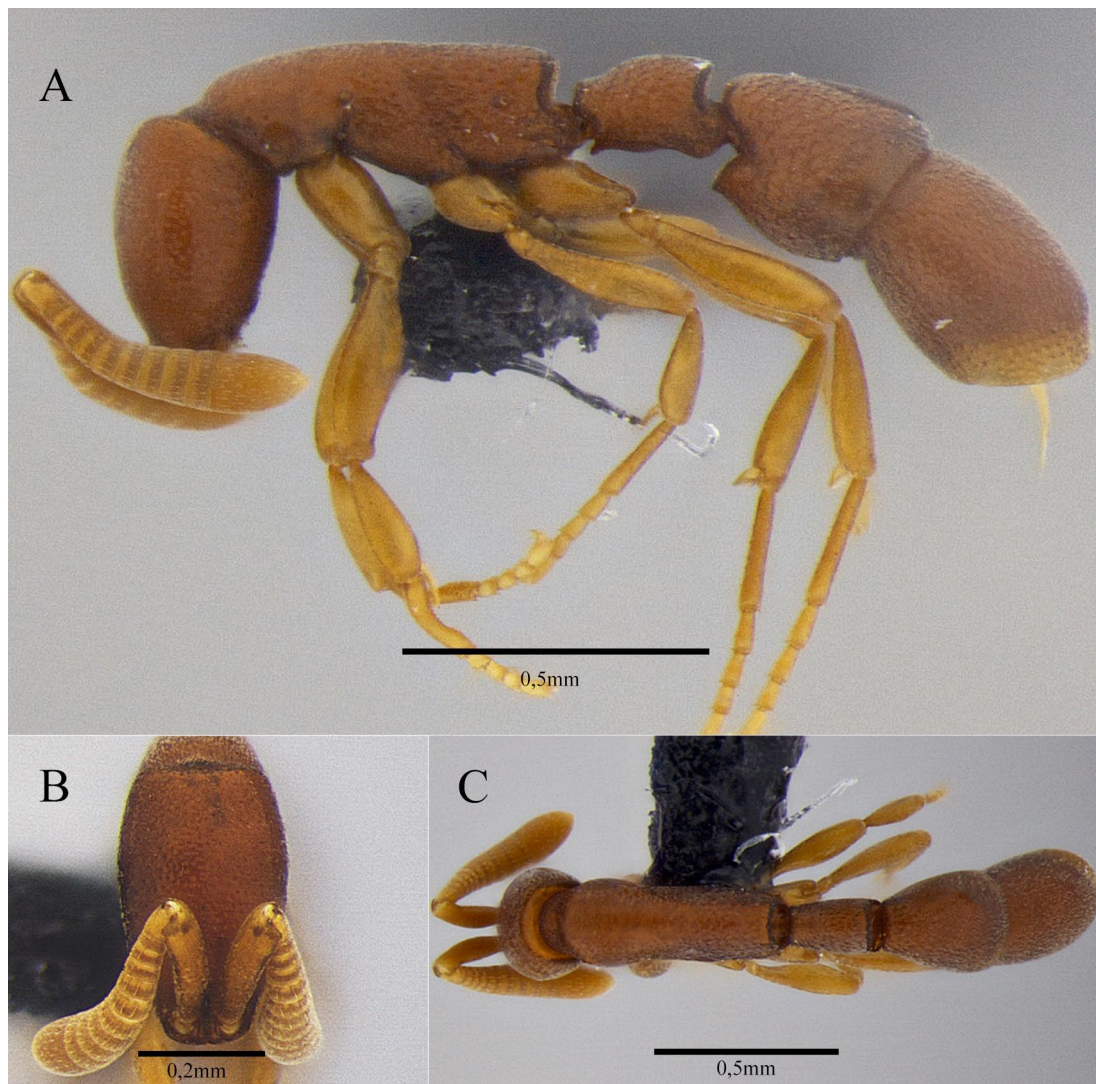
**Diagnosis:** Propodeum and petiole entirely emarginated posteriorly by a conspicuous lamella, without teeth. Postero-ventral lobe of petiole short and subquadrate. Subpetiolar process weakly developed. Prora weakly developed and dorsal protuberance on the posterior region of the first gastral tergite weakly developed.

**Worker measurements:** (n=1) HL 0.50; HW 0.30; SL 0.30; WL 0.59; PL 0.30; PW 0.24; PH 0.20; TL 2.11; CI 59.3; SI 59.3; PI 78.5.

**Worker description:** Frontoclypeal shelflike projection micropunctate; mandibles foveated; external surface of mandibular basal margin large and imbricated (Fig. 24B – esm). Antennal funiculi with pits; tip of apical segment of antennae bearing different sized pits (Fig. 24C – Ap). Mesopleuron foveate and micropunctate; metapleuron alveolate and foveated; lateral faces of propodeum foveated and micropunctate; alveoli denser just above metapleural gland orifice; opening of metapleural gland large, with smooth anterior region, surrounded by rows of hairs (Fig. 24D). Petiolar node and postero-ventral lobe of petiole with incomplete foveae and micropunctures; latero-ventral region of petiole and subpetiolar process alveolate (Fig. 24E). Posterior region of second gastral tergite with transversal rows of deep rounded pits.



**FIGURE 24.** SEM micrography of *Probolomyrmex lamellatus* sp. n. (holotype worker). A. Habitus. B. Mandibles (he = hypostomal margin; esm = external surface of basal region of mandible). C. Antenna (ap = antennal pit; lah = long appressed hair; sh = short hair). D. Metapleural gland. E. Petiole (pil = postero-inferior lobe of petiole; sp = subpetiolar process).



**FIGURE 25.** *Probolomyrmex lamellatus* sp. n. (holotype worker). A. Habitus. B. head in frontal view. C. dorsal view.

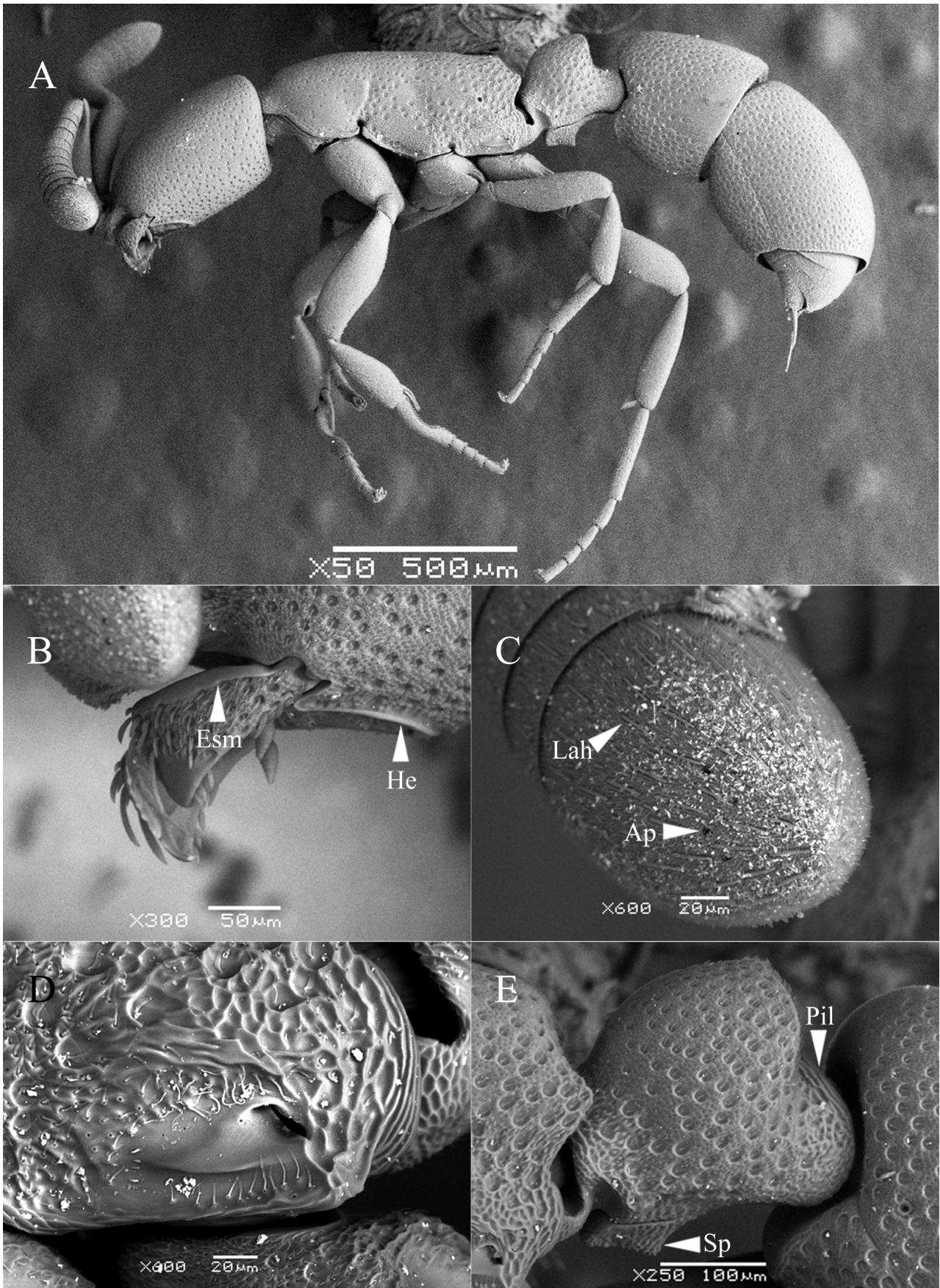
Space between mesosomal foveae covered by dense pubescence.

Head 1.8 times longer than wide (Fig. 25B). Hypostomal margin curved (Fig. 24B – he). Antennal scapes extend to head midlength, distance from scape apex to of head more than two times pedicel length (SI 59.3). Propodeum and petiole entirely emarginated posteriorly by a dark lamella, without teeth (Fig. 25A); Petiole 1.5 times longer than high (PI 78.5) posterior face short, straight, and smooth; postero-ventral lobe short and subquadrate; subpetiolar process weakly developed (Fig. 24E). First gastral segment with weakly developed prora and dorsal protuberance on posterior region of tergite weakly developed (Figs. 24A, 25A).

**Etymology:** The epithet refers to the posterior lamella of the propodeum and petiole, an exclusive characteristic of this species.

**Distribution** (Fig. 29): Brazil (PA).

**Comments:** *Probolomyrmex lamellatus* is similar to *P. cegua*, but the head is comparatively longer, the propodeum and petiole are unarmed and completely emarginated by a dark lamella, and the postero-ventral lobe of petiole is subquadrate. The single known specimen came from a leaf-litter sample collected at in mature lowland Amazon forest.



**FIGURE 26.** SEM micrography of *Probolomyrmex petiolatus* (worker - CASENT0610407). A. Habitus. B. Mandibles (he = hypostomal margin; esm = external surface of basal region of mandible). C. Antenna (ap = antennal pit; lah = long appressed hair; sh = short hair). D. Metapleural gland. E. Petiole (pil = postero-inferior lobe of petiole; sp = subpetiolar process).

*Probolomyrmex petiolatus* Weber, 1940

(Figs. 26, 27)

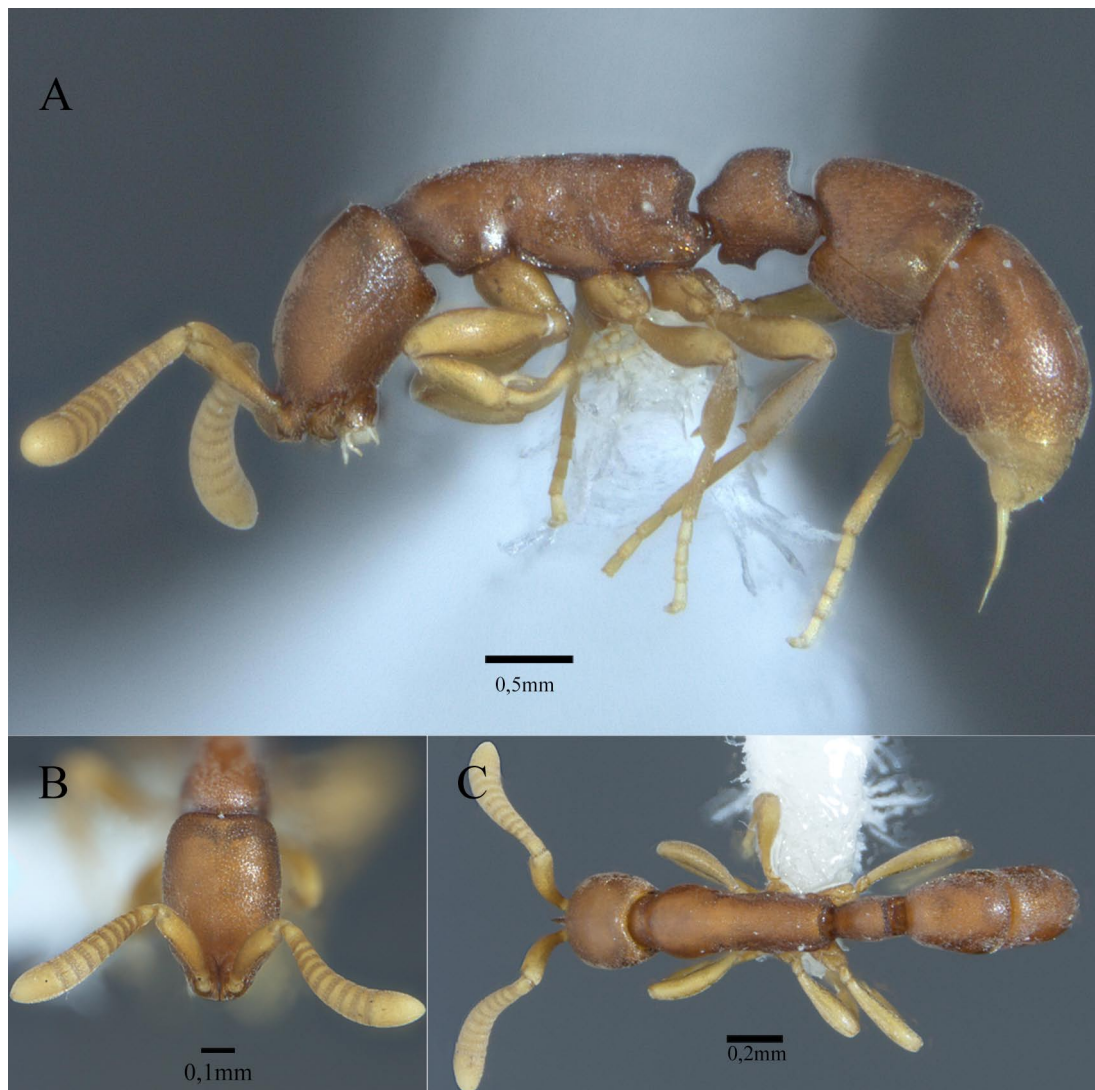
**Holotype:** PANAMÁ: Canal Zone: Barro Colorado Island, 30.vi.1938, N.A. Weber, 906-32203 (worker) [MCZ] [examined].

**Diagnosis:** Postero-ventral lobe of petiole long and subquadrate. Subpetiolar process well developed and sub-rectangular. Prora and dorsal protuberance on posterior region of first gastral tergite absent.

**Worker measurements:** (n=3) HL 0.50–0.57; HW 0.34–0.37; SL 0.26–0.30; WL 0.63–0.69; PL 0.26–0.30; PW 0.27–0.30; PH 0.28–0.30; TL 2.13–2.33; CI 61.5–68.5; SI 51.5; PI 93.5–107.

**Worker description:** Frontoclypeal shelflike projection micropunctate. Mandibles foveated, interval between foveae covered by micropunctures; external surface of mandibular basal margin smooth (Fig. 26B – esm); tip of apical segment of antennae bearing minute pits (Fig. 26C – Ap). Mesopleuron and metapleuron alveolate and foveated; lateral faces of propodeum foveated and micropunctate; alveoli denser just above metapleural gland orifice; opening of metapleural gland narrow, with smooth anterior region, surrounded by rows of hairs (Fig. 26D). Petiolar node and postero-ventral lobe of petiole with incomplete foveae and micropunctures; subpetiolar process alveolate (Fig. 26E). Posterior region of second gastral tergite with foveae (Fig. 26A).

Space between mesosomal foveae covered by dense pubescence. Pygidium with dense pubescence and some long and thick hairs.



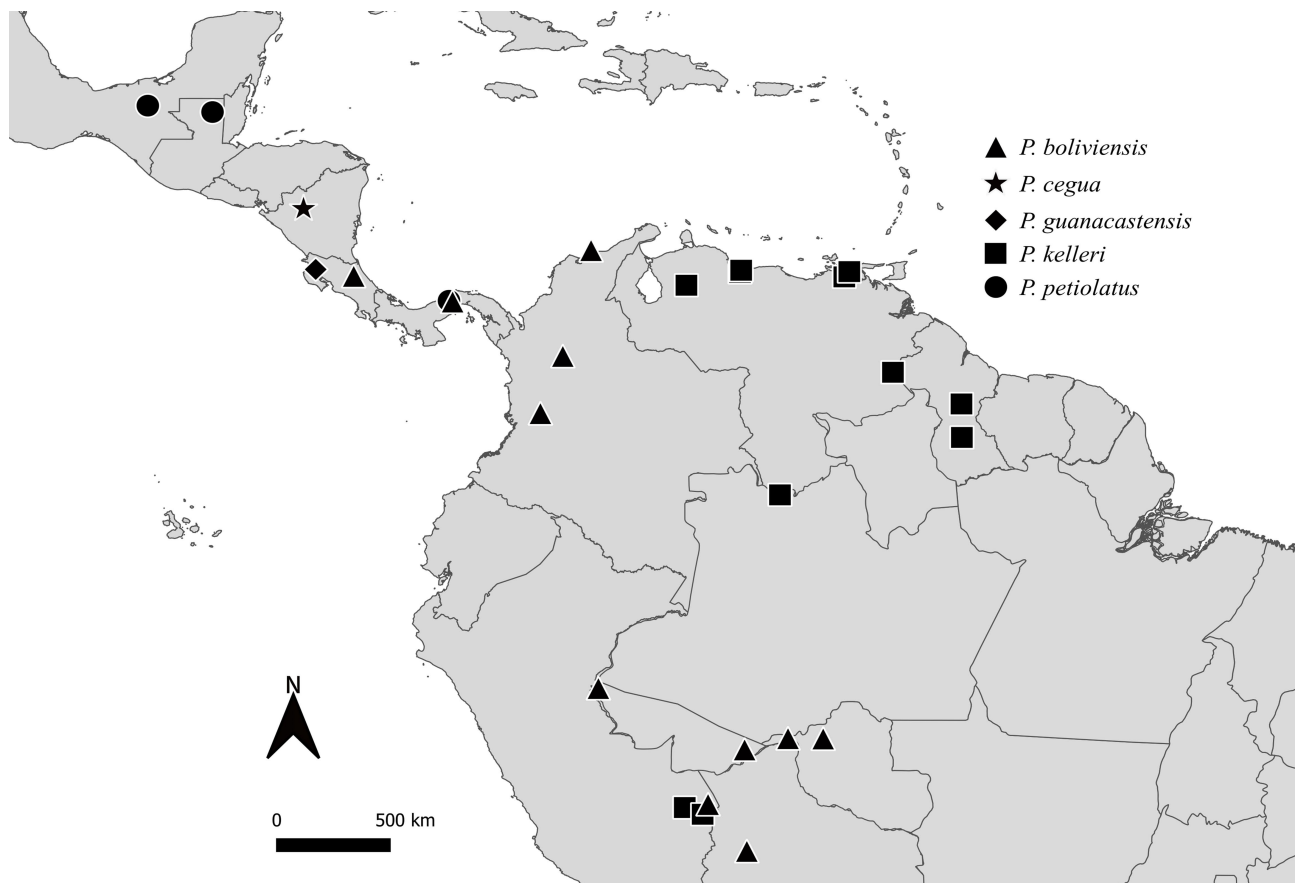
**FIGURE 27.** *Probolomyrmex petiolatus* (worker - JTLC00014514). A. Habitus. B. head in frontal view. C. dorsal view.

Head 1.5 times longer than wide (Fig. 27B). Hypostomal margin curved (Fig. 26B – he). Antennal scapes extend head midlength, distance from scape apex to of head more than two times the pedicel length (SI 51.5). Propodeum emarginated posteriorly on each side by a narrow carina, with teeth at their apices. Petiole as long as high (PI 93.5–107), without teeth; posterior face short, straight and smooth; postero-ventral lobe long and subquadrate; subpetiolar process well developed and subrectangular, with the postero-ventral angle acute and directed ventrally (Fig. 26E). First gastral segment without prora and dorsal protuberance on posterior region of tergite (Figs 26A, 27A).

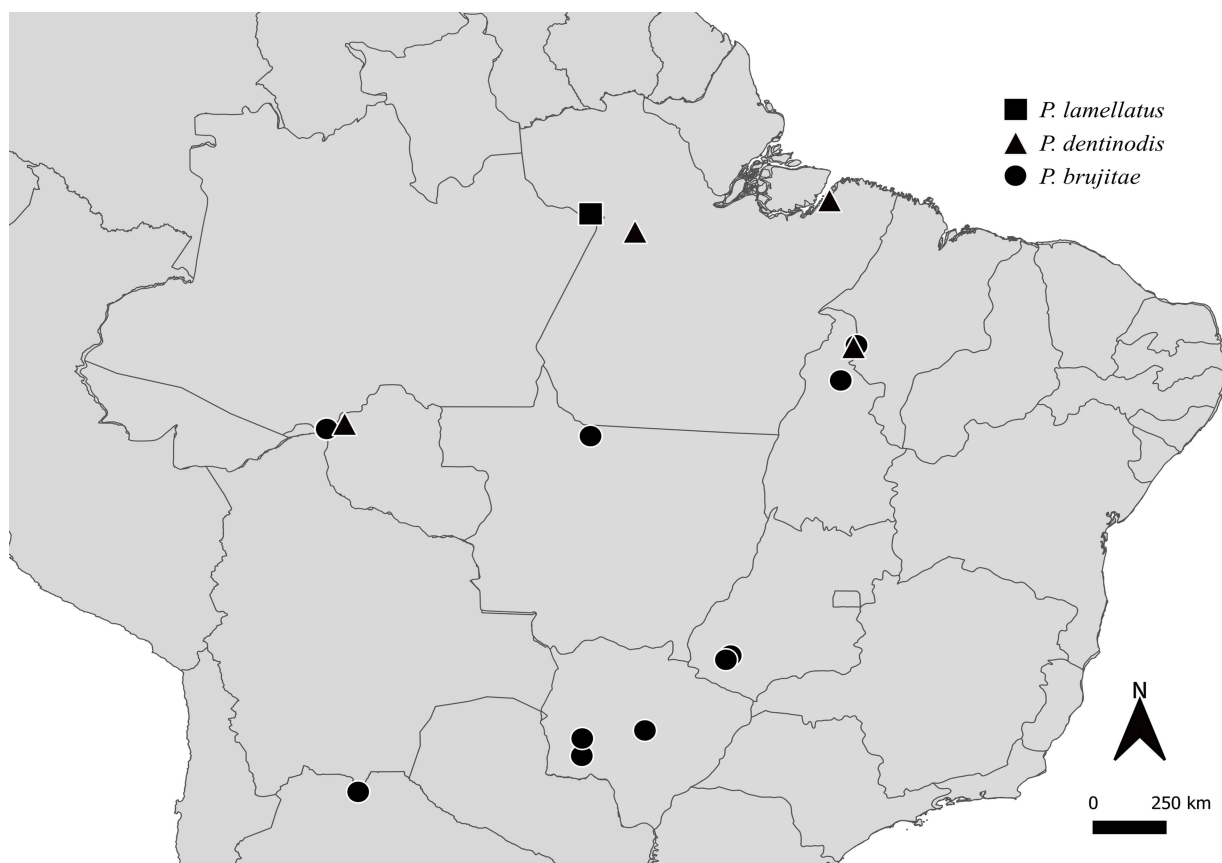
**Distribution** (Fig. 28): Guatemala, Mexico, and Panama.

**Comments:** The subrectangular shape of the subpetiolar process makes this species similar to *P. dentinodis*. However, the latter has a pair of petiolar teeth, the postero-ventral lobe of the petiole is short and rounded, and there are a prora and dorsal protuberance on the gaster. The holotype of *P. petiolatus* was collected among leaves and humus on the rainforest floor in Panama. There is a Brazilian record in the literature for this species (Delabie *et al.* 2001), but these are described here as a new species, *P. dentinodis*.

**Additional material examined (n=11): GUATEMALA: Petén:** Parq. Nac. Tikal, 17.24037 - 89.61990, 270m, 22.v.2009, LLAMA, #Wa-B-05-2-47 CASENT0610407 (1 worker) [JTLC]. **MEXICO: Chiapas:** 8km SE Salto de Agua, 17.51438° N 92.29498° W 70m, 14.vi.2008, LLAMA, Wa-A-08-1-04 JTLC000014514 (1 worker) [JTLC]. **PANAMA: Canal Zone:** Barro Colorado Island: LN 9°9' LW 079°51' 20-50m, v-viii.2007, J.Z.Shik, Mekou 064252 (1 worker) [DZUP]; Mekou 063866 (2 workers) [MZSP]; Mekou 063803 (3 workers) [MZSP]; 1.vi.1983, L.A Mound, CASENT0102222 (1 worker) [BMNH]; 30.vi.1938, A. Newton, Leaf litter forest floor (1 worker) [MCZ].



**FIGURE 28.** Distribution map for the Neotropical species of *Probolomyrmex*.



**FIGURE 29.** Distribution map for the Neotropical species of *Probolomyrmex*.

## Acknowledgments

We would like to thank Jack Longino (JTLC), Lívia P. Prado (MPEG); Jacques Delabie (CPDC), John Lattke (MIZA/DZUP), Carlos Brandão and Mônica Ulysséa (MZSP), Ted Shultz (NHMN) and all the colleagues who provided us with *Probolomyrmex* specimens. We are deeply indebted to John Lattke, Francisco Hita-Garcia, Marek Borowiec, and Jack Longino for the critical reading of a previous version of this manuscript. This work was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), grants 132561/2018-2, 131363/2017-4 and 302462/2016-3, and the Partnerships for Enhanced Engagement in Research (PEER) Science Program (NAS/USAID – award number AID-OAA-A-11-00012 - project 3-188).

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