



## Ants of the genus *Protalaridris* (Hymenoptera: Formicidae), more than just deadly mandibles

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**Abstract.** The ants of the genus *Protalaridris* are revised based upon their morphology. Seven species are recognized; the type species (*P. armata* Brown, 1980) and six species described as new: *P. aculeata* Lattke & Alpert, sp. n., *P. arhuaca* Guerrero, Lattke & Alpert, sp. n., *P. bordoni* Lattke, sp. n., *P. leponcei* Delsinne & Lattke, sp. n., *P. loxanensis* Lattke, sp. n., and *P. punctata* Lattke, sp. n. The genus is patchily distributed in mesic forested areas from western Panama to northern Venezuela and along the Andes to the Amazon watershed of southwestern Peru. The generic description is modified to accommodate a short-mandibulate species. Sporadic biological observations of one long-mandibulate species suggest they are sit-and-wait ambush predators that open their jaws to approximately 180° when stalking. All species are described and imaged, an identification key and a distribution map is provided. Comparing the mandibular morphology of long-mandibulate *Protalaridris* with other extant and extinct ants bearing elongate, dorsoanterior arching mandibles suggests the supposed mandibular apex in these taxa is actually a hypertrophied, preapical tooth and their supposed basal mandibular tooth is the main mandibular shaft.

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### INTRODUCTION

The leaf litter of the American tropics harbors several rare ant genera, known from scant specimens, and virtually lacking natural history data. One such genus is *Protalaridris*, described in 1980 by William Brown, Jr. from workers taken from humid forests in Ecuador and Colombia. It was considered a member of the Tribe Basicerotini, along with 5 other genera: *Basiceros* Schulz, 1906; *Eurhopalothrix* Brown & Kempf, 1961; *Octostruma* Forel, 1912; *Rhopalothrix* Mayr, 1870, and *Talaridris* Weber, 1941, until the revisionary work of Ward et al. (2015) transferred these genera to the Tribe Attini. We will refer to these genera as the *Basiceros* group. The genus *Octostruma* was revised by Longino (2013a), the Central American and Caribbean species of *Eurhopalothrix* were reviewed by Longino (2013b), and *Rhopalothrix* was reviewed by Longino & Boudinot (2013). The increasing use of leaf-litter sifting for both taxonomic/faunistic collecting as well as ecological studies, has enabled the recovery of additional species belonging to *Protalaridris*, extending its geographic distribution south to Peru and north to Venezuela and Cen-

tral America. Amongst ants, most *Protalaridris* are easily recognizable due to their dramatic jaws: slender and widely separated at the base with one or two massive ventral preapical teeth and an exquisitely pointed apical tooth that make for a sophisticated tridimensional trapping structure. But mandibles alone do not make a genus, as has been demonstrated in *Strumigenys* F. Smith, 1860, the senior synonym of close to 30 names that were each considered a proper genus some 30–40 years ago (Bolton, 2000). Differences in mandibular morphology were the main argument for proposing most of these genera but subsequent work has shown that long-mandibulate species are nested within the short-mandibulate groups (Ward et al., 2015). The discovery of a new species with all the characteristics of the traditional *Protalaridris* habitus, except for the elongate mandibles, obliges a reconsideration of the genus. This revision redescribes the genus as well as the type and the, until now, only known species, *Protalaridris armata* Brown, 1980, and describes an additional six species. All species are imaged, an identification key and distribution map are included as well as a discussion of their natural

history. Considerations of the unusually shaped, dorsally arching mandibles of the long-mandibulate species of *Pro-talaridris*, and comparisons with similarly shaped mandibles in both extant and extinct ant taxa, lead to a reinterpretation of their mandibular morphology.

## MATERIALS AND METHODS

### Generalities

The alpha taxonomy is based upon direct observation of specimens and comparative study of their morphology. Most morphological terms used are standard for ant taxonomic descriptions, as defined in Hölldobler & Wilson (1990), Bolton (1994), and Shattuck (1999). Descriptive terms for cuticular sculpturing follow Harris (1979), pilosity stature follows Wilson (1955), and wing venation follows Yoshimura & Fisher (2012) for vein and cell names and Mason (1986) for vein development terms. Tubular veins are sclerotized and raised on both the ventral and dorsal wing surfaces, while sclerotized nebulous veins and unsclerotized spectral veins are raised on the dorsal surface only. For describing hair shapes, the terms defined by Bolton (2000) are used as well as some botanical terms used for describing leaf shapes (Harris & Harris, 2001). Despite their origins in botanical morphology they are readily applicable to ant hairs. The following terms describe hair shapes:

clavate – club-shaped, with a cylindrical basal section and a swollen, but not flattened distal section. Similar in outline to a spatulate hair, but the latter is flattened.

lanceolate – lance-shaped, with the widest part basad (Fig. 1G).

linear – long and narrow, much more so than oblong, with parallel to subparallel sides (Fig. 1B).

oblong – flattened, two to four times longer than broad with parallel or subparallel sides (Fig. 1C).

ovate – egg-shaped, flattened, with the widest part basad (Fig. 1E).

reniform – kidney-shaped, flattened and widest close to mid-length, the base is between two shallow convex lobes and the lateral and apical margins describe a broad convexity (Fig. 1F).

spatulate – elongate and flattened, gradually tapering basad with the widest part close to the apex (Fig. 1D).

subspatulate – similar to spatulate but with a lesser degree of tapering, not exactly oblong but not spatulate (Fig. 1A).

Many of the descriptions and diagnoses describe outlines of particular body part margins; these (in particular the shape of cer-

tain teeth and hairs) are best seen by using reflected background lighting. For recognizing species, we used discontinuities in the variation of a set of morphological characters between groups of ants that share distinctive characters and continuous variation for said character, or others, as indicative of reproductive isolation between groups. The characters we found most useful for alpha taxonomy are listed in the results.

### Specimen repositories

Specimens from the following collections were studied:

ARCE – Ant Reference Collection Ecuador, Instituto de Ciencias Biológicas, Escuela Politécnica Nacional, Quito, Ecuador.

CAS – California Academy of Sciences, Dept. of Entomology, San Francisco, California, U.S.A.

DZUP – Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil.

FMNH – Field Museum of Natural History, Chicago, Illinois, USA.

ICN – Instituto de Ciencias Naturales Insects Collection, Universidad Nacional de Colombia, Bogotá, Colombia.

JTLC – John T. Longino Collection, Department of Biology, University of Utah, Salt Lake City, Utah, U.S.A.

MCZC – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

MIZA – Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela.

NHMUK – The Natural History Museum, London, England, U.K.

QCAZ – Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

RBINS – Royal Belgian Institute of Natural Sciences, Entomology Collection, Brussels, Belgium.

USNM – National Museum of Natural History, Washington, D.C., U.S.A.

UTPL – Universidad Técnica Particular de Loja, Loja, Ecuador.

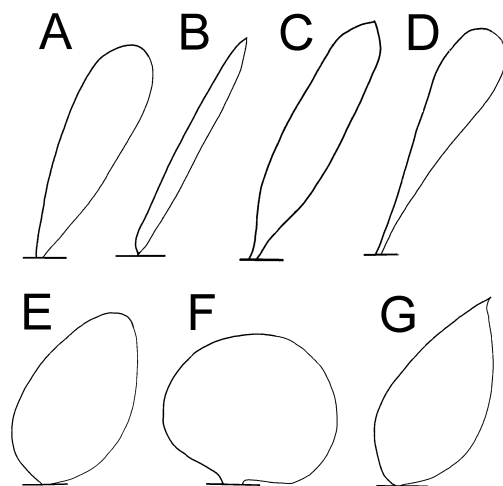
### Images

High resolution digital images of *P. aculeata* sp. n. and *P. arhuaca* sp. n. were taken using a Leica DFC290 camera attached to a Leica Z6APO stereomicroscope. Image stacks were taken using Leica Application Suite v3.8 (2003–2011) and united with Combine ZP (<http://combinezp.software.informer.com/>). The images of *P. armata* were taken with a motorized Leica M16Z imaging system using a Canon 7D camera mounted on the scope. LED dome lights were used for illumination, image stacks were processed with Helicon Focus Pro 6.7.1 and final rendering with Photoshop CS6. The *P. loxanensis* sp. n. wing images were taken with a Leica DFC 500 camera mounted on a motorized Leica MZ1 stereoscope and processed with Leica LAS 3D Viewer and Leica LAS Montage 4.7 with final rendering using GIMP 2.8. All other images were taken with a Leica MC170HD camera attached to a Leica S8APO stereomicroscope. Each image stack was taken using Leica Application Suite ver. 4.3.0 (2003–2013) and united with Combine ZP. Final editing was done with Adobe Photoshop CS5. The distribution map was created using QGIS v2.14 (Quantum GIS Development Team, 2016).

### Measurements and indices

Most morphological measurements were made using a stereoscopic microscope with an ocular micrometer. The following measurements are adopted from Brown & Kempf (1960) and are expressed in millimeters:

HL – Head length: mid-line length of the cephalic capsule, measured in full-face (dorsal) view, from the anterior margin of



**Fig. 1.** Hair shape terms. A – subspatulate; B – linear; C – oblong; D – spatulate; E – ovate; F – reniform; G – lanceolate.

the clypeus to the midpoint of a line drawn across the occipital margin.

HW – Head width: maximum width of head, measured in the same plane as HL.

ML – Mandible length: straight-line maximum length of a mandible, measured from the base at the insertion into the head capsule, to the apex. Not measured in the same plane as HL, but in a dorsal view of the mandible itself (in *P. leponcei* sp. n., the mandible was measured in the same plane as HL as it is also its dorsal view).

EL – Eye length: maximum length of the compound eye, measured perpendicular to the eye.

SL – Scape length: maximum length of the first antennal segment, as measured from the anteriormost margin of the basal lobe or angle to the apex.

PW – Pronotal width: maximum width of pronotum in dorsal view.

WL – Weber's length of the mesosoma: diagonal length, measured in lateral view from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the metapleural lobe.

PH – Petiole height: height of the petiole measured in profile from the ventralmost point of the petiole vertically to a line intersecting the dorsal-most point of the node.

PL – Petiole length: the length of the petiole measured in profile from the anterior process to the posteriormost point of the tergite, where it surrounds the postpetiolar articulation.

DPW – The maximum width of the petiole in dorsal view.

PPL – The maximum length of the postpetiole in dorsal view.

PPW – The maximum width of the postpetiole in dorsal view.

The following indices were calculated from the preceding measurements: CI – Cephalic index: HW/HL; MI – Mandibular index: ML/HW; OI – Ocular index: EL/HW; SI – Scape index: SL/HW; LPI – Lateral Petiole Index: PH/PL; DPI – Dorsal Petiole Index: DPW/PL.

## RESULTS

### Characters

In this study the following characters proved to be the most helpful in separating species. *Head*: General shape, sculpture of dorsal surface, presence or absence of transverse carina, shape of antennal fossa. *Compound eye*: General shape, number of ommatidia, relative distance from cephalic dorsum and antennal fossa. *Mandible*: General shape, angle formed with dorsal cephalic surface, relative length, number of teeth/denticles along dorsal and ventral preapical margins, number of large ventral teeth; general sculpture pattern; shape and orientation of setae along internal mandibular border. *Antenna*: Shape of scape and number of standing hairs along anteroventral margin of scape. *Labrum*: General shape, development of anteromedian notch, number and shape of labral hairs, geometry of hairs. *Mesosoma*: General shape of dorsal margin in lateral view, curvature of propodeal declivity anterad of tooth; shape of propodeal tooth.

### Species list

#### *armata* group

*P. aculeata* Lattke & Alpert, sp. n. (southwestern Peru)

*P. arhuaca* Guerrero, Lattke & Alpert, sp. n. (northeast Colombia)

*P. armata* Brown, 1980 (central Ecuador to western Panama)

*P. bordoni* Lattke, sp. n. (northcentral Venezuela)

*P. loxanensis* Lattke, sp. n. (southcentral Ecuador)

*P. punctata* Lattke, sp. n. (northcentral Venezuela)

#### *leponcei* group

*P. leponcei* Delsinne & Lattke, sp. n. (southcentral Ecuador)

### Identification key for workers of *Protalaridris*

- 1 Mandible long and slender. Dorsal margin in lateral view concave, forming obtuse angle with clypeal plane. In frontal view, first basal tooth of mandible separated from basal rim by diastema. Eye separated from dorsal cephalic surface by at most one its diameter (*armata* group) ..... 2
- Mandible short, stout, and triangular. Dorsal margin in lateral view strongly bowed with basal portion in same plane as clypeus and apical portion strongly bent downward. In frontal view, first basal tooth of mandible continuous with basal rim. Eye well separated from dorsal cephalic surface by twice its diameter (Fig. 6c) (*leponcei* group) ..... *leponcei* sp. n.
- 2 Cephalic dorsum bears prominently elevated frontovertexal ridge that is separated from occipital carina by broad and concave sulcus, especially evident in lateral view of head (Figs 2c, 5c) ..... 3
- Frontovertexal ridge variably developed, but never so elevated that it forms a distinct concavity with the occipital carina when seen laterally. Cephalic margin posterad of ridge straight to convex in lateral view (Figs 4c, 7c, 9c) ..... 4
- 3 Large ventral mandibular tooth situated closer to mandibular base than to its mid-length; anterior margin of scape with 6–7 erect hairs; eye with 3–4 relatively indistinct ommatidia; dorsal surface of mandible and lateral surface of tibiae with abundant tubercles ..... *aculeata* sp. n.
- Large ventral mandibular tooth situated closer to mandibular mid-length than to its base; anterior margin of scape with 8–9 erect hairs; eye reduced to 1 apparent ommatidium; dorsal surface of mandible and lateral surface of tibiae rugulose at most, lacking tubercles ..... *bordoni* sp. n.
- 4 Each mandible with single prominent and massive preapical tooth that crosses that of opposing mandible, tooth closer to mandibular base than mandibular mid-length and easily visible in lateral view; one or two more slender preapical teeth may overlap (Figs 3b, 5b, 7b, 9b), but these teeth are not visible in lateral view; eye separated from dorsal cephalic surface by at least half a diameter ..... 5
- Each mandible with two prominent and massive preapical teeth, proximal tooth situated close to mandibular mid-length and distal tooth closer to mandibular apex; both teeth cross their opposite counterpart and are visible in lateral view (Fig. 4b); eye borders on dorsal cephalic margin ..... *armata* Brown
- 5 Anterior labral margin in dorsal view weakly sinuate, median emargination not deeper than one-fourth of labral length; labrum relatively narrow, its lateral basal margins clearly visible in full face view, uncovered by mandibles (Fig. 7a) ..... *loxanensis* sp. n.
- Anterior labral margin medially cleft; median notch deeper than one-fourth of labral length; lateral basal margins of labrum in full-face view totally covered by mandibles ..... 6
- 6 Labrum with angular to bluntly angular anterolateral lobes; mandible apicad of large ventral tooth with series of short teeth, none crossing or touching their opposite counterparts (Fig. 9b) ..... *punctata* sp. n.

- Labrum with rounded anterolateral lobes; mandible apicad of large ventral tooth with single large tooth that touches or crosses its opposite counterpart (Fig. 3b).....*arhuaca* sp. n.

### Genus *Protalaridris* Brown, 1980

*Protalaridris* Brown, 1980: 36. Type-species: *Protalaridris armata* Brown, 1980, by original designation.

Baroni Urbani & De Andrade, 2007: 88 (as junior synonym of *Basiceros* Schulz, 1906).

Ward et al., 2015: 77 (transferred from *Basicerotini* to *Attini*).

**Worker.** Head in dorsal view about as long as wide, widest posterior to eye; cephalic dorsum with transverse blunt frontovertexal ridge, posteriorly broad convex; occasionally ridge sharp and narrow (*P. aculeata* sp. n. & *P. bordoni* sp. n.). Vertex broad and convex when ridge is blunt, mostly concave when ridge is sharp with narrow flat strip bordering the occipital carina. Brief median longitudinal carina present on frontal area, extending posterad from posteromedian clypeal margin. Epistomal suture well defined, shaped as open inverted V; clypeus posterolaterally forms anterior part of antennal fossa, anterior margin of frontal lobe meets posterior clypeal margin through narrowly arched space. Vertex both posterior and anterior to frontovertexal ridge feebly but broadly impressed on each side; anterior clypeal margin generally with broad median concavity. Head in lateral view with broadly convex posterodorsal margin that meets dorsal margin at an angle; cephalic dorsal margin straight to broadly concave.

Compound eye relatively small, directed anterolaterally, with 1–12 usually indistinct ommatidia; eye separated from dorsal cephalic surface by at least one diameter, sometimes less but never directly bordering the dorsal cephalic surface. No erect pilosity on cephalic dorsum but *P. leponcei* sp. n. bears one erect spatulate hair on each side of head, posterior to compound eye and lateral to frontal carina; medially pointing subspatulate to lanceolate appressed hairs generally present. Antenna issues forth on each side through a deep semicircular notch in the dorso-lateral cephalic margin; antennal fossa shaped as sinuous emargination along anterolateral cephalic margin in full-face view, interior of fossa mostly finely areolate; antennal scrobe very shallow and broad, extending posterad of compound eye. Antenna 9-segmented with 2-segmented club, pedicel suboval, segments 3–7 short and transverse, apical segment longer than preceding seven segments. Scape flattened, robust with flat to convex dorsal surface, ventral surface finely areolate, anterior basal lobe slightly expanded, except in *P. aculeata* sp. n. where the lobe is lamellate, anterior margin with 5–10 spatulate to reniform hairs.

Mandible: 1. *armata* species-group: mandibles long and slender, in full length view straight to slightly arched, insertions remote, shafts crossing at apices when completely closed, each tapering apicad towards medially directed apical tooth, tooth dark brown, shining, and acutely pointed. Mandibles form complex cradle or cage mainly bound by the main axis of each mandible as well as one, or two, prominent ventral teeth. Base of mandible at cephalic insertion expands into flange with smooth rim and areolate dor-

sal surface; mandibular dorsum strongly sculpted, ventral surface weakly sculpted; apical tooth and apex of massive ventral tooth/teeth smooth. In lateral view mandibular dorsal margin concave or forms obtuse angle with main longitudinal axis of cephalic capsule. Mandible generally with two internal rows of preapical teeth, one ventral another dorsal; dorsal teeth sometimes absent or reduced in number (*P. armata*). Dorsal preapical teeth numbering 1–7 pointing mesad, relatively small, never crossing each other; ventral preapical teeth numbering 4–5, of varying size with at least some teeth that cross, including one or two massive ventromedially directed teeth. Mandibular dorsum with abundant appressed and elongate lanceolate to simple hairs that arch anterad. 2. *leponcei* species-group: mandible short, stout, and triangular; dorsal margin in lateral view strongly bowed with basal portion in same plane as clypeus and apical portion strongly bent downward. Masticatory margin with single row of 9 preapical teeth of irregular size, protruding dorsomedially. Apical and longest preapical teeth crossed with mandibles closed. In frontal view first basal tooth of mandible continuous with basal rim.

Labrum extended, shape varying from rounded to rectangular with an anteromedian notch ranging in depth from shallow to over half the length of the labrum, six to 32 usually flattened hairs present along margins, the longest anterolaterally placed and the shortest posterolaterally placed and within the anterior notch. With head in dorsal view the labrum mostly visible with mandibles closed in *armata* group but entirely hidden from view in the *leponcei* group.

Mesosoma subpyriform to pyriform in dorsal view, broadest across anterior pronotum, cervix marked off by a blunt arcuate margin. Mesosomal dorsal margin continuously convex in lateral view, curvature ranging from weakly convex to strongly convex; no sutures evident across dorsum, except for shallow narrow furrow usually obscured by particulate matter, immediately anterad of transverse carina marking top of concave dorsal part of the propodeal concavity, and presumably marking the anterior margin of propodeum. Propodeal spiracle surrounded by elevated ring of cuticle, opening faces posterolaterally, located approximately at half length of declivity less than one diameter from tooth; dorsal propodeal margin very brief; declivity finely areolate ventrad of upper margin of teeth, rugulose dorsad, separated from dorsum by distinct transverse carina, not covered by debris or encrustations. Petiole relatively short with poorly developed node, node transverse in dorsal view, obliquely subtruncate in lateral view, postpetiole twice as wide as petiole, rounded above, with trace of median longitudinal sulcus posterad, and weak median posterior emargination. Underside of petiole biconvex, anteroventral process shaped as discrete angle or lacking. No erect hairs on dorsum of mesosoma, petiole, and postpetiole; mesosomal lateral surface without standing pilosity. Encrustations present on dorsal surface of petiolar node and postpetiole.

Abdominal tergite IV with broadly convex main dorsal surface, dorsolaterally bordered by longitudinal blunt ridge that defines elongate lateral vertical region of tergite, trans-

verse ridge present along anterior margin; gastral tergum with 20–50, sometimes more, erect to suberect spatulate hairs arranged in at least four longitudinal rows; antero-ventral gastral process lacking. Legs short and compact, femora gradually thickened apicad, and tibiae even thicker, tarsi more slender; 1–2 spatulate hairs present on apex of tibiae, meso- and metatarsal segments with pairs of erect spatulate hairs in V; tarsal claws small. Venation (for *P. bordoni* sp. n. and *P. loxanensis* sp. n. gynes). (Fig. 8) Fore wing with 4 closed cells (costal, basal, submarginal, and subbasal); veins C, Sc+R, M+Cu, Cu, cu-a, and 1A tubular; Cu tubular for a distance; Rs partly spectral between M and 2rs-m; separation of Cu from M-Cu occurs at a distance from cu-a; 1A continues briefly apicad of cu-a. Hind wing with tubular C+Sc+R, Sc+R, and Rs+M; 1A briefly tubular and M+Cu partially tubular.

**Comments.** The inclusion of *Protalaridris leponcei* sp. n., with its strikingly different mandibles, obliged a redefinition of the genus, but most changes are limited to mandibular morphology, as the majority of other characters are shared, including the number of antennal segments. The labral margin hairs are very short in *P. leponcei* sp. n. with none longer than 1/4 the labral width while in the other species some hairs will always exceed half the labral width in length. A monotypic genus could have been proposed but there is a long history of ant genera established because of variances in mandibular morphology, with further studies forcing a taxonomic weeding out of excess names. Differences in mandibular morphology and antennal segmentation have traditionally been important in separating genera within the *Basiceros* and *Strumigenys* groups, but recent work has gathered convincing evidence to the contrary, especially in the latter genus. It was only after the extensive work of several myrmecologists (Baroni Urbani & De Andrade, 1994; Bolton, 1999; Ward et al., 2015) that many genus-group names were sunk as junior synonyms of *Strumigenys*. A tipping point was finally reached when J. Longino and M. Branstetter graciously shared the preliminary results of their UCE molecular analysis of the *Basiceros* group of genera and these clearly indicate the inclusion of *P. leponcei* sp. n. as an ingroup within *Protalaridris*.

The two strikingly different mandibular morphologies permit easy recognition of two informal species groups within the genus: (1) The *armata* group, with elongate mandibles, and (2) the *leponcei* group, with short, triangular mandibles. Most species of the *armata* group have the frontovertexal ridge arching laterally until it either meets the eye or misses it by an ocular diameter, whereas in *P. leponcei* sp. n. the ridge is separated from the eye by several times its diameter. This latter condition is also found in the *ascrobicula* group of *Octostruma* (Longino, 2013a). Within the *armata* group *P. aculeata* sp. n. and *P. bordoni* sp. n. share the prominent frontovertexal ridge and a mostly concave vertex except for a narrow flat strip that borders the occipital carina, in sharp contrast with the blunt frontovertexal ridge with a mostly convex vertex of the other known species.

Only a few winged individuals are known for the genus. The following discusses differences and similarities between the wing venation of *Protalaridris* and some of the genera of the *Basiceros* group. The fore wing of *P. bordoni* sp. n. and *P. loxanensis* sp. n. is very much like that of *Basiceros scambognathus* (Brown, 1949) as illustrated in Brown & Kempf (1960: 173), but the Cubital vein separates from M-Cu at the junction with cu-a in *B. scambognathus* whereas in *Protalaridris* the separation of Cu occurs at a distance from cu-a. In *Protalaridris* 1A continues briefly apicad of cu-a but it stops at cu-a in *Basiceros*. The fore wing of *P. loxanensis* sp. n. has the costal cell well-defined between tubular veins C and Sc+R as in *Rhopalothrix* Mayr, 1870; basal cell well-defined between tubular veins Sc+R and M+Cu (similar to *Rhopalothrix* but M+Cu darker, better defined in *Protalaridris*); submarginal cell mostly well-defined though Rs is partly spectral between M and 2rs-m; subbasal cell closed as M+Cu, 1A, and cu-a markedly tubular; Cu tubular for a distance. Fore wing with 4 closed cells in *Protalaridris* and *Basiceros* (costal, basal, submarginal, and subbasal); in *Rhopalothrix* with 2 (costal and basal). The hind wing in *P. loxanensis* sp. n. has tubular C+Sc+R, Sc+R, and Rs+M; 1A is briefly tubular and M+Cu is also partially tubular. In contrast the fore wing venation of *Rhopalothrix subspatulata* Longino & Boudinot, 2013 is relatively reduced, with Rs+M, M, and Rs apicad of M all reduced to spectral veins, cu-a is absent and A has a vestigial tubular section (Longino & Boudinot, 2013). Additionally the hind wing of *R. subspatulata* has only C+Sc+R developed as tubular veins whilst Sc+R and Rs+M are spectral. As in *Protalaridris*, 1A is briefly tubular but M+Cu is totally spectral.

## SPECIES ACCOUNTS

### *Protalaridris aculeata* Lattke & Alpert, sp. n.

(Figs 2a–d)

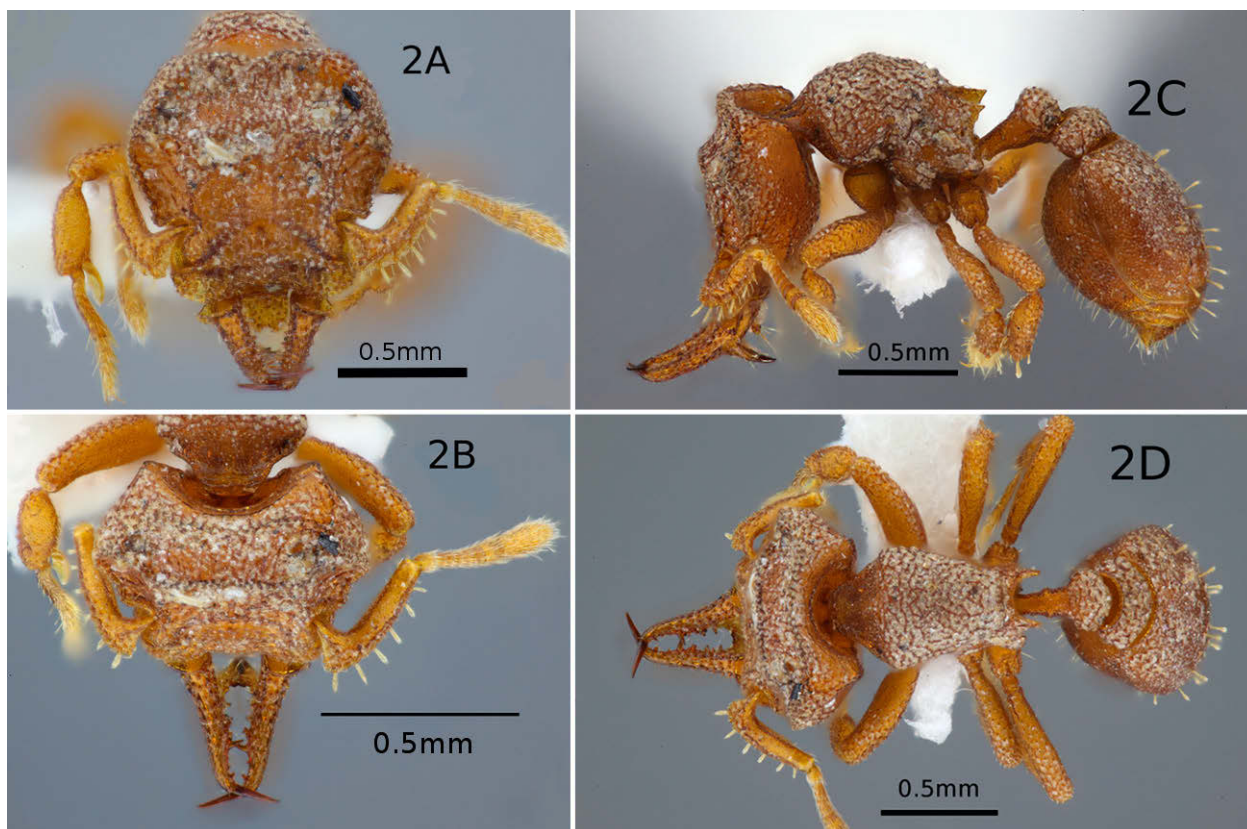
ZooBank taxon LSID:

067C6EC4-5150-4464-A544-FCFC2C1FC104

**Worker diagnosis.** Mandibular shaft with massive tooth projecting ventromesad close to mandibular base, mandible with abundant tubercles; labrum in frontal view rectangular and narrow, anterior margin with six long hairs. Basal angle of scape well-developed, lamellate; scape anterior margin with 6 spatulate hairs. Cephalic dorsum with median rectangular raised area. External tibial surfaces with abundant tubercles.

**Holotype measurements.** HL 0.67, HW 0.70, ML 0.37, EL 0.03, SL 0.35, PW 0.38, WL 0.60, PH 0.18, PL 0.25, DPW 0.18 mm. CI 1.05, MI 0.52, OI 0.05, SI 0.50, LPI 0.73, DPI 0.73.

**Worker description.** With head in frontal view anterior clypeal margin with broad median concavity, laterally broadly convex; lateral cephalic margin posterad of antennal fossa convex, head widest at posterior two-thirds, lateral cephalic margins mostly converging anterad; posterior cephalic margin with medial emargination, posterolaterally convex with inconspicuous occipital lobe; cephalic dorsum posterad of antennal fossa with well-defined, carinate bor-



**Fig. 2.** *P. aculeata* sp. n. Worker holotype: A – head dorsal view; B – mandible, full length view; C – body lateral view; D – body, dorsal view. Images by G. Alpert.

ders. Frontal lobe dorsally convex, anterior margin forms narrow angle with posterior clypeal margin, width less than half that of fossa. Eye with 3–4 relatively indistinct ommatidia, facing anterolaterally, separated from antennal fossa along lateral cephalic margin by not more than 3 diameters, separated from dorsal face less than one diameter in lateral cephalic view.

Cephalic dorsum mostly rugulose reticulate, rugulae directed longitudinally posteriorly and obliquely laterally, space between rugulae shining; cephalic dorsum divided into elevated central area, convex transverse posterior area and vertical lateral convex area. Central elevation rectangular, extending posterad approximately two-thirds of cephalic length; lateral margin of elevation vertical, extends from frontal carina, elevation bordered posterad by transverse carina, carina broadly concave medially, rugulose reticulate with longitudinal elevated median area. Cephalic dorsum between transverse carina and posterior cephalic carina convex in lateral cephalic view. Cephalic dorsum with mesially pointing subspatulate to lanceolate appressed hairs; occiput areolate, posterolateral region areolate-rugulose. Cephalic ventrum mostly areolate to areolate-rugulose, posterolaterally densely punctulate and shining. Antennal scrobe shallow but distinct, posteriorly ending just beyond eye.

Mandible in full length view with both shafts converging until just anterad of mandibular mid-length, then each is weakly convex, bending at base of apical tooth. Mandible with prominent ventromedially directed tooth, situ-

ated closer to mandibular base than apex in mandibular full length view; ventral tooth in dorsal view tapering apicad, internal margin edentate, apically broadly concave. Internal surface of ventral tooth mostly smooth and shining. With mandibles closed the apices of each ventral tooth cross; apical and ventral tooth ferruginous brown, smooth and shining. Mandibular dorsum with low but distinct, blunt tubercles and rugulae, ventral surface anterior of ventral tooth rugulose and with appressed pilosity directed apicad; smooth and shining sculpture limited to posteroventral area, ventral tooth, and mandibular apex.

In cephalic lateral view mandibular dorsal margin forms broad concavity with dorsal cephalic surface, ventral tooth tapers posteroventrally, mostly straight, its length about 1/3 that of lateral mandibular width. Mandibular dorsum with short, arched, slender hairs pointing apicad or mesad. Dorsal mandibular margin with 5–6 preapical denticles, besides medium sized tooth set at mid-length between massive ventral tooth and base of apical tooth; dorsal mandibular margin with decumbent slender hairs, directed anteromesad. Ventral mandibular margin with 8 denticles between base of apical tooth and ventral massive tooth.

Labrum rectangular and narrow, lateral margins visible in dorsal view with mandibles closed, basal ridge broadly arched; apically rounded with distinct but shallow median notch. Median ventral surface with abundant hairs, dorsal surface sculpted, not smooth and shining. Anterior margin of labrum with six long hairs, third and second hairs from labral cleft the longest, slender and weakly lanceolate. In-

ternal hairs weakly spatulate with rounded apex. Labral cleft with 2 very short hairs. Palpal formula unknown. Scape in dorsal view with weak basal lobe, anterior margin broadly convex and lamellate; scape in general broadly arched. External margin dorsad of lamella with 6 elongate spatulate hairs, ventral margin with 10 slender hairs; anterior scape face rugulose and shining, anterobasal lobe weakly expanded anterad, dorsum with very fine short hairs. Cross-section of scape at mid-length triangular, anterior convex margin, dorsal margin broadly convex, ventral margin mostly straight.

Mesosomal dorsal margin in lateral view convex, promesonotal suture marked by shallow concavity, mesonotum with narrow anterior margin, mesonotal dorsal margin mostly straight, dorsal propodeal margin brief; declivitous margin covered by triangular tooth; base of tooth broadly concave, apex pointed, posterior margin lamellate, briefly concave. Mesosomal dorsum and dorsolateral half of pronotum rugulose, with decumbent and arched weakly lanceolate hairs, mostly directed posteromesad. Half of lateral pronotum, part of mesopleuron, and propodeum punctulate to areolate, wanting pilosity, metapleuron punctulate; mesopleuron with rugulae. Pronotum with anterior transverse areolate strip with scattered rugulae, not marked off by transverse carina from dorsal surface; promesonotal suture marked as shallow transverse trough.

Petiolar node strongly convex in lateral view, anterior petiolar margin mostly straight to broadly concave, anteroventral process triangular small, postpetiolar dorsal margin in lateral view broadly convex. Petiole with long straight hair on ventrolateral surface, posterolaterally directed. Postpetiole transverse in dorsal view, anterior margin concave and shorter than convex posterior margin, dorsum of petiolar node and postpetiole areolate-rugulose with posteriorly directed appressed, arched hairs. Dorsal margin of abdominal tergum IV broadly convex in lateral view, ventral margin markedly convex, with greatest height just anterad of gastral mid-length; abdominal tergum IV with transverse carina along anterodorsal margin that separates dorsum from brief transverse anterior surface; dorsal pilosity consisting of sparse arched subdecumbent lanceolate hairs, and some 22–26 suberect, spatulate hairs. Abdominal sternite IV densely areolate anterad becoming punctate posterad, sparsely clothed by arched decumbent hairs pointing posterad. Tarsal claws simple, long and slender; legs stout, not elongate; protibial apex with lateral spatulate hair. Meso- and metatibial apices each with anterolateral and posterolateral spatulate hairs, anterior hairs largest. External surface of tibiae with numerous low tubercles. Body mostly ferruginous, darker tint on transverse cephalic carina and cephalic dorsum posterad of carina, apex of mandible and ventral mandibular tooth, mesosomal dorsum and propodeal lamella, including tooth, and gaster throughout.

**Queen and male.** Unknown.

**Type material.** Holotype worker (MCZC). Peru. Madre de Dios: Cuzco Amazónico, 15 km NE Puerto Maldonado [–12.5312° –69.0713°], 200 m, 16.VII.1989, SP Cover, JE Tobin

CA-879 leg. Plot IE20. Matute Tierra Firme Forest, ‘Burhenuvia’ [*Buchenavia*] fruit fall berlesate.

**Type locality.** Madre de Dios, Peru.

**Etymology.** The species epithet is derived from the Latin neuter plural of *aculeātus* “having stingers or spines”, also “stinging”, and alludes to the numerous tubercles on the mandibles and tibiae of this species.

**Distribution.** Only known from type locality.

**Biology.** It is the only *Protalaridris* found outside of pre-montane and montane rainforest, in a lowland site of the Amazon basin relatively close to the Andes. It represents the southernmost known limits of the distribution range for the genus, separated by a gap of close to 1500 km from the closest known *Protalaridris* in southern Ecuador. *Buchenavia* Eichler, 1866 is a tree genus of the Combretaceae family with several species known from the Amazonian forest.

**Comments.** Even though this species is described from a single specimen, its morphology is very distinct within the genus, particularly the tuberculate sculpturing on the mandibular and lateral tibial surfaces. Most *Protalaridris* have 8 or more spatulate hairs along the anterior margin of the scape but there are only 5 or 6 hairs in *P. aculeata* sp. n. and *P. loxanensis* sp. n. A crust of dirt or debris covers most of the body, ventrolateral cephalic surface, and most of abdominal tergum IV, though the tergal crust is apparently thinner than that of the head. The occiput, propodeal declivity, and a transverse strip anterad to the anterior carina on abdominal tergum IV are contrastingly clean and devoid of any debris. The number and arrangement of erect hairs on the gastral tergum should be considered provisional as it can vary in other species.

A label accompanying the specimen discloses it was recognized as an undescribed species by B.H. Dietz in 2002. It is probably a rare ant as a two week long ant taxonomy course in July of 2012 involving over 25 students and instructors collecting intensively at a locality (Sachavacayoc Centre, –12.8587° –69.3552°, 235 m) just 38 km SW of the type locality of *P. aculeata* sp. n. failed to detect this ant. The 2013 edition of Ant Course was held at a site 251 km EEW (Villa Carmen Station, –12.8947° –71.4031°) of the type locality, closer to the Andes, with a large group of students and instructors intensively collecting ants between the altitudes of 500–700 m, but no specimens were found. The type locality is 55 km W from the Bolivian border and under 200 km S from the Brazilian border, suggesting the presence of this genus in these countries.

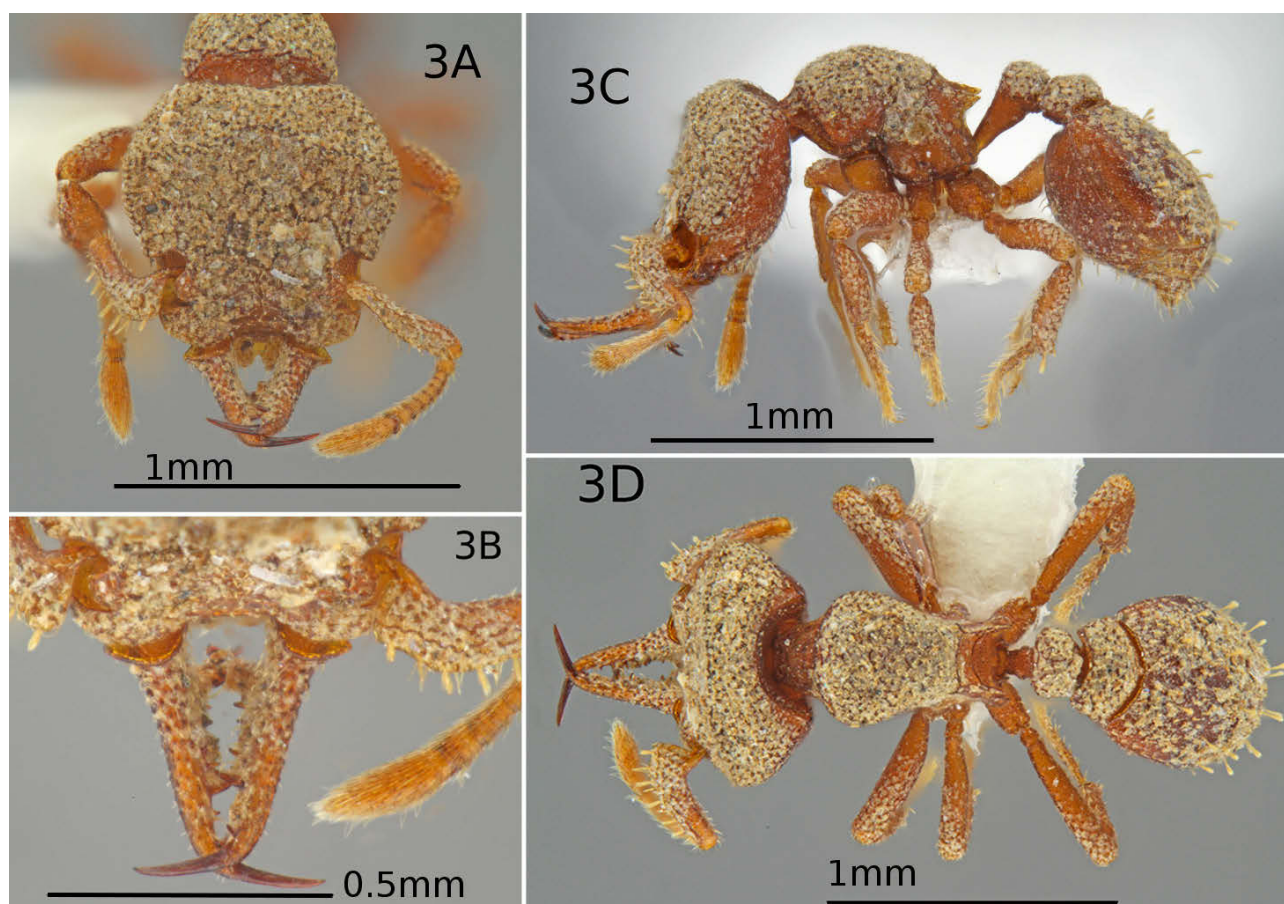
***Protalaridris arhuaca* Guerrero, Lattke & Alpert, sp. n.**

(Figs 3a–d)

ZooBank taxon LSID:

ADBBC186-0CD1-4DB3-8951-746FC140DF4E

**Worker diagnosis.** Cephalic vertex with median subquadrate elevation. Labrum wider than long, deeply cleft with 8 large anterolateral hairs and no hairs in labral cleft. Overlapping preapical mandibular teeth between mid-length of mandible and base of apical tooth belong to dorsal row. Frontovertextal ridge with abundant small pro-



**Fig. 3.** *P. arhuaca* sp. n. Worker paratype: A – head dorsal view; B – mandible full length view; C – body lateral view; D – body dorsal view. Specimen CASENT0633240. Images by G. Alpert.

tubercles. Dorsum of head, most of mesosoma, petiolar node, and postpetiole torose-rugulose.

**Measurements of type specimens.** Holotype (paratypes,  $n = 3$ ): HL 0.84 (0.82–0.87); HW 0.87 (0.86–0.90); ML 0.53 (0.53–0.57); EL 0.04 (0.05–0.06); SL 0.49 (0.47–0.51); PW 0.49 (0.48–0.52); WL 0.72 (0.73–0.79); PH 0.20 (0.20–0.22); PL 0.37 (0.36–0.43); PPL 0.20 (0.19–0.24); PPW 0.38 (0.34–0.39); DPW 0.26 (0.25–0.27) mm. CI 1.04 (1.05–1.07); MI 0.61 (0.60–0.63); OI 0.04 (0.06–0.07); SI 0.56 (0.54–0.56); LPI 0.54 (0.51–0.58); DPI 70 (63–72).

**Worker description.** Head slightly wider than long in full-face view; posterior margin broadly concave to straight with small median emargination; lateral cephalic margin posterior to antennal fossa forming blunt obtuse angle with straight to weakly convex sides, widest at frontovertexal ridge, lateral margin forms discrete angle with posterior margin of antennal fossa; lateral cephalic margin briefly concave along posterior half of antennal fossa, then gradually curves convex towards clypeus. Anterior clypeal margin medially concave with lateral convex lobe next to basal mandibular flange. Cephalic lateral margin bordered by raised, blunt carina that curves medially to form strongly raised frontovertexal ridge shaped as broad, anteriorly facing concavity, continuously arching except for brief median concavity that forms anterior margin of median vertexal protuberance. Antennal fossa conspicuous, as long as wide, reaching barely half the length of the head, anterior

margin straight, internal margin sinuous; anterior margin of fossa brief and transverse, frontal carina with anterior half convex and posterior half shaped as subquadrate to convex emargination. Internal surface of the fossa densely foveolate, without pilosity. Cephalic dorsal surface irregularly rugulose from frontovertexal ridge to anterior clypeal margin; head posterad of ridge with abundant rounded, protuberances connected by short and thick sharply-crested rugulae, sculpture more accentuated posterolaterally; bunched series of longitudinal rugulae extend posteriorly from frontal carina forming low, broad crest that almost touches frontovertexal ridge. Ill-defined longitudinal median ridge present, extending posterad from posterior clypeal margin. Area between longitudinal and lateral carinae strongly concave, area posterad to frontovertexal ridge with median, subquadrate-shaped raised area (best seen in dorsal view of the posterior cephalic margin) laterally bound by ovoid depression. Cephalic dorsum with short and apically acute, appressed hairs, each hair separated by distance equal to or greater than its length.

Mandible elongate, external and internal margins in full-length view mostly parallel, cross-section at one-third anterior-length is convex externally and straight (vertical) internally; mandible tapers to medially directed, acutely pointed apical tooth, as long as 1/3 mandibular length. Mandibular internal margin with longitudinal dorsal row of 4 teeth and 3–4 denticles: teeth situated apicad of massive

ventral tooth, from the base apicad, teeth 1–3 relatively small and non-overlapping; tooth 4 large, approximately twice as long and as wide at base than preceding teeth. Tooth 4 situated anterad of mandibular mid-length and overlapping with large tooth of other mandible, 2–3 denticles situated apicad of tooth, 1 or two denticles situated basad of tooth 1; mandibular internal margin with ventral row of 5–6 denticles best seen ventrally, posteriormost denticle largest in size and situated on base of large ventral tooth. Ventral tooth placed closer to mandibular base than to mid-length, crossing opposing tooth from other mandible, internal ridge with low triangular flange. Mandibular dorsum mostly rugulose-torulose, ventrally mostly smooth and shining, including ventral tooth and apical tooth; mandibular basal flange finely areolate. Mandible with sparse curved decumbent hairs along lateral margin, apex of each hair contacting mandibular surface; ventral mandibular surface with 2 rows of very short erect hairs between base of ventral tooth and base of apical tooth; 6–8 obliquely positioned, long hairs present from mandibular base to basal half of ventral tooth.

Labrum wider than long, anterolaterally bluntly angular and lateral margin convex, anteromedially with narrow V-shaped incision as long or longer than labral mid-length; dorsal surface shining and rugulose with fine punctae; labrum anterolaterally with 4 thick, cylindrical hairs, 2 hairs on anterior margin and 2 hairs on anterolateral margin, lateralmost hair the shortest, no hairs in median emargination, apex of some hairs flattened; ventral surface of labrum with erect pubescence and subspatulate hairs, some apically cleft.

Scape barely reaches frontovertexal ridge; in dorsal view with two oblique surfaces separated by longitudinal carina, internal surface with bead-like projections arranged in rows and low carinae, external surface with two longitudinal concavities separated by median lamella; external margin with 2 rows of hairs, dorsal row with 6 lamellate thick hairs, ventral row of 9–10 cylindrical thick hairs, narrower than dorsal hairs. Scape opaque, funiculus shining. Antenna with pedicel as wide as long, campaniform; segment 3 trapezoid, slightly wider than long, segments 4–8 trapezoid, serially increasing in length, 2–8 punctulate, apical segment smooth; scape apex with semierect hairs, following segments with abundant decumbent to subdecumbent hairs as long as pedicel. Eye reduced to single ommatidium, separated from dorsal cephalic surface by distance equal to less than one diameter.

Dorsal margin of mesosoma in lateral view mostly convex, dorsal propodeal margin concave to apex of tooth; pronotal collar opaque and finely punctate; propleuron finely areolate. Mesometapleuron briefly cleft along ventral margin, mesopleuron mostly flat, rugulose ventrally; metapleuron mostly flat except for anterodorsal depression next to propodeum, depression and propodeum joined by carina; mesopleuron posteroventrally convex. Spiracle rounded, posteriorly facing; dorsal propodeal face separated from declivity by transverse carina. Mesosoma trapezoid in dorsal view, widest anterad, most of mesosomal

dorsum and lateral surfaces of pronotum and mesonotum torose-rugulose. Propodeal declivity finely areolate; narrow posteroventral strip of pronotum, mesometapleuron, and lateral propodeal face pruinose with shallow foveolae. Anteroventral margin of pronotum with shallow, roughly scrobiculate sulcus. Mesosomal dorsum lacking standing hairs. Petiole as long as propodeal declivity in lateral view, dorsal margin straight, ventral margin slightly sinuous; node discrete, rectangular in dorsal view, wider than long; postpetiole twice as wide as long, anterior margin strongly concave, posterior margin very convex, lateral margins posteriorly diverging. Most of petiole densely foveolate, dorsum of petiolar node and postpetiole torose-rugulose. Fourth abdominal tergite anteriorly concave in dorsal view, complementing posterior convex margin of postpetiolar tergite; fourth abdominal segment makes up 3/4 of gaster, dorsum of tergite foveolate-rugose; sides of fourth abdominal tergite, all gastral sterna, and rest of tergites densely foveolate; gastral dorsum with more than 10 erect, subspatulate hairs; sparse pubescence also present; sternites with sparse erect hairs.

Coxae finely areolate. Femora with anterior, posterior, and ventral surfaces relatively flat, dorsally convex; erect and semierect hairs present on both internal and external femoral surfaces; tibiae laterally compressed, dorsal margin in lateral view straight and ventral margin convex; meso- and metatibia longer than protibia. First tarsomere of each leg half as long as respective tibia, tarsomeres 2–4 each slightly longer than wide. Coxae and lateral tibial surfaces densely foveolate; dorsum and apical-lateral surface of profemur mostly torulose-rugulose, meso- and metafemora apically torulose-rugulose, basally foveolate. Tibiae with thick flattened hairs on ventral surface, hairs as long as half tibial width. Lateral apex of tibiae each with flattened spatulate hair, mesotibial apex with small flattened hairs on posterior side. Head, scape, mandible, promesonotum and most of dorsal propodeal face and rest of abdomen brown; funiculus, mesometapleuron, lateral and declivitous propodeal faces, and most of legs yellowish-brown; mandibular apical tooth reddish-brown.

**Queen and male.** Unknown.

**Type material.** Holotype worker (point-mounted; ICN): COLOMBIA. Magdalena: 9 km SE Minca, 11.08972° –74.06021° ±100 m, 1650 m, 28 May 2017, R. Guerrero, J. Longino#9848-s. Taken in secondary growth montane wet forest from sifted leaf litter. Holotype bears red label with unique specimen identifier 'ICN 093589'. Paratypes: Three point-mounted workers with same data as holotype: One with unique specimen identifier CASENT0644163 and a Q code, deposited in DZUP. One with unique specimen identifier CASENT0644170 and a Q code, deposited in JTLC. One with unique specimen identifier CASENT0644171 and a Q code, deposited in JTLC.

**Additional material.** COLOMBIA. Magdalena: 4 km SE La Minca, 11.12257° –74.08508°, ±20 m, 1180 m, 4.xii.2014, MG Branstetter 2452, CASENT0633240, ADMAC DNA voucher, 1 worker (JTLC).

**Type locality.** Magdalena, Colombia.

**Etymology.** The species epithet is in recognition of the Arhuaco people, an indigenous group with ancestral lands close to the type locality of the species.

**Distribution.** Only known from the Sierra Nevada of Santa Marta, Magdalena, Colombia

**Biology.** All specimens of *P. arhuaca* have been collected from sifted leaf-litter in premontane rain forest between 1180 and 1650 m on the northwestern slopes of the Sierra Nevada de Santa Marta. The holotype and specimen CASENT0644163 were found in the lower site, a dense forest with closed canopy and abundant leaf-litter. Specimens CASENT0644170 & CASENT0644171 were taken from secondary growth forest with an open canopy and some scattered large trees. The site is surrounded by pastures and crossed by trails. The litter in this site was taken from the base of the largest trees.

**Comments.** *P. arhuaca* sp. n. is similar to *P. loxanensis* sp. n., also having a large apical tooth that overlaps its counterpart on the opposing mandible. In *P. arhuaca* sp. n. this tooth is part of the dorsal row of dentition, in contrast with *P. loxanensis* sp. n. where the tooth is part of the ventral row of preapical mandibular dentition. Their respective head lengths and labral configuration also permit separation. The head length of *P. arhuaca* sp. n. is the longest in *Protalaridris*, including *P. loxanensis* sp. n. (HL > 0.80 mm vs. 0.76–0.78 mm, respectively). *P. arhuaca* sp. n. has a subquadrate head compared with the subrectangular shape in *P. loxanensis* sp. n. (CI ≤ 1.07 vs. ≥ 1.10). Although other *Protalaridris* may have quadrate to subquadrate heads, their respective widths and lengths are less than in *P. arhuaca* sp. n. In a dorsal cephalic view the

mandibles, when closed, cover the lateral margins of the labrum in *P. arhuaca* sp. n., but in *P. loxanensis* sp. n. these margins are visible despite full mandibular closure. The labrum in *P. loxanensis* sp. n. has a weak anterior concavity but in *P. arhuaca* sp. n. the labrum is deeply cleft. *P. punctata* sp. n. also has a relatively wide labrum with a deep emargination, as in *P. arhuaca* sp. n., but this cleft forms an acute angle in *P. punctata* sp. n. and in *P. arhuaca* sp. n. it forms an obtuse angle.

#### *Protalaridris armata* Brown, 1980

(Figs 4a–d)

*Protalaridris armata* Brown, 1980: 37, Figs 1–8 (worker).

*Basicerus armata*: Baroni Urbani & De Andrade, 2007: 90.

**Worker diagnosis.** Mandibular shaft with two massive overlapping ventromesially projecting teeth, dorsal mandibular margin lacking preapical teeth or denticles except for a single denticle at base of apical tooth; mandibular shaft slender, in full-length view very gradually tapering apicad. Lateral margin of labrum with three anterolaterally projecting hairs; abdominal tergite IV with 12–16 erect hairs.

**Worker measurements.** (n = 10): HL 0.60–0.87; HW 0.69–0.93; ML 0.40–0.58; EL 0.04–0.09; SL 0.36–0.47; PW 0.40–0.64; WL 0.64–0.87; PH 0.21–0.29; PL 0.22–0.27; DPW 0.11–0.27 mm. CI 0.95–1.15; MI 0.53–0.65; OI 0.06–0.11; SI 0.50–0.53; LPI 0.83–1.20; DPI 0.42–1.10.



**Fig. 4.** *P. armata* Brown 1980. Worker paratype: A – head dorsal view; B – mandible, full length view; C – body lateral view; D – body dorsal view. Specimen CASENT0900943. Images by Will Ericsson, Antweb.

**Worker description.** Head slightly wider than long in dorsal view; posterior margin mostly broadly convex to bluntly angular, occipital lobe projects posterad as blunt angle, lateral cephalic margin posterior to eye broadly convex to bluntly angular. Cephalic lateral margins anterad of maximum head width converge anteriorly; anterior clypeal margin medially concave, anterolaterally forming blunt angle, clypeus bordered posterolaterally by antennal fossa. Eye distinct, partially visible in frontal view, oval, apparently 4–5 partially fused ommatidia, facing anterolaterally, separated from antennal fossa by one diameter or less in lateral view, dorsal ocular margin at same level as dorsal cephalic margin in lateral cephalic view. Head widest along dorsolateral ridge. Cephalic lateral surface elongate, facing lateroventrad in lateral view, mostly occupied by broad and shallow antennal scrobe that fades posteriorly at same distance as dorsal transverse carina; head widest along dorsolateral ridge. Cephalic dorsum mostly densely punctate with abundant brief longitudinal rugae, commonly encrusted with dirt and debris that obscure cuticle; dorsum traversed at widest point by broadly concave to bluntly angular carina that forms elevated crest dividing cephalic dorsum into two sloping surfaces; frontovertexal ridge always obvious but may vary in vertical development. Low but distinct longitudinal carina present between posterior clypeal midpoint and frontovertexal ridge. Cephalic dorsum with short appressed, mostly transverse lanceolate ground hairs; posterolateral and ventral cephalic surfaces densely punctate, pilosity sparse.

Mandibles form cradle mainly bound by the main axis of each mandible as well as two prominent ventral teeth. Mandible in full length view progressively tapers apicad, mostly straight, bending mesad just before base of apical tooth, in lateral view dorsal mandibular margin sinuous, convex up to level of basal ventral tooth and concave apicad. Base of mandible at cephalic insertion expands into flange with smooth rim and areolate dorsal surface. Mandibular dorsum mostly punctate with scattered rugulae basad, abundant appressed and elongate to lanceolate or linear hairs that arch anterad present throughout mandibular shaft, densest on basal half; ventral mandibular surface mostly shining, with scattered punctulae. Mandibular dorsal margin sinuous in lateral view, forms weak obtuse angle with dorsal cephalic surface, mandibular base emarginate at junction with clypeus; massive ventral teeth pointing mostly mesad, ventral projection of tooth in lateral view less than contiguous thickness of mandibular shaft. Dorsal mandibular margin lacking preapical dentition except for denticle close to base of apical tooth. Mandibular ventral margin with 4 preapical teeth: teeth 1 and 3 massive, mesoventrally directed and overlapping with their counterparts, basal tooth largest, apically cleft; tooth 3 simple; tooth 2 small, closer to tooth 3 than tooth 1, tooth 4 at base of apical tooth. Ventral tooth in dorsal view tapering apicad; in anterior view relatively straight with decumbent tooth along anterodorsal margin. Mandibular apical tooth dark brown shining and sharply pointed.

Labrum entirely visible in frontal view, basal margin posteriorly convex, labrum wider posterad than anterad; bilobed with apically blunt median cleft almost extending to labral mid-length, lateral margin weakly concave. Ventral surface mostly shining, dorsal surface with scattered punctulae, not as shining. Labral margins with lanceolate flattened hairs; lateral margin with 3 anterolaterally directed hairs, progressively becoming longer anterad, anterior margin with 2 hairs, and internal margin with 2–3 anteromedially directed hairs. Palpal formula unknown. Scape in dorsal view with longitudinal rugulae anterad, posterad sparsely punctate, subparallel anterior and posterior margins, slightly wider basad than apicad, posterior margin broadly concave, anterior margin broadly convex, antero basal lobe weakly expanded anterad, thin longitudinal lamella usually present between antero basal lobe and apex; dorsum with arched hairs particularly anterad. Cross-section of scape at mid-length subrectangular, dorsal margin broadly convex, ventral margin mostly straight, anterior margin concave to convex, posterior margin straight to weakly concave; scape anteroventral margin bears 8 prominent apically truncate hairs; basal hair simple and longest, other hairs spatulate, weakly arching anterad, apical-most 4 hairs smallest of all.

Mesosomal dorsum in lateral view weakly convex, dorsal propodeal margin very brief; propodeal tooth broadly triangular, posterior base prolonged ventrally as broadly concave lamella, in dorsal view relatively thick not lamellate. Pronotum, mesosomal dorsal and dorsolateral surfaces rugulose, including anepisternum and dorsal extremes of metapleuron and lateral propodeum. Numerous decumbent ground hairs on lateral pronotum, mesonotum and propodeum, mostly directed postero to posteromesad; no decumbent hairs on mesometapleuron; no erect hairs on dorsum of head, mesosoma, petiole, and postpetiole. Katepisternum, most of metapleuron, and base of propodeal tooth punctate to areolate; katepisternum lacking transverse rugulae. Pronotum with defined anterior face separated from dorsal face by abrupt curvature, collar with few longitudinal carinae; promesonotal suture barely distinguishable.

Petiolar node subquadrate with anterior petiolar margin evenly and broadly concave in lateral view, dorsal margin straight to weakly convex, posterior margin brief and vertical, length less than half that of dorsal margin. Petiolar anteroventral process shaped as weak angle to absent, ventral margin posterad of process broadly concave to sinuate; postpetiolar dorsal margin in lateral view mostly broadly convex, curvature more pronounced posterad. Petiolar node and postpetiole transverse in dorsal view; postpetiole broadly concave anteriorly and convex posteriorly, dorsum and dorsolateral surfaces of petiolar node and postpetiolar tergum areolate-rugulose with posteriorly directed appressed, linear to lanceolate ground hairs. Petiolar anterior surface smooth and shining with abundant punctae, laterally and ventrally opaque and areolate; postpetiolar ventrum transverse, opaque and areolate.

Dorsal margin of abdominal tergite IV broadly convex in lateral view, ventral margin of sternite IV markedly convex except for brief, anterior vertical margin; tergum densely punctulate, space between depressions less than their diameters; ventrite IV densely punctate, space between the depressions may be opaque to shining. Abdominal tergum IV with transverse carina along anterodorsal margin that separates dorsum from very narrow transverse anterior surface. Pilosity on tergite IV consisting of 12–16 erect to suberect arched spatulate hairs generally forming 4 longitudinal rows on the posterior half: 2 median rows of 3 or more hairs each flanked by a row of 2 or more hairs, 2 median hairs present just anterad of mid-length. Ground pilosity consists of abundant arched and appressed lanceolate hairs mostly pointing posterad on dorsal surface, pilosity much reduced to absent along lateral face of tergum and most of ventrum. Tarsal claws simple and slender, about as long as fifth tarsomere; legs stout; protibial apex with long spatulate hair anterolaterally, plus another more slender hair just posterad; rest of hairs on protibia mostly short and arched, hairs towards tibial apex longer. Mesotibial and metatibial apex each with two prominent spatulate hairs, one longer than the other; lateral surface of meso- and metatarsi each with two longitudinal rows of elongate, spatulate hairs. Body mostly dark brown; antennae and legs lighter; mandible mostly brown with apical tooth dark brown.

**Queen description.** ( $n = 3$ ): HL 0.76–0.82; HW 0.82–0.98; ML 0.49–0.60; EL 0.13–0.13; SL 0.38–0.49; PW 0.60–0.76; WL 0.87–1.00; PH 0.24–0.29; PL 0.31–0.36; DPW 0.40–0.51 mm. CI 1.09–1.19; MI 0.59–0.62; OI 0.14–0.16; SI 0.45–0.50; LPI 0.79–0.93; DPI 1.29–1.57. Head very much as in worker but with 3 ocelli, lateral ocelli directed laterally and anterior ocellus directed anterad. Compound eye large, 12–15 ommatidia across. Mesonotum with mostly longitudinal rugulae. Petiolar node relatively smaller, lower and peduncle more elongate than in worker. All of lateral mesosoma densely punctate. Propodeal tooth triangular with posterior weakly convex keel.

**Male.** Unknown.

**Type material examined.** ECUADOR. Pichincha: 20–30 km ENE Allurquin on Chiriboga Rd., VI.1975, S. & J. Peck, 1w, MCZC B-301, moss forest (holotype); Tinalandia, 16 km SE Santo Domingo de los Colorados, 9.V.1976, S. & J. Peck, 1w MCZC P-106 (paratype); Tinalandia, 16 km SE Santo Domingo de los Colorados, 680 m, no date, S. & J. Peck, 1w MCZC B-300 (paratype); 3 km E Tandapi, 1300 m, 2.VI.1975, S. & J. Peck, 1w MCZC, litter, wet ravine (paratype); 3 km E Tandapi, 1300 m, 2.VI.1975, S. & J. Peck, 2w MCZC B-303 (paratype); 3 km E Tandapi, 1300 m, VI.1975, S. & J. Peck, 1w MCZC (paratype); Tinalandia, 16 km SE Santo Domingo de los Colorados, 680 m, 1975, S. & J. Peck, 1w MCZC B-300 (paratype); Tinalandia, 16 km SE Santo Domingo de los Colorados, 4.VI.1975, S. & J. Peck, 1w MCZC (paratype); 4 km SE Santo Domingo de los Colorados, 500 m, 8.VI.1976, S. & J. Peck, 1q MCZC B-342 (paratype); 20–30 km ENE Allurquin on Chiriboga Rd., 1400–1800 m, 1975, S. & J. Peck, 1w MCZC B-301, moss forest (paratype).

**Other material examined.** COLOMBIA. Chocó: 10 km SW San José del Palmar, Finca Los Guaduales, Río Torito 800 m, 1-449, vi.1978, C. Kugler, 3w MCZC, Guadua Litter. ECUADOR. Otongachi, 850 m, 0°18'49"S, 78°57'15"W, ix.2013, 1w

UTPL; Otongachi, 850 m, 0°18'49"N, 78°57'15"W, 13.vii.2011, G. Ramón, 1q QCAZ VD-1137, LL10 W14; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 13.vii.2011, G. Ramón, 1q QCAZ VD-998, LL10 W19; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 13.vii.2011, G. Ramón, 1q QCAZ VD-508, LL11 W3; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 4.viii.2008, D. Donoso, 1q QCAZ KT-694, LL6 W2; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 13.vii.2011, G. Ramón, 1q QCAZ VD-1166, LL11 W10; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 6.viii.2009, G. Ramón, 1q QCAZ KT-514, WLL-E, ART-F10; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 6.viii.2009, G. Ramón, 1q QCAZ KT-1018, WLL-E, NAT-F7; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 3.viii.2011, G. Ramón, 1q QCAZ VD 354, LL 12, W16; Río Toachi, 900 m, -0.3304° -78.9414°, 5.ix.2003, D. Donoso, 1q, 2w QCAZ LL1 P4, W484, QCAZ 59326; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 3.viii.2011, G. Ramón, 1w QCAZ VD-720, LL12, W12; Río Toachi, 900 m, -0.3304° -78.9414°, 5.ix.2008, D. Donoso, 2w, QCAZ XC199, LL1P4, W48 h; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 13.vii.2011, G. Ramón, 1w QCAZ VD-928, LL10 W3; Río Toachi, 900 m, -0.3304° -78.9414°, 5.ix.2003, D. Donoso, 3w QCAZ LL1 P9, W484, xc250, QCAZ 59331; Río Toachi, 900 m, -0.3304° -78.9414°, 5.ix.2003, D. Donoso, 1w QCAZ LL1 P6, W484; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 4.viii.2008, D. Donoso, 1w QCAZ KT-1640, LL6-W1; Río Toachi, 900 m, -0.3304 -78.9414, 5.ix.2003, D. Donoso, 1w QCAZ LL11 W484, xc230, QCAZ 59332; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 3.viii.2011, G. Ramón, 1w QCAZ VD-1164, LL12 W4; Otongachi, 850 m, 0°18'49"S, 78°57'15"W, 13.vii.2011, G. Ramón, 1w QCAZ VD-1038, LL10 W18. PANAMA. Chiriquí: Finca Lérida near Boquete, 2370 m, 8.8129° -82.4836°, 17.iii.1959, H.S. Dybas, 2w FMNH FMNH-INS 95868/9; 2 km Cerro Punta, 2200 m, 8.8495° -82.5489°, 1.vi.1977, S. & J. Peck, 1w, 1q FMNH FMNH-INS 95862/3. Unknown: Cerro Bollo, 1800 m, 20.i.1981, W.R. Suter, 1w, 1q, FMNH FMNH-INS 95866/7, BS-2575, ex litter under broad leaf epiphyte.

**Type locality.** Pichincha, Ecuador.

**Distribution.** Western Panama to central Ecuador, the broadest distribution within the genus.

**Biology.** Known from premontane to montane forests with the highest altitudinal records from Panama at close to 2400 m and the lowest in Ecuador at 680 m. Most records are from few individuals but in central Ecuador they may be common in the Otongachi Reserve and to a lesser extent in one site along the Toachi River. At the southern limit of its range it may be sympatric or parapatric with *P. loxanensis* sp. n. but field work is necessary to corroborate this conjecture.

**Comments.** This is the type species for the genus. *P. armata* is easy to separate from other species on account of its two very prominent ventral teeth on each mandible. All other species have only one such tooth. Compared with other *Protalaridris* these ventral teeth project mesad more than ventrally, in lateral view their length is relatively less than that of other species. Some specimens of *P. loxanensis* sp. n. may have a well-developed ventral tooth apicad of the basal ventral tooth that approaches the condition in *P. armata*. *P. armata* has the dorsal mandibular margin mostly devoid of denticles whilst other *armata* group species have several. *P. armata* has distinct posterolateral occipital lobes; each lobe has a dorsal convex surface, distinct from

the curvature of the rest of the posterodorsal cephalic surface. The lobes in *P. punctata* are relatively smaller and lack distinct curvature. In all species the frontovertexal ridge, upon reaching the lateral cephalic margin, curves and continues anterad until reaching the antennal fossae, defining the dorsal cephalic surface. The eye in *P. armata* is placed at the edge of the dorsal cephalic surface, forming part of its lateral margin, but in most other species the eye is separated from the dorsal surface by at least one ocular diameter, half a diameter in *P. arhuaca* sp. n. This location of the eye, along with the well-impressed antennal scrobe in *P. armata* combines to give the impression the eye is situated along a ridge as wide as the eye. All other species have the eye on a broadly curving surface, either because of the distance separating it from the dorsal cephalic surface or because of a shallowly impressed antenna scrobe, or both.

*P. armata* specimens have their mandibles, part of the mesosoma, and gastral tergum frequently encrusted with debris that obscure features such as denticles and sculpturing. On the mesosoma the presence of decumbent hairs seem to coincide with the dorsolateral parts with crusts. The number and arrangement of erect hairs on the gastral tergum is variable. Specimens from Panama are more ferruginous in color and have the anterolateral edges of the head carinate, their mandibular denticulation is more variable in other populations, and their anterior ventral tooth is not as developed as in samples from Colombia and Ecuador. The tooth between the two massive ventral teeth is smaller and sometimes placed closer to the anterior tooth,

which may be apically cleft. The Panama specimens also have the transverse cephalic crest consistently well-developed, whilst in specimens from other sites the crest may be poorly developed. The Chocó specimens are generally darker with the gastral sternites shining and finely punctate. The Cerro Bollo locality could not be found with a degree of reasonable doubt. A search through different sources gave similarly named localities in Chiriquí and in Ngöbe Buglé at altitudes of 1800 m or less.

### *Protalaridris bordoni* Latke, sp. n.

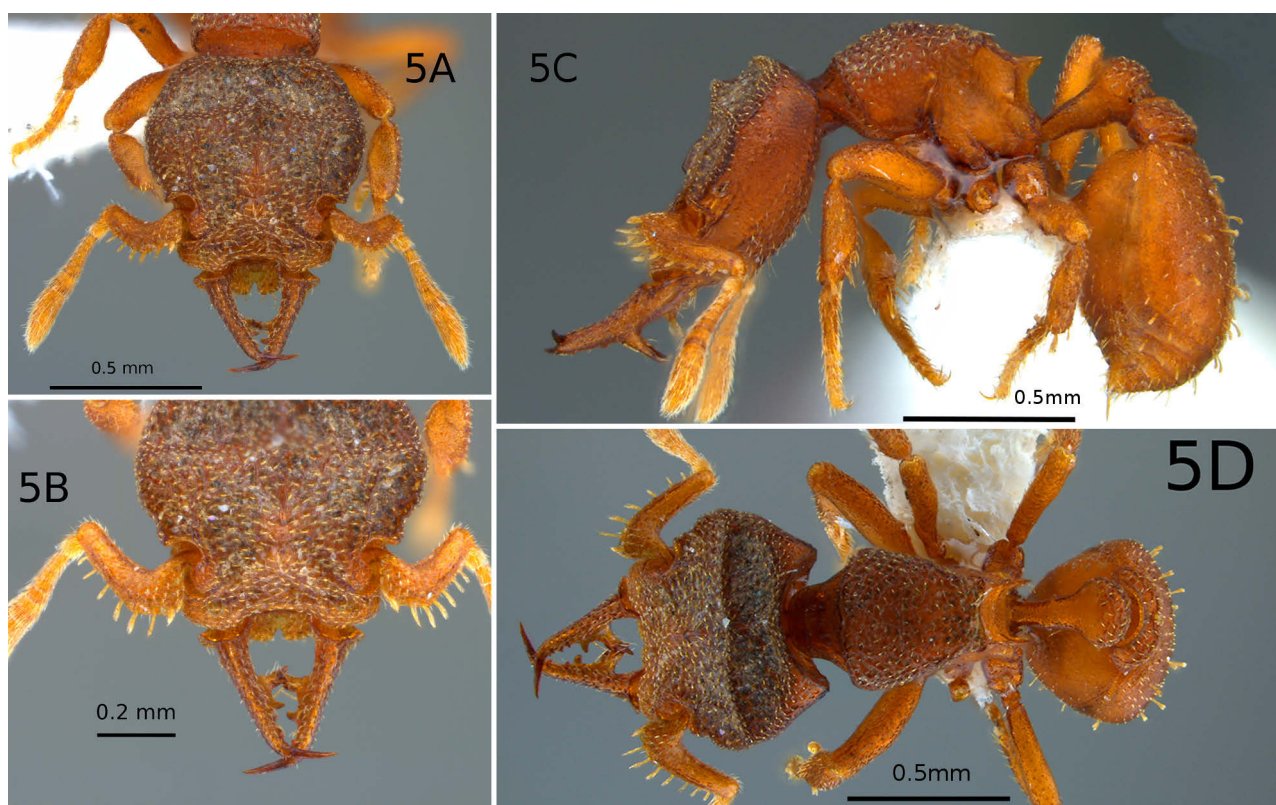
(Figs 5a–d)

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**Worker diagnosis.** Cephalic dorsum with prominent transverse carina situated posteriorly at approximately three-fourths cephalic length, cephalic dorsum with brief and rough longitudinal carina extending posterad from opening of frontal carina, cephalic discal area brief longitudinal carina. Compound eye with single ommatidium. Anteromedian labral cleft deep, reaching at least to labral mid-length.

**Measurements of type specimens.** Holotype (paratypes,  $n = 5$ ): HL 0.63 (0.62–0.67); HW 0.67 (0.63–0.68); ML 0.35 (0.33–0.35); EL 0.05 (0.03–0.04); SL 0.35 (0.32–0.35); PW 0.38 (0.37–0.40); WL 0.62 (0.62–0.62); PH 0.18 (0.17–0.18); PL 0.28 (0.25–0.28); DPW 0.20 (0.18–0.20) mm. CI 1.05 (1.03–1.07); MI 0.53 (0.50–0.53); OI 0.08 (0.05–0.06); SI 0.53 (0.48–0.53); LPI 0.65 (0.63–0.73); DPI 0.71 (0.69–0.77).



**Fig. 5.** *P. bordoni* sp. n. Worker holotype: A – head dorsal view; B – mandible, full length view; C – body lateral view; D – body dorsal view. Specimen MIZA0021677. Images by T. Delsinne.

**Worker description.** Cephalic dorsum with well-defined, carinate borders; clypeus with broad median concavity along anterior margin, broadly convex laterally; lateral cephalic margin posterad of antennal fossa convex, head widest at posterior two-thirds, most of lateral margins converge anterad; posterior cephalic margin weakly emarginate medially, occipital lobe inconspicuous. Frontal lobe dorsally convex, width in dorsal view less than half of fossa. Eye reduced, but distinct, to apparently one ommatidium, facing anterolaterally, separated from antennal fossa along lateral cephalic margin by not more than 3 diameters, separated from dorsal face by not more than one diameter in lateral cephalic view. Cephalic dorsum mostly weakly areolate-rugulose, commonly encrusted with dirt and debris that obscure cuticle; dominated by prominently raised transverse carina, carina with median blunt angle, laterally joins with carina that defines lateral cephalic margin. Cephalic dorsum between transverse carina and posterior cephalic carina convex in lateral cephalic view. Frons with median longitudinal carina present on weakly raised swelling, both fading just anterad of transverse carina. Another longitudinal carina projects posterad from antennal fossa, longer and better developed than median carina, but failing to reach transverse cephalic carina. Cephalic dorsum with mesially pointing subspatulate to lanceolate appressed hairs; occiput areolate, posterolateral region areolate-rugulose. Cephalic ventrum mostly areolate to areolate-rugulose, posterolaterally densely punctulate and shining.

Mandibles form complex cradle or cage bound by the main axis of each mandible as well as prominent ventral tooth. Mandible in full length view slender, progressively tapering towards apex, mostly straight until base of apical tooth, at which it bends mesad. Base of mandible at cephalic insertion, expands into flange with smooth rim and areolate dorsal surface. Mandible mostly with scattered rugulae and appressed pilosity directed apicad; smooth and shining sculpture limited to posteroventral area, ventral tooth, and mandibular apex. Mandible apicad of crossing dark brown and sharply pointed. Mandibular dorsal margin forms broad concavity with dorsal cephalic surface in cephalic lateral view, ventral tooth tapers posteroventrally, mostly straight, its length about 1/3 that of lateral mandibular length. Dorsal mandibular margin with 2–3 preapical denticles, one may be present posterior to ventral tooth, and the rest apicad to ventral tooth; dorsal mandibular margin with decumbent slender hairs, directed anteromesad. Ventral internal mandibular margin with short stout tooth, not more than half mandibular width at that point, just apicad of ventral tooth; 2 denticles also present, one at base of apical tooth. Stout tooth sometimes with basal angle or lobe. Mandible with prominent ventromedially directed tooth, situated closer to mandibular base than apex in mandibular full length view; ventral tooth in dorsal view tapering apicad, posterior margin edentate and broadly concave; length approximately equal to length of smooth apex of mandible in full length view. In anterior view, ventral tooth relatively straight with small decumbent tooth along anter-

odorsal margin; apex of tooth tapering, not forked. Internal surface of ventral tooth mostly smooth and shining. With mandibles closed the apex of each ventral tooth cross; apical and ventral tooth ferruginous brown, smooth and shining. Single hair, almost as long as ventral tooth inserted just apicad of tooth and subparallel to it.

Lateral extremities of labrum not visible in dorsal view with mandibles closed, though at least one base may be visible, basal ridge weakly but distinctly sinuous; anteromedially a deep incision forms an acute angle not quite one-half the length of the labrum, dividing it into two lobes. Ventral surface mostly smooth and shining, dorsal surface sculpted, not smooth and shining. Anterolateral margin of each lobe with three long hairs, second hair from labral cleft the longest, slender and lanceolate. Other hairs weakly spatulate with apex truncate, and apical half twisted so plane of hair is directed longitudinal to cephalic axis. Labral cleft with 1 or 2 short, spatulate hairs; labral hairs parallel to ventral tooth in lateral view and of approximately same length, two internal hairs of each lobe ventrally directed in dorsal view, whilst external hair lateroventrally directed. Palpal formula unknown. Scape in dorsal view longitudinally rugulose with apical two-thirds mostly straight and parallel, anterobasal lobe weakly expanded anterad, dorsum lacking hairs. Cross-section of scape at mid-length triangular, dorsal margin broadly convex, ventral margin mostly straight. External scape margin defined by narrow longitudinal lamella, one along ventral margin and another along dorsal margin; external scape margin bears 8–9 weakly erect hairs that stem from anteroventral margin; one short ovate hair close to basal angle, with following hair slender, weakly lanceolate and the longest, remaining hairs spatulate, bluntly pointed. Head ventrolaterally punctulate.

Mesosomal dorsum in lateral view convex, dorsal propodeal margin brief; declivitous margin covered by tooth; base of tooth broadly concave, apex pointed, posterior margin briefly concave, then vertical. Mesosomal dorsum and dorsolateral one-third of pronotum rugulose, with numerous decumbent, weakly lanceolate hairs, mostly directed posteromesad; no erect hairs on dorsum of head, mesosoma, petiole, and postpetiole. Most of lateral pronotum, mesopleuron, and propodeum punctulate to areolate, wanting pilosity, metapleuron smooth; katapisternum lacking series of transverse rugulae. Pronotum with anterior transverse carina that separates a strongly sloped anterior facing strip and the pronotal collar; promesonotal suture marked as rough transverse carina, anteriorly broadly convex. Promesonotal surface overhanging lateral pronotal surface; propodeal dorsum not as wide as lateral surface, lateral metapleural – propodeal surface not or barely visible in dorsal mesosomal view.

Petiolar node convex to subquadrate in lateral view, anterior petiolar margin mostly straight to weakly concave, anteroventral process lacking or present as low swelling at best, postpetiolar dorsal margin in lateral view mostly flat, posterior margin convex. Postpetiole transverse in dorsal view, slightly shallower medially than laterally, an-

terior margin concave and shorter than convex posterior margin, dorsum of petiolar node and postpetiole areolate-rugulose with posteriorly directed appressed, weakly lanceolate-shaped hairs. Dorsal margin of abdominal tergum IV broadly convex in lateral view, ventral margin markedly convex, with greatest height just anterad of gastral mid-length; densely punctulate, space between depressions less than their diameters; pilosity consisting of sparse arched subdecumbent lanceolate hairs, and some 25–30 suberect, truncate hairs forming 6–8 ill-defined longitudinal rows, hairs are spatulate along anterior of tergum IV and become progressively linear towards posterior of tergum IV, pilosity not obscuring sculpturing.

Abdominal tergum IV with transverse carina along anterodorsal margin that separates dorsum from brief transverse anterior surface. First gastral ventrum with dense, scalloped punctures, abruptly impressed anterad and gradually impressed posterad, sparsely clothed by decumbent hairs pointing posterad, and sparse suberect simple hairs. Sting stout. Tarsal claws simple, long and slender; legs stout, not elongate; protibial apex with spatulate hair anterolaterally, plus two flattened linear hairs, one lateral the other posterolateral, posterolateral hair longest; rest of hairs on protibia short, arched. Lateral surface of meso- and metatarsi each with two longitudinal rows of spatulate hairs, apex of lateral surface of meso- and metatibia each with single spatulate hair, apically wider than that of protibia. Body mostly ferruginous, darker tint on transverse cephalic carina and cephalic dorsum posterad of carina, apex of mandible and ventral mandibular tooth, mesosomal dorsum and propodeal lamella, including tooth, and gaster throughout.

**Queen description.** Measurements. HL 0.78; HW 0.78; ML 0.50; EL 0.17; SL 0.45; PW 0.60; WL 0.95; PH 0.20; PL 0.38; DPW 0.25 mm. CI 1.00; MI 0.64; OI 0.21; SI 0.57; LPI 0.52; DPI 0.65. Only the measurements and indices are offered as the specimen was measured but left in MIZA by the senior author upon relocating from Venezuela before he could write a description. The present conditions in Venezuela preclude sending specimens through the mail. Images of this gyne can be accessed in Antweb using the unique specimen identifier CASENT0248768.

**Male.** Unknown.

**Type material.** Holotype worker: VENEZUELA. Aragua: Parque Nacional Henri Pittier, Rancho Grande, La Cumbre, 10°21'34"N, 67°41'06"W, 1450 m, 12.ix.2007, M. Riera 100, C. Rodriguez, J. Valera leg. Point-mounted worker found by soil washing. Property of MIZA [unique specimen identifier MIZA0021677] but presently in DZUP. Paratypes: VENEZUELA. Aragua: Pq. Nac. Henri Pittier, Rancho Grande, La Cumbre, 10°21'34"N, 67°41'06"W, 1400 m, 4.xi.1986, C. Bordon leg., 1 queen in CAS with two unique specimen identifiers MIZA0021727, CASENT0248768 (flight intercept trap); Pq. Nac. Henri Pittier, Rancho Grande via La Cumbre, 10°21'17"N, 67°40'55"W, 1225 m, 26.i.2008, M. Riera 161, R. Lujan, J. Valera leg., 1 worker in MCZC; Pq. Nac. Henri Pittier, Rancho Grande, La Cumbre, 10°21'34"N, 67°41'06"W, 1450 m, 12.ix.2007, M. Riera 100, C. Rodriguez, J. Valera leg., 1 worker in MIZA; Pq. Nac. Henri Pittier, Rancho Grande via La Cumbre, 10°21'17"N, 67°40'55"W, 1225 m, 10.iii.2007, M. Riera 33, J. Lattke, O. Riera,

C. Cardona, C. Rodriguez leg., 1 worker in NHMUK; same data as previous except M. Riera 34, 1 worker in DZUP, 548781.

**Type locality.** Aragua, Venezuela.

**Etymology.** The species epithet is a patronym honoring Carlos Bordon (1921–2012), an amateur entomologist that avidly collected insects in Henri Pittier National Park (Venezuela). He generously shared his time and material resources with MIZA and budding entomologists as well, including the senior author.

**Distribution.** Known only from the type locality.

**Biology.** At present one of the two only known localities where two *Protalaridris* species are sympatric is the cloud forest above 1200 m in the Rancho Grande sector of Henri Pittier National Park in the Coastal Cordillera of Venezuela (the other locality is RBSF in Ecuador with *P. leponcei* sp. n. and *P. loxanensis* sp. n.). Specimens of the two species were found only 10 m distant from each other along the same sampling transect. Both species have been found in either leaf litter samples or soil samples. The different denotation between the two species as well as the contrastingly shaped labral hairs, suggest that prey may be different for the two species. Most specimens of *P. bordoni* sp. n. have the dorsal body surfaces caked with a thin layer of light colored matter that seems to accumulate more within cuticular impressed areas, such as the bottom of punctae or rugulae. In contrast most *P. punctata* sp. n. specimens were found free of encrustations.

**Comments.** This species is morphologically very different from the sympatric *P. punctata* sp. n. (see “Comments” for the latter).

***Protalaridris leponcei* Delsinne & Lattke, sp. n.**

(Figs 6a–d)

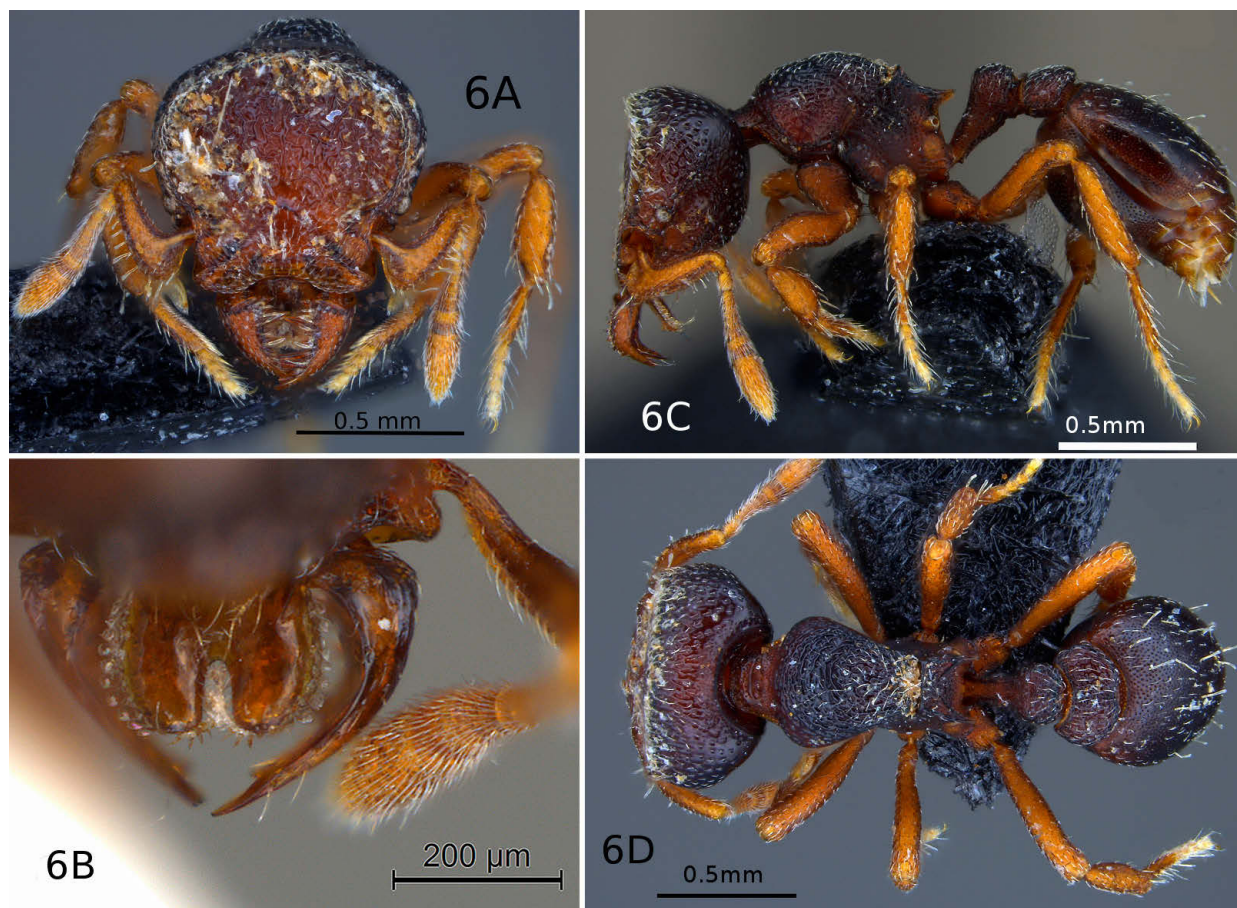
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**Worker diagnosis.** Mandible highly distinctive: short, stout, triangular, and strongly bowed. Basal mandibular tooth continuous with basal rim, not separated by diastema. Frontal lobe covering most of antennal fossa in dorsal view. Frontal carina and frontovertexal ridge delimiting anterodorsally truncated area in head capsule. Eye well separated from head dorsum by twice diameter length. Labrum with anteromedian cleft extending over half its length, and with numerous translucent hairs along its margin (up to 32 hairs in holotype). Head truncated area and dorsum of pronotum rugo-reticulate.

**Holotype measurements.** HL 0.73; HW 0.81; ML 0.21; EL 0.06; SL 0.41; PW 0.48; WL 0.76; PH 0.36; PL 0.38; DPW 0.23; PPL 0.19; PPW 0.38 mm. CI 1.12; MI 0.26; OI 0.08; SI 0.51; LPI 0.95; DPI 0.6.

**Worker description.** Head in frontal view slightly wider than long, widest at posterior one fourth. Posterior cephalic margin straight, without median emargination, posterolaterally convex, with inconspicuous occipital lobe. Lateral cephalic margin posterior to eye broadly convex, in continuity with occipital convexity. Lateral cephalic margins anterior to eye almost straight, converging anteriorly. Frontal lobe covering most of fossa in dorsal view except for anteriormost part. Frontal carina sharp, continuous with



**Fig. 6.** *P. leponcei* sp. n. Worker holotype: A – head dorsal view; B – labrum ventral view; C – body lateral view; D – body dorsal view. Specimen RBINS33008. Images by T. Delsinne.

raised frontovertexal ridge that arches across vertex (“facial arc” sensu Longino & Boudinot, 2013). Eye reduced, but distinct and visible in frontal view, 10–12 partially fused ommatidia, facing anterolaterally, separated in lateral view from antennal fossa by one diameter or less and from dorsal face by nearly two diameters. One spatulate hair on each side of ridge, posterior to eye and lateral to frontal carina.

Cephalic dorsum delimited by frontal carinae and ridge flattened (truncated) in lateral view. Cephalic dorsum posterior to frontovertexal ridge convex, curving posteriorly to form cephalic posterior margin and broadly convex ventral margin. Antennal scrobe ventrad of eye running from anterior ventral cephalic margin to occipital corner; its anterior half shallow but distinct, delimited ventrally by faint carina and dorsally by fossa ventral margin, its posterior half very shallow, not delimited by carina or flange and progressively vanishing. Occipital carina sharp and extending ventrally across posterior fourth of cephalic capsule, roughly equidistant from postgenal bridge and ventral scrobe margin. Postgenal suture visible as darker line across the head ventral area. Hypostoma sharp and projecting a little above buccal cavity as translucent lamina. Clypeus smooth and shining. Area delimited by frontal carinae and frontovertexal ridge strongly rugo-reticulate, without clear median longitudinal carina, encrusted with dirt and debris that obscure shining cuticle. Cephalic dorsum posterad of ridge,

including lateral cephalic region above eye, with longitudinal rugulae, fading to smooth and shining with sparse punctae near occipital carina. Scrobe from anterior margin to eye level shallowly but densely foveolate, then with sparse punctae. Ventral head area with shallow foveolae and with irregular mostly transverse rugae. Cephalic dorsum with short appressed hairs, pointing anteromedially. Head ventrum with both short appressed hairs and 10–12 sparse longer suberect hairs.

Mandible short, stout, and triangular. Dorsal margin in lateral view strongly bowed with basal portion in same plane as clypeus and apical portion strongly bent downward. Base of mandible at cephalic insertion expands into flange with smooth rim. Mandible with 10 teeth, tooth 1 robust and continuous with basal rim, tooth 3 at least twice as long as teeth 1, 2, 4–6, these teeth subequal in length, except tooth 5 slightly longer. Teeth 7–10 forming an apical fork perpendicular to base of dorsal face, tooth 7 long and separate, tooth 8 about 1/3 length of tooth 7 (and subequal in length to teeth 1, 2, 4, and 6), tooth 9 slightly sharper than tooth 8, joined to tooth 10 at mid-length between tooth 8 and 10 (or could be interpreted as single tooth bifid at the tip), tooth 10 longer than tooth 7 (but, as the mandible is bent, teeth 7 and 10 reach the same level in dorsal view); dorsal surface of mandible roughened, ventral surface narrow, smooth and shining; interior surface strongly concave, smooth and highly polished. Mandibular dorsum with very

short appressed hairs. Masticatory mandibular margin with series of translucent, flattened, lanceolate hairs inserted among teeth 1–7. Apex of mandible, close to teeth 7–10, with longer thin hairs. Single long hair, flexuous at the tip, inserted ventrally at and perpendicularly to the base of the mandible, very close to the mandible insertion with cephalic capsule.

Labrum hardly visible in dorsal view with mandibles closed; with outer lateral margin and apex forming a continuous convexity, and with acute anteromedian cleft extending over one-half labrum's length. Both dorsal and ventral surfaces mostly smooth and shining. Hairs inserted along labral margin directed ventrally and shaped as follows: outer lateral margin of each lobe with fringe of at least 11 translucent, flattened, subrectangular hairs, serially increasing apicad in both length and width; lobe apex with single thin hair, three times as long as preceding subrectangular hair; close to cleft, 3–4 aciculate hairs, roughly as high as the apical-most subrectangular hair; minute hairs may be present within cleft. Palpal formula unknown. Scape in dorsal view with faint longitudinal rugulae with apical two-thirds mostly straight and parallel, anterobasal lobe slightly expanded anterad. Cross-section of scape at mid-length flattened, subrectangular, with external margin roughly as wide as internal margin, dorsal and ventral margins straight. External and internal scape margins defined by narrow longitudinal lamella, one along ventral margin and another along dorsal margin. Scape with sparse short decumbent hairs, denser along its internal margin. External scape margin with series of 8–10 weakly spatulate (apically fringed at 80x) erect hairs; hair closest to apex of basal lobe longest.

Promesonotum in lateral view broadly convex. Dorsal propodeal margin concave, confluent with triangular and sharply pointed propodeal tooth. Declivitous margin of propodeum straight; short lamella present from base of propodeal tooth to propodeal spiracle. In dorsal view, pronotal cervix polished, with sparse punctae and with short medial transverse carina, posteriorly marked by narrow, shallow furrow. Promesonotum covered by transversely arching rugo-reticulation, with short appressed hairs. Promesonotal suture barely distinguishable, not interrupting sculpture. Promesonotum and propodeum separated by shallow furrow obscured by particulate matter, immediately anterad of strongly raised transverse carina marking anterior margin of propodeum. Propodeal dorsum very short with rugulae and punctae, lacking pilosity, separated from declivitous face by transversely arched carina confluent with inner margin of propodeal teeth. Declivitous face finely areolate. Lateral pronotum, mesometapleuron, and propodeum irregularly foveolate, with oblique rugulae on posterior region of pronotum and on anepisternum; wanting pilosity. Metapleural gland opening forming vertical slit covered by cuticular flange and not visible in lateral view. Bulla visible through cuticle. Petiolar node in lateral view convex to subquadrate, anterior petiolar margin mostly straight to weakly concave, anteroventral process shaped as low angular lobe, postpetiolar dorsal margin in lateral view broadly convex,

convexity increasing posterad. Postpetiole flattened, transverse in dorsal view, anterior margin concave and shorter than convex posterior margin. Dorsum of petiolar peduncle finely areolate, lateral region densely foveolate. Dorsum of petiolar node with transverse rugulae; dorsum of postpetiole with fovae and fainter rugulae; both dorsa with posteriorly directed appressed short hairs.

Dorsal margin of abdominal tergum IV broadly convex in lateral view, ventral margin markedly convex, with greatest height in anterior half of gaster. Dorsum densely punctulate, space between depressions equal to 1–2 of their diameters; smoother areas present on lateral and posterior parts of tergite; pilosity consisting of sparse appressed short hairs, and some 16–20 suberect, spatulate (apically fringed) longer hairs; pilosity not obscuring sculpturing. Abdominal tergum IV with transverse carina along anterodorsal margin, separating dorsum from anterior surface. First gastral ventrum densely punctate, with appressed pilosity pointing posterad and sparse suberect spatulate hairs. Sting not visible. Tarsal claws simple, long, slender, poorly diverging (delimiting an angle of 50–60°) and strongly bent; legs stout, not elongate; protibial apex with spatulate hair anterolaterally, plus one hair posterolaterally; rest of hairs on protibia short, appressed. Meso- and metatibial apices each with anterolateral and posterolateral spatulate hairs, anterior hairs largest. Trochanters finely areolate to punctulate. Tibiae and femora finely areolate, with faint longitudinal striae on apical dorsum for tibiae. Body mostly ferruginous, darker tint along facial arc. Appendices (mandibles, antennae, legs) lighter, brownish. Tarsi except basitarsi pale yellow.

**Queen and male.** Unknown.

**Type material.** Holotype worker (point-mounted; RBINS). ECUADOR. Zamora-Chinchipe: 13 km E Loja, Reserva Biológica San Francisco, “forester plot”,  $-3.97504^{\circ}$   $-79.07631^{\circ}$ , 1970 m, 23.IX.2007, M. Leponce coll., in 1 m<sup>2</sup> of sifted litter extracted during 48 h (Winkler sample). Unique specimen code RBINS33008 from sample code RBINS33700. DNA extracted from two legs by John Longino and Michael Branstetter (University of Utah). Paratypes 4 workers in RBINS, all preserved in ethanol, same data as holotype except: 1 worker, specimen code RBINS33010 from sample code RBINS33710; 1 worker, specimen code RBINS33011 from sample code RBINS33694; 1 worker, specimen code RBINS33007 from sample code RBINS33695; 1 worker, specimen code RBINS33009 from sample code RBINS33688.

**Type locality.** Loja, Ecuador.

**Etymology.** The species epithet is a patronym to honor our colleague and friend Maurice Leponce, myrmecologist at the Royal Belgian Institute of Natural Sciences, and collector of the type series. Maurice was one of the supervisors of T. Delsinne's PhD thesis and regularly provides help to the authors with ant digitization, analyses or specimen sharing.

**Distribution.** Only known from the type series collected at the Reserva Biológica San Francisco, which borders the Podocarpus National Park on the eastern Andean slope of southern Ecuador.

**Biology.** It was found at 1970 m in the leaf litter of an evergreen lower montane forest in nearly pristine condition

(Homeier et al., 2008). Five workers were found in 5 samples (20%) of a grid of  $5 \times 5$  (25) Winkler 10 m apart from each other. Sampling points with *P. leponcei* sp. n. were separated by 10 to 50 m. At the type locality, *P. leponcei* sp. n. seems therefore frequent although at low abundance. Interestingly, a worker of *P. loxanensis* sp. n. was found in another Winkler sample of this very grid, resulting in the second case of sympatry recorded for the genus. It is possible that *Protalaridris leponcei* sp. n. is very restricted in distribution as intense sampling [ $> 430$  Winkler samples ( $0.5 \text{ m}^2$  of leaf-litter extracted during 48 h)] carried out in the same continuous forest, 1.1 km away, at 2070 m did not result in the collection of additional specimens. Nevertheless, this second site was closer to the mountain ridge and some undetermined variables (e.g. soil properties, sun exposition, vegetation height) were perhaps sufficiently different to prohibit the occurrence of *P. leponcei* sp. n. in that part of the forest.

**Comments.** The species can be very easily separated from any other known *Protalaridris* species by the unique shape of its mandibles. In addition, the eye is relatively more developed (up to 11–12 ommatidia rather than 1–5 ommatidia in other species), and it is placed lower on the lateral cephalic region, at a further distance from the cephalic dorsum. The frontal lobe is more expanded laterally and covers most of antennal fossa in dorsal view. The connection of the frontal carina with the frontovertexal ridge, defining a truncated area on the cephalic dorsum, is also unique. The carina separating the promesonotum from the propodeum is more marked and elevated. In some aspects, *Protalaridris leponcei* sp. n. is more reminiscent of the *Octostruma ascribicula* species-group than of its congeneric species. In particular, these ants share similar mandibular shape (strongly bowed) and a basal tooth confluent with the mandibular rim. However, careful observation of tooth size show differences (for instance, tooth 3 is much larger than teeth 2 and 4 in *P. leponcei* sp. n., but much smaller in *O. ascribicula* species-group). Other similarities are the truncated area delimited by the frontal carinae and the conspicuous facial arc (although these carinae are not confluent in some *Octostruma* species, such as *O. convallisur* Longino, 2013), presence of at least two erect spatulate hairs on cephalic dorsum (except in *O. limbifrons* Longino, 2013), and eye distant from the cephalic dorsum by at least twice its diameter. However, *P. leponcei* sp. n. differs by its 9-segmented antenna (8-segmented in *Octostruma*), its labrum divided in two lobes by an acute anteromedian cleft (labrum subrectangular without deep anteromedian incision in *O. ascribicula* species-group), and by the presence of suberect hairs on the first gastral tergite (some are also present in *O. ascribicula* species-group but are always restricted to the posterior margin of gastral tergite I). SEM images of the holotype are available on Antweb: <https://www.antweb.org/specimenImages.do?name=rbins33008>.

***Protalaridris loxanensis* Lattke, sp. n.**

(Figs 7a–e, 8)

ZooBank LSID

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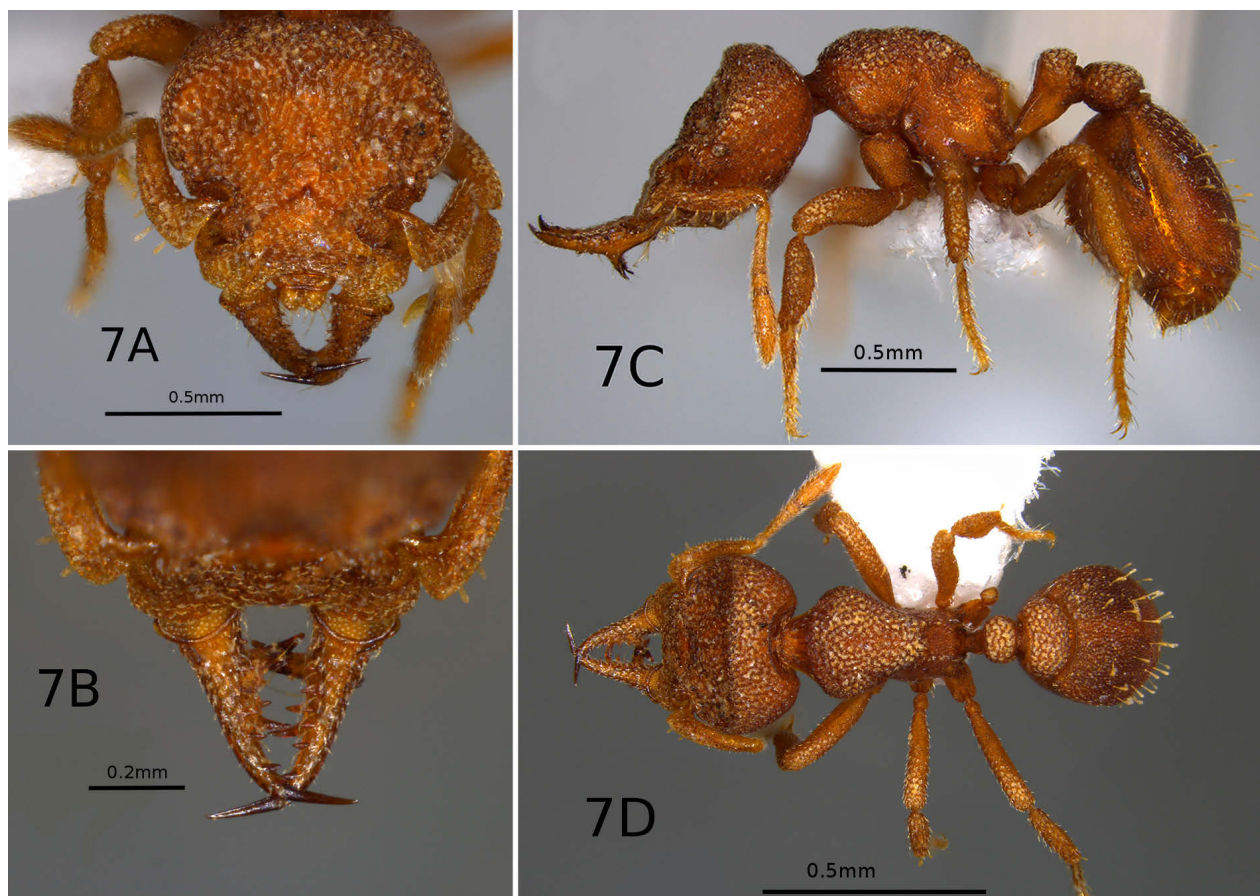
**Worker diagnosis.** Mandibular shaft relatively short and stocky, base relatively wide in full length view, rapidly tapering apicad; dorsal mandibular margin with 6–7 preapical teeth. Anterior margin of scape with 5–6 erect hairs; lateral labral margin with three hairs, two basal short lanceolate hairs directed laterally and long anterior hair directed anterolaterally. Abdominal tergite IV with 18–20 subdecumbent spatulate hairs.

**Measurements of type specimens.** Holotype (paratype): HL 0.78 (0.76); HW 0.84 (0.87); ML 0.51 (0.43); EL 0.06 (0.04); SL 0.43 (0.41); PW 0.51 (0.45); WL 0.77 (0.69); PH 0.22 (0.20); PL 0.43 (0.45); DPW 0.22 (0.33) mm. CI 1.08 (1.15); MI 0.61 (0.49); OI 0.07 (0.05); SI 0.51 (0.47); LPI 0.52 (0.45); DPI 0.75 (0.52).

**Worker description.** Head slightly wider than long in dorsal view; posterior margin mostly transverse with weak median emargination, occipital lobe inconspicuous, lateral cephalic margin posterior to eye convex; head widest at posterior one fourth, cephalic lateral margins converging anteriorly; clypeus with small shining posteromedian area. Eye reduced, but distinct, apparently 3–5 partially fused ommatidia, facing anterolaterally, separated from antennal fossa along lateral cephalic margin by not more than 2 diameters, separated from dorsal face by not more than one diameter in lateral cephalic view.

Cephalic dorsum mostly broadly concave in lateral view with short posterior convexity that curves posteriorly to form cephalic posterior margin and broadly convex ventral margin; lateral cephalic surface continuously curves with ventral surface; scrobe shallow and inconspicuous, ending anterad of compound eye. Cephalic cross-section at compound eye approximately bowl shaped with dorsal surface forming a mostly horizontal line on top of broad convexity. Cephalic dorsum mostly weakly areolate-rugulose, commonly encrusted with dirt and debris that obscure cuticle; dorsum traversed by arching, broadly concave carina that laterally curves anterad to posterior margin of antennal fossa, defining elongate posterior cephalic region elevated above anterior median cephalic region. Frons with weakly raised median swelling. Cephalic dorsum with short appressed spatulate ground hairs; occiput areolate, posterolateral region areolate-rugulose; ventral surface mostly areolate to areolate-rugulose, posterolaterally densely punctulate and shining.

Mandibles form complex cradle or cage mainly bound by the main axis of each mandible as well as one prominent ventral tooth. Mandible in full length view progressively tapers apicad, mostly straight until base of apical tooth, at which it bends mesad. Base of mandible at cephalic insertion expands into flange with smooth rim and areolate dorsal surface. Mandible relatively short and robust, dorsum mostly with scattered rugulae and short arched hairs that point anterad on dorsal and internal margins; appressed pilosity present, directed apicad; ventral mandibular surface mostly shining, weakly sculpted. Mandibular dorsal margin forms weak obtuse angle with dorsal cephalic surface in cephalic lateral view, ventral tooth points ventrally, mostly straight, its length under 1/3 that of mandible. Dorsal mandibular margin with 6–7 preapical short and



**Fig. 7.** *P. loxanensis* sp. n. Worker holotype: A – head dorsal view; B – mandible full length view; C – body lateral view; D – body dorsal view. Images by T. Delsinne.

acute teeth. Mandibular ventral margin with 4 preapical teeth (1–4), teeth 1 and 3 overlapping counterparts of other mandible. Tooth 1 (basal-most) massive and mesoventrally directed, tooth 3 large and medially directed. Teeth 2 & 4 short and acute: one between large teeth and other close to base of apical tooth. Basal tooth in dorsal view tapering apicad; in anterior view relatively straight with decumbent tooth along anterodorsal margin. Single long hair, almost as long as basal tooth, inserted just apicad of basal tooth and subparallel to it. Mandibular apical tooth dark brown shining and sharply pointed.

Labrum totally visible in frontal view, lateral extremes of base may be partially obscured by mandibles; shape subquadrate to weakly bilobed, lateral margin convex, anterior margin with median concavity of variable development, labrum wider posterad than anterad. Ventral surface mostly shining, dorsal surface sculpted, not shining. Lateral labral margin with three flattened hairs, two basal, short lanceolate hairs directed laterally and anterior long flagellate hair directed anterolaterally. Anterior margin with 4 flattened hairs, two lateral elongate lanceolate hairs directed anteriorly and median pair of short, converging or subparallel lanceolate hairs. Palpal formula unknown. Scape in dorsal view longitudinally rugulose, subparallel, slightly wider basad than apicad, internal margin broadly concave, external margin broadly convex, anterobasal lobe weakly expanded anterad, dorsum lacking hairs except for sparse

erect pubescence. Cross-section of scape at mid-length subrectangular, dorsal margin broadly convex, ventral margin mostly straight, external margin concave, internal margin convex; external scape anteroventral margin bearing 5–6 spatulate, apically truncate hairs; additional short arched hair placed close to basal angle; remaining pilosity sparse, short, and simple. Head ventrolaterally punctulate, ventromedially rugose.

Mesosomal dorsum in lateral view broadly convex, dorsal propodeal margin very brief; propodeal tooth relatively short, broadly triangular to acutely triangular, posterior base prolonged as lamella. Mesosomal dorsal and dorsolateral surfaces rugulose, with numerous decumbent ground hairs, mostly directed posteromesad. Most of lateral pronotum, mesopleuron, and propodeum punctate, punctae not as dense on metapleuron; katepisternum lacking transverse rugulae, mesosomal lateral surface without standing pilosity. Pronotum with anterior transverse rugae that separate collar region, collar with longitudinal carinae; promesonotal suture indistinguishable.

Petiolar node convex to subquadrate in lateral view, anterior petiolar margin weakly concave, anteroventral process lacking, postpetiolar dorsal margin in lateral view broadly convex. Petiolar node and postpetiole transverse in dorsal view; postpetiole weakly concave anteriorly and convex posteriorly, dorsum of petiolar node and postpetiole areolate-rugulose with posteriorly directed appressed,

ground hairs. Dorsal margin of abdominal tergum IV broadly convex in lateral view, ventral margin of sternite IV markedly convex; tergum densely punctulate, space between depressions less than their diameters; pilosity on tergite IV consisting of 18–20 arched subdecumbent spatulate hairs forming 6 longitudinal rows, appressed ground pilosity present. Abdominal tergum IV with transverse carina along anterodorsal margin that separates dorsum from very narrow transverse anterior surface. First gastral ventrum with densely punctate, sparsely clothed by decumbent hairs pointing posterad. Tarsal claws simple, long and slender; legs stout, not elongate; protibial apex with spatulate hair anterolaterally, plus smaller single arched hair just posterad; rest of hairs on protibia short, arched. Mesotibial apex with two spatulate hairs, metatibial apex with single spatulate hair, lateral surface of meso- and metatarsi each with two longitudinal rows of oblong hairs. Body mostly ferruginous brown, gaster darker; apex of mandible and ventral mandibular tooth, brown.

**Queen description.** Measurements. HL 0.76; HW 0.83; ML 0.56; EL 0.15; SL 0.43; PW 0.57; WL 1.00; PH 0.24; PL 0.43; DPW 0.44 mm. CI 1.10; MI 0.67; OI 0.18; SI 0.51; LPI 0.57; DPI 1.04. Head very much as in worker but with 3 ocelli, lateral ocellus directed laterodorsad, median ocellus directed anterad. Compound eye large, 12–15 ommatidia across, clearly visible in cephalic frontal view. Pronotal margin vertical in lateral view, mesonotum with anterior convex margin and mostly flat dorsally. Mesonotum with mostly longitudinal rugulae. Petiolar node relatively smaller, lower, and with peduncle more elongate than in worker. Mesosoma laterally densely punctate. Propodeal tooth triangular with posterior keel weakly convex. Gastral tergum with over 50 slender spatulate standing hairs, ventrum with abundant slender hairs; very sparse appressed pilosity also present on gaster. See genus description and discussion for venation.

**Male.** Unknown.

**Type material.** Holotype worker (point-mounted; to be deposited in QCAZ): ECUADOR. Loja: Reserva El Madrigal,  $-4.0466^{\circ}$   $-79.1758^{\circ}$ , 6.3 km SSE of Loja, 2350 m, 5.III.2015, J. Lattke 3708. Found by sifting leaf litter. Paratypes: ECUADOR. Loja: Reserva El Madrigal,  $-4.0466^{\circ}$   $-79.1758^{\circ}$ , 6.3 km SSE of Loja, 2350 m, 28.VIII.2014, J. Lattke 3590-5. One point-mounted worker found by sifting leaf litter and deposited in ARCE. ECUADOR. Zamora-Chinchipe: Reserva Biológica San Francisco,  $-3.9823^{\circ}$   $-79.0835^{\circ}$ , 13 km E of Loja, 2070 m, 24.III.2011, hand-collected, T. Delsinne coll., RBINS, specimen-ID 46586-01 from sample 46586. One point-mounted alate queen presently in DZUP, to be deposited in RBINS.

**Other material examined.** Zamora-Chinchipe: Reserva Biológica San Francisco,  $-3.97504^{\circ}$   $-79.07631^{\circ}$ , 13 km E Loja, “forester plot”, 1970 m, 23.ix.2007, M. Leponce coll., in 1 m<sup>2</sup> of sifted litter extracted during 48 h (Winkler sample), one point-mounted worker lacking the gaster, RBINS, specimen-ID 33006 from sample 33692.

**Type locality.** Loja, Ecuador.

**Etymology.** The species epithet is an adjective in the nominative singular derived from “Loxa”, the old Spanish name for the town of Loja, Ecuador, not far from the type locality. It translates into “from Loja”.



**Fig. 8.** *P. loxanensis* sp. n. Gyne paratype: Wing. Costal margin and anal margin slightly folded dorsad so Costal cell and Anal lobe appear more slender than if wing were spread flat. Image by K. Morais.

**Distribution.** Forests surrounding the town of Loja in southern Ecuador.

**Biology.** This species is sympatric with *P. leponcei* sp. n. at Reserva Biológica San Francisco. In *Protalaridris*, only *P. punctata* sp. n. and *P. bordonii* sp. n. are also known to be sympatric. Some localities may share an even higher number of *Protalaridris* species as *P. loxanensis* sp. n. and *P. leponcei* sp. n. may also be sympatric with *P. armata* as their known ranges are only separated by 390 km. The few specimens of *P. loxanensis* sp. n. have been taken from cloud forests and secondary vegetation above 2000 m near the southern Ecuadorian town of Loja. The Reserva Madrigal is a private reserve 7 km SSE from Loja that neighbors Podocarpus National Park. It was previously a dairy farm and its fields have been undergoing conversion towards forest during the last fifteen years. One specimen was taken from a single 1 m<sup>2</sup> leaf litter sample along a 200 m long transect and a second one was later collected by sifting litter from the same site. The site is mostly secondary vegetation ranging from trees forming a loose canopy approximately 15 m high to more open bracken-fern dominated understorey with scattered trees and shrubs. Neighboring slopes across the stream from the sampling site have dense forest with a canopy not more than 15 m high. The area has an estimated average annual rainfall of 2500–3000 mm (Richter et al., 2013). The Estación Científica San Francisco ( $-3.9717^{\circ}$ ,  $-79.07917^{\circ}$ ) is situated within the Eastern Cordillera of the Ecuadorian Andes at an altitude of 1860 m with the focal experimental site in the RBSF (Reserva Biológica San Francisco) ranging from 1600 to 3140 m. The surrounding vegetation mostly corresponds to an evergreen upper montane forest (Homeier et al., 2008) and the mean annual precipitation is 3500–4000 mm (Richter et al., 2013). The San Francisco Station is situated 11.5 km NE from the Madrigal Reserve. A single worker was collected at 1970 m from a grid of 25 Winkler samples. One alate queen was hand-collected in the same natural reserve, at a slightly higher elevation (2070 m), in the morning of 24.iii.2011, after it landed on the white T-shirt of our colleague Tania M. Arias-Penna. At that elevation, no other

specimen was discovered despite robust sampling (>430 Winkler samples (0.5 m<sup>2</sup>), >380 pitfall traps, >140 soil samples (15 × 15 × 15 cm), visual search in dead wood) carried out either in March–May 2009, 2010 and 2011, or in September 2009. However, this sampling was geographically restricted as it was mainly done inside six 20 × 20 m experimental plots close from each other. A single ALL transect carried out in August of 2014 (J. Lattke, unpubl. data) in a forest 2.5 km SW from the San Francisco Station at 2105 m failed to retrieve any *Protalaridris*.

**Comments.** Besides the characters used in the key, *P. armata* and *P. loxanensis* sp. n. may be separated on account of the following: The mandibles in *P. armata* lack a dorsal row of preapical teeth as present in *P. loxanensis* sp. n.; the labrum is relatively much larger in *P. armata* with a deep anteromedian concavity whilst in *P. loxanensis* sp. n. the anterior labral margin bears a weak median emargination at most. *P. armata* has small, but distinct, posterolateral cephalic lobes that form a different surface from the mostly convex vertex between the vertexofrontal ridge and occipital carina. *P. loxanensis* sp. n. lacks such lobes and has a uniformly convex vertex. The antennal scrobe is nonexistant in *P. loxanensis* sp. n. making for a uniformly concave ventral margin in a transverse section of the head at eye level, whilst in *P. armata* the same section is mostly convex but with a lateral concavity because of the antennal

scrobe. In lateral view the eye in *P. armata* is situated on a narrow surface between the cephalic dorsum and the antennal scrobe whilst in *P. loxanensis* sp. n. the eye is situated on a broad cuticular surface. The setae along the anterior scape margin in *P. armata*, when seen laterally, are arched and in dorsal view tend to be feather-shaped, contrasting with the straight setae in *P. loxanensis* sp. n. that progressively widen to a truncate apex. In *P. armata* these setae are placed between a narrow furrow formed by two longitudinal parallel ridges that run along the anteroventral scape surface, in contrast with the scape in *P. loxanensis* sp. n. that lacks such ridges. A transverse section of the scape in *P. armata* has a convex anterodorsal margin, but in *P. loxanensis* sp. n. the dorsal margin forms a right angle with the anterior margin.

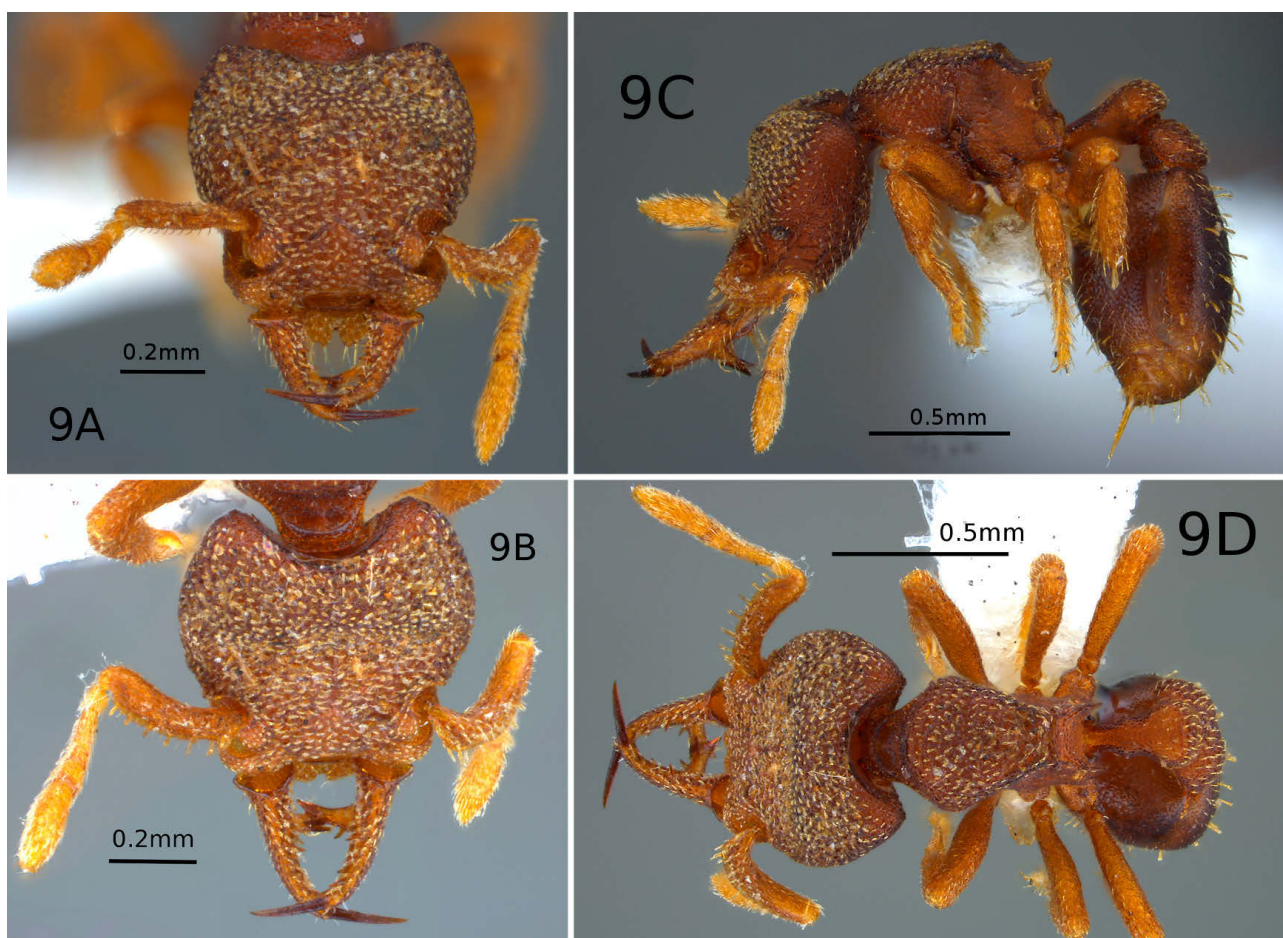
***Protalaridris punctata* Lattke, sp. n.**

(Figs 9a–d)

ZooBank LSID

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**Worker diagnosis.** Mandible with dorsal row of 5–8 preapical teeth of varying length, cephalic dorsum without brief longitudinal carina extending posterad from antennal insertion, external scape margin with 8–10 erect hairs. In lateral view mesosomal dorsal margin mostly flat to weakly convex, joining propodeal tooth through broadly convex



**Fig. 9.** *P. punctata* sp. n. Worker holotype: A – head dorsal view; B – mandible full length view; C – body lateral view; D – body dorsal view. Specimen MIZA0021675. Images by T. Delsinne.

dorsal margin; propodeal tooth broad, roughly shaped as equilateral triangle.

**Measurements of type specimens.** Holotype (paratypes,  $n = 5$ ): HL 0.63 (0.62–0.67); HW 0.67 (0.63–0.68); ML 0.35 (0.33–0.35); EL 0.05 (0.03–0.04); SL 0.35 (0.32–0.35); PW 0.38 (0.37–0.40); WL 0.62 (0.62–0.62); PH 0.18 (0.17–0.18); PL 0.28 (0.25–0.28); DPW 0.20 (0.18–0.20) mm. CI 1.05 (1.03–1.07); MI 0.53 (0.50–0.53); OI 0.08 (0.05–0.06); SI 0.53 (0.48–0.53); LPI 0.65 (0.63–0.73); DPI 0.71 (0.69–0.77).

**Worker description.** Head in frontal view shaped as irregular hexagon ( $L \approx W$ ): lateral angle broadly convex; anterolateral margin more than twice as long as posterolateral margin; posterior margin broadly cleft, forming bluntly angular lateral occipital lobes. Eye reduced but distinct, anteroventrally oriented, separated from antennal fossa along lateral cephalic margin by 3 diameters. Cephalic dorsum mostly areolate-rugulose; dominated by broadly posteriorly convex, blunt, transverse crest that originates laterally just posterad of eye, and separates elevated posterior cephalic region from lower anterior region by anterior facing slope, the latter larger than the former; small smooth area present just posterad of posteromedian clypeal apex, frons with median longitudinal carina present on weakly raised longitudinal crest, both fading just anterad of transverse crest. Cephalic dorsum with mesially facing oblong appressed hairs, apically cuspidate; frontal lobe with similar hairs but facing anterad, and broader; occipital carina fine and arched, width less than pronotal width, occiput areolate, posterolateral region areolate-rugulose. Cephalic ventrum mostly areolate to areolate-rugulose, posterolaterally densely punctulate.

Mandibles form complex cradle or cage bound by the main axis of each mandible as well as prominent ventral tooth. Mandible in full length view slender, progressively tapering towards apex, slightly arched until close to 2/3 length, at which mandibles cross, each bending approximately 40 degrees mesad. Base of mandible, close to cephalic insertion, expands into flange with smooth rim and areolate dorsal surface. Mandible dorsally and dorsolaterally with scattered rugulae and decumbent oblong pilosity directed apicad; ventrally, ventrolaterally, and internal surface smooth and shining. Mandible apicad of crossing dark brown, smooth and exquisitely pointed. Mandible extends anterodorsally at a 45° angle relative to the dorsal cephalic surface in lateral view, ventral tooth tapers posteroventrally, slightly arched, its length about 1/3 that of lateral mandibular length. Mandibular cross-section at mid-length crescent-shaped, dorsal margin with 5–8 teeth of varying lengths, longest at mandibular mid-length, length of each tooth not more than mandibular width at base of tooth; dorsal mandibular margin with series of apically truncate spatulate hairs, each longer than longest preapical tooth and arching mesad. Ventral internal mandibular margin with 3 small teeth close to mandibular crossing point. Mandible with prominent ventromedially directed tooth, situated closer to mandibular base than apex in mandibular full length view; ventral tooth in dorsal view tapering apicad, posterior margin edentate and broadly concave; length

approximately equal to length of smooth apex of mandible in full length view. In anterior view, ventral tooth relatively straight with 1–2 small decumbent, acute teeth along anterodorsal margin; apex of tooth expanded into asymmetrical fork with stout dorsal preapical tooth, at least 3× longer than smaller teeth, apical tooth with broad base and broadly concave dorsal margin. Dorsal surface of ventral tooth smooth and shining with single long hair at mid-length. With mandibles closed the apex of each ventral tooth cross; apical and large preapical tooth ferruginous brown, smooth and shining.

Lateral extremities of labrum not visible in dorsal view with mandibles closed, basal ridge weakly but distinctly sinuous; anteromedially a deep incision forms an acute angle over one-half the length of the labrum, dividing it into two lobes. Ventral surface mostly smooth and shining, dorsal surface sculpted, not smooth and shining. Anterolateral margin of each lobe with four long aciculate hairs, each on low triangular lobule, second hair from labral median cleft the longest. Two hairs closest to cleft parallel and directed ventrally, anterolateral hairs weakly diverging and directed lateroventrally; two to four minute hairs may be present within cleft. Labral hairs parallel to ventral tooth in lateral view and of same length as tooth. Palpal formula unknown. Scape in dorsal view longitudinally rugulose with apical two-thirds mostly straight and parallel, anterobasal lobe weakly expanded anterad, short decumbent hairs present on scape. Cross-section of scape at mid-length flattened, external margin wider than internal margin, dorsal margin broadly convex, ventral margin mostly straight. External scape margin defined by narrow longitudinal lamellae, one along ventral margin and another along dorsal margin; external scape margin bears 8–10 weakly spatulate, erect hairs that stem from anteroventral margin, apically either truncate, bifid or trifurcate; one hair close to basal angle, usually third or fourth from anterior margin noticeably longer than others and parallel-sided, in oblique view spatulate hairs weakly arched.

Mesosomal dorsum in lateral view straight to broadly convex, sometimes pronotum and mesonotum each form weak convexity, dorsal propodeal margin straight to weakly convex; declivitous margin anteriorly concave, confluent with lamellate, triangular and sharply pointed propodeal tooth, posterior declivitous margin straight to concave. Mesosomal dorsum rugulose, with numerous decumbent, weakly spatulate hairs; promesonotal suture present as shallow transverse sulcus. Lateral pronotum, mesometapleura, and propodeum densely punctulate, wanting pilosity; pronotum lacking transverse crest or carina delimiting pronotal collar from rest of sclerite, coarse areolae present along dorsolateral region, besides appressed hairs; transverse rugulae present on katepisternum. Promesonotal surface overhanging lateral pronotal surface; propodeal dorsum not as wide as lateral surface, lateral metapleural – propodeal surface visible in dorsal mesosomal view.

Petiolar node in lateral view convex, anterior petiolar margin mostly straight to weakly concave, anteroventral process shaped as low angular lobe, postpetiolar dorsal

margin in lateral view broadly convex, convexity increasing posterad. Postpetiole transverse in dorsal view, with shallow median longitudinal sulcus separating low lateral convexities, anterior margin concave and shorter than convex posterior margin, dorsum of petiolar node and postpetiole areolate-rugulose with posteriorly directed appressed and slender lanceolate hairs. Dorsal margin of abdominal tergum IV broadly convex in lateral view, ventral margin markedly convex, with greatest height just anterad of gastral mid-length; densely punctulate, space between depressions less than their diameters; pilosity consisting of sparse arched subdecumbent flattened hairs, and some 25–32 suberect, weakly spatulate, truncate hairs forming 6–8 ill-defined longitudinal rows, most hairs situated on posterior two-thirds of tergite, pilosity not obscuring sculpturing. Abdominal tergum IV with transverse carina along anterodorsal margin, separating dorsum from anterior surface. First gastral ventrum with dense, scalloped punctures, abruptly impressed anterad and gradually impressed posterad, sparsely clothed by short decumbent hairs pointing posterad, and sparse suberect hairs. Sting stout.

Tarsal claws simple, long and slender; legs stout, not elongate; protibial apex with spatulate hair anterolaterally, plus two flattened linear hairs laterally and posterolaterally, lateral hair longest; rest of hairs on protibia short, arched. Mesotibial apex with spatulate hair, lateral surface of meso- and metatarsi each with two longitudinal rows of spatulate hairs, apex of lateral surface of each with single spatulate hair, apically wider than that of protibia. Body mostly ferruginous, darker tint on transverse cephalic carina and cephalic dorsum posterad of carina, apex of mandible and ventral mandibular tooth, mesosomal dorsum and propodeal lamella, including tooth, and gaster throughout.

**Queen description.** Measurements: HL 0.70; HW 0.37; ML 0.13; EL 0.37; SL 0.55; PW 0.95; WL 0.22; PH 0.33; PL 0.23; DPW 0.23 mm. CI 1.07; MI 0.49; OI 0.18; SI 0.49; LPI 0.65; DPI 0.70. The queen bears great resemblance to the worker save characters typical for a queen. Head with frontovertexal carina better developed in full-face view, head posterior to transverse carina gradually protruding dorsad mesially, highest point at ocelli, ocelli inconspicuous, compound eye weakly convex but distinctly visible in full face view. Mesoscutum dorsally flattened with shallow posteromedian concavity, mostly with longitudinal roughened costulae; transscutal articulation posteriorly convex, finely impressed but distinct; scutoscuteellar suture anteriorly convex, deeper and broader than transscutal articulation; axilla transverse, shaped as elongate scalene triangle; scutellum extends posterad as a blunt lobe. Pronotum with vertical anterior face in lateral view of mesosoma, separated from lateral face by blunt vertical ridge, lateral face mostly smooth with abundant punctae and posterior margin that projects into anepisternum as rounded lobe. Anapleural suture broad and deep. Dorsal mesosomal margin, from scutum to scutellum, horizontal, abruptly dropping posteriorly. Propodeal spiracle facing posterad, declivity areolate. Gastral tergum I with more than 50 erect hairs.

Images of the paratype queen can be seen by searching for CASENT0248769 in Antweb.

**Male.** Unknown.

**Type material.** Holotype worker. VENEZUELA. Aragua: Parque Nacional Henri Pittier, Rancho Grande via La Cumbre, 10°21'17"N, 67°40'55"W, 1225 m, 26.i.2008, M. Riera 160, R. Luján, J. Valera, leg. One point-mounted worker to be deposited in MIZA but presently in DZUP. Paratypes. Same series as the holotype: 2 workers to be deposited in USNM, 2w CAS, 2w MCZC, 2w DZUP 548782, 3w MIZA, 2w ICN, 2w RBINS. One MIZA paratype is point-mounted on the same pin as the holotype, but the holotype has its point stained red. As with the holotype, the MIZA paratypes will be temporarily kept in DZUP.

**Other material.** VENEZUELA. Aragua: Parque Nacional Henri Pittier, Rancho Grande, La Cumbre, 10°21'34"N, 67°41'06"W, 1450 m, 14.ix.2007, M. Riera 104, C. Rodríguez, J. Valera, legs. 1q MIZA. Parque Nacional Henri Pittier, Rancho Grande, La Cumbre, 10°21'34"N, 67°41'06"W, 1400 m, 10.vi.1986, Carlos Bordón leg. Ex sifted leaf-litter. Unique specimen identifier CASENT0178630, 1 worker deposited in MIZA. Images of this specimen available in Antweb. Specimen with an identification label by J. Lattke 1987 mistakenly determined as *P. armata*.

**Type locality.** Aragua, Venezuela.

**Etymology.** The species epithet is derived from the Latin *punctus*, to prick or puncture, in allusion to the exquisitely pointed and smooth mandibular apex, suggesting impalement of its prey.

**Distribution.** Only known from the type locality.

**Biology.** This species, along with *P. bordoni*, are presently only known from the cloud forests in the vicinity of the Estación Biológica of the Universidad Central de Venezuela in the Coastal Mountains of Venezuela. Most specimens of this species come from a single 1 m<sup>2</sup> leaf litter sample taken at 1225 m during a study of ant diversity in the Rancho Grande cloud forest (Lattke & Riera, 2012). The same field work uncovered a dealate queen in a soil sample taken at an altitude some 200 m higher.

**Comments.** The labral hairs of this species are apparently not flattened, in contrast with all other *Protalaridris*, though this could be an artifact of preservation methods. Better resolution could be gained using SEM and dissecting the mouth-parts. The mandibles of *P. punctata* sp. n. are relatively shorter than other *armata* group species and their dorsal margin is not concave in lateral view but straight, forming an obtuse angle with the dorsal cephalic margin.

*Protalaridris bordoni* sp. n. can be separated from *P. punctata* sp. n. by the following differences, amongst others: The transverse carina of the cephalic dorsum is more prominent and higher than the surrounding integument, and the median clypeal carina is longer and more prominent as well. The posterolateral cephalic border is convex with a weakly impressed median concavity in full-face view. The frontal lobes are smaller in but each has a posterior longitudinal carina that reaches the level of the posterior end of the median cephalic carina. The external margin of the scape has 7 spatulate erect hairs. The mandible presents two large pre-apical teeth; the basal tooth is the largest, ventromesially projecting and crossing with opposing tooth, not apically bifurcate, and with a low preapical den-

ticle; the other tooth projects mesoventrally and is smaller, not touching the opposing tooth when the mandibles are closed. Its labrum is elongate with the apex of each lobe having three flattened lanceolate hairs that twist approximately 90° at mid-length, so the basal plane faces anterad, but the apical plane faces laterad. Also present are 1–2 very short, weakly spatulate hairs along the internal margin of the median labral cleft. The mesosomal dorsum is convex in lateral view and the pronotum has an obliquely transverse anterior carina that defines a steep slope that falls onto the pronotal collar.

Besides the characters used in the key *P. armata* may be separated from *P. punctata* sp. n. by the broad labral setae that contrast with the narrow setae in the latter species, *P. punctata* sp. n. also has an angularly cleft labrum, not curved as in *P. armata*. The mandible in *P. punctata* sp. n. bears a dorsal row of arched, mesially projecting spatulate setae that bear no resemblance to the multitude of slender arching setae along the interior mandibular surface of *P. armata*. *P. punctata* sp. n. also has a dorsal row of preapical teeth on the mandible, a feature lacking in *P. armata*. In a lateral view the dorsal mandibular margin of *P. armata* is sinuous, convex basally and then concave apicad of the basal ventral tooth, but in *P. punctata* sp. n. this margin is mostly straight with no sinuosity. The mesosomal dorsum is flattened in *P. punctata* sp. n. and has slender, sharp propodeal spines that contrast with the broadly triangular spines of *P. armata* and its weakly convex mesosomal margin.

### ***Protalaridris* natural history**

Until now, the known specimens of this genus have been taken from leaf litter samples and no nests have been uncovered. One litter sample from Venezuela contained several workers and a queen of *P. punctata* sp. n., implying a ground nesting site within leaf litter or decomposing branches, twigs or other plant matter. *Protalaridris* is found in mesic forests ranging from 200 to 2500 m a.s.l., although by far most records are from montane cloud forests between altitudes of 800 and 2000 m. Most have been taken from isolated collecting events though some may be locally abundant. Specimens were collected in 10 percent of 2 transects using the ALL protocol in cloud forests of the Venezuelan Coastal Range on the southern facing slopes between 1225 to 1450 m (Lattke & Riera, 2012), but none were recorded from one cloud forest transect, 16 km to the west, also using the ALL protocol, at 1100 m on north facing slopes (Rodriguez & Lattke, 2012). In some localities they may be quite frequently encountered such as in the cloud forest Otongachi Reserve at 850 m in the western Andean slopes of Central Ecuador, where *P. armata* has been found in 20% of leaf litter samples (Donoso & Ramon, 2009) or in Reserva Biológica San Francisco, in the eastern range of the south Ecuadorian Andes, where two species of *Protalaridris*, *P. leponcei* sp. n. and *P. loxanensis* sp. n., have been found in a total of 6 (24%) out of 25 Winkler samples (but with only one specimen in each sample). Nevertheless sampling montane cloud forests in northern South America does not guarantee finding these

ants as surveys in apparently suitable sites in SW Colombia failed to recover any specimens (Estrada & Fernandez, 1999; Bustos & Ulloa-Chacon, 1997). An unpublished survey (Farfán, 2014) using the ALL protocol in three cloud forest sites situated between 1300–1700 m in the Sierra de Aroa mountains of northern Venezuela, 122 km W from the Rancho Grande locality, also failed to detect any *Protalaridris*. See the biology for *P. aculeata*, *P. leponcei* sp. n. and *P. loxanensis* sp. n. for additional information on the inferred absence – presence of these species. Fig. 10 summarizes the species distribution in *Protalaridris*. Given the large areas of potentially suitable habitat in Colombia and Peru it is expected that more species of *Protalaridris* should be uncovered in these countries. Its presence in Bolivia and Brazil is also possible considering the few kilometers separating the type locality for *P. aculeata* sp. n. from the borders of these countries. During the course of this study we had access to images of a disarticulated specimen of long-mandibulate *Protalaridris* from Risaralda, Colombia. Its cephalic and mandibular morphology indicate it represents an undescribed species.

No field observations of habits are yet recorded for this genus though the mandibular morphology suggests specialized predation. The biology of most *Basicerus* group species is poorly known as they are generally described from leaf litter samples. Casual observations of a single live worker of *P. loxanensis* sp. n. taken by JEL from a leaf litter sample offered some clues to their predatory habits. It was placed in a petri dish with a humid paper towel. The ant would walk slowly with its head directed anterad, elevated from the ground. Whilst walking the head would slowly sweep right and left with the antennae describing vertical elongate ovals. During movement the mandibles would be either closed or open up to 90 degrees. The labrum and its surrounding hairs project forward. Several times it was observed with its mandibles opened almost 180°, but only when it was immobile. During this stance it would keep its body and head closer to the ground than when walking, its scapes extended posteroventrally and tucked beneath the head with the funiculus extending anterolaterally. A fine-hair paint brush as well as a human hair glued to a toothpick were both used in attempts to stimulate the ant into closing its mandibles, but in both cases it would close its mandibles slowly and back away. Thus, the mandibles may not be of the rapidly closing type or the attempts to stimulate a reaction simply failed.

With mandibles closed and in lateral view, it is possible to discern the major anteroventral tooth and the protruding labrum with its suite of long hairs (Fig. 7c). The labral hairs are subparallel to the ventral tooth, and their apices frequently surpass in length the tooth's apex. The labrum protrudes at a roughly 45° angle with the ventral mandibular margin in all studied specimens. The mandibles can be opened with comparative ease in ethanol-preserved specimens (*P. armata* and *P. loxanensis* sp. n.) to a gape of approximately 180°, such as in trap-jaw ants of the genera *Odontomachus* Latreille, 1804, *Anochetus* Mayr, 1861, *Acanthognathus* Mayr, 1887, or *Strumigenys* F. Smith,

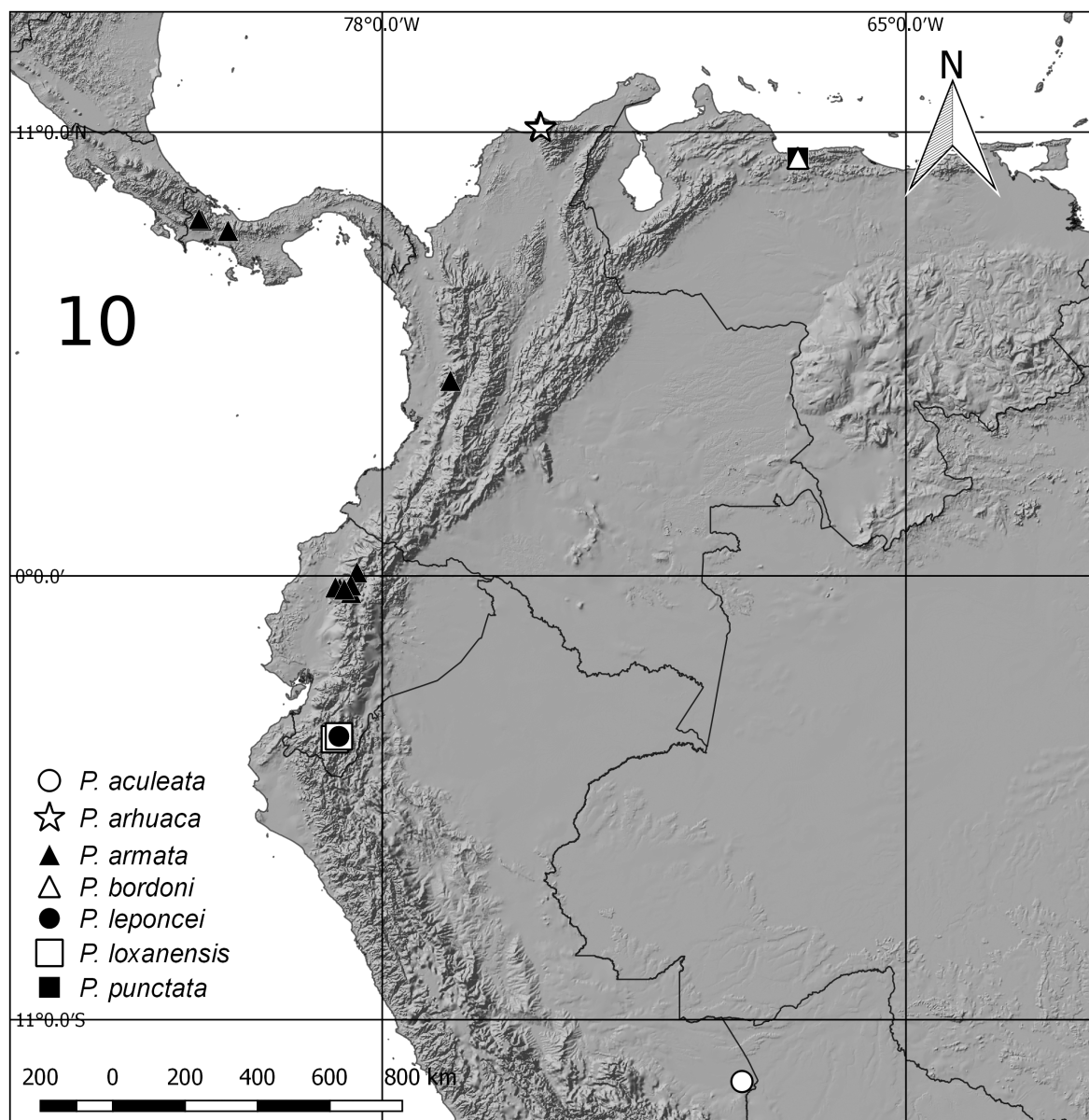


Fig. 10. Distribution map of *Protalaridris* species.

1860. The finely pointed and polished apices of both the mandible and its ventral tooth suggest either penetration of the body of its prey or a more secure grip to facilitate use of its sting, or both. The protruding labrum with the row of long apical hairs suggest a latch mechanism controlled by trigger hairs that make contact with the prey (Cerdá & Dejean, 2011). But Bolton's (1999) studies of mandibular morphology indicate that a T-shaped labrum is associated with a sudden release, kinetic mode of mandibular closure. The labral morphology in *Protalaridris* is more like that of a static mandibular closing mechanism, but the wide gape is typical of ants with a kinetic mechanism. Another, closely related genus, *Rhopalothrix*, also presents acutely pointed mandibles and a similarly protruding labrum with specialized hairs, and it is also possible to open their mandibles to a gape as in *Protalaridris* (Longino & Boudinot, 2013) but they lack the well-developed basal mandibular process. There is no conclusive evidence regarding the na-

ture of the jaw closure mechanism in *Protalaridris*. The Otongachi Reserve in Ecuador offers excellent opportunities for natural history studies of this genus or for collecting nests for lab study as *P. armata* is relatively common there.

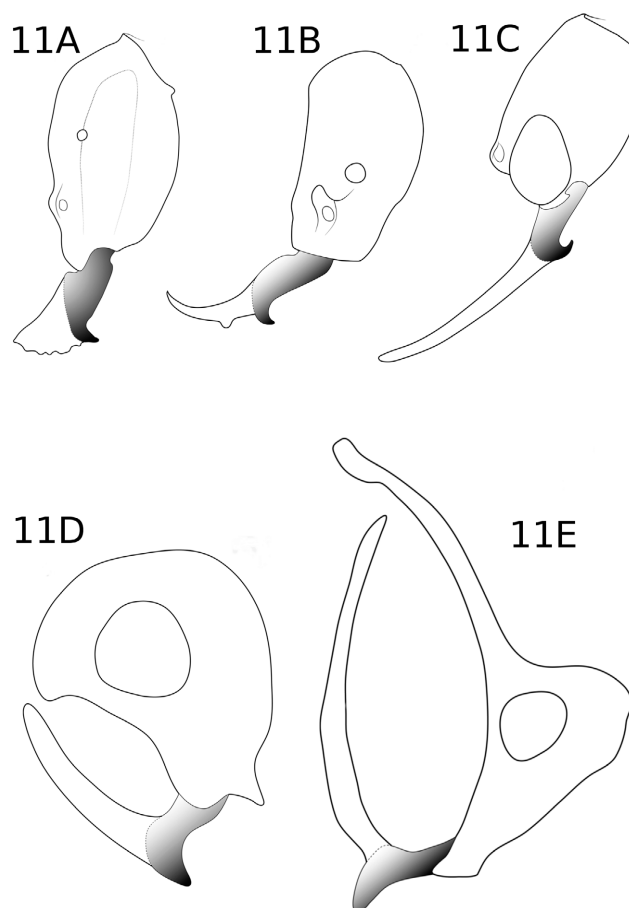
#### Mandibular morphology

The mandibular morphology of the *armata* group contrasts with that of most other ant genera due to its upturned dorsal margin when seen laterally. In Hymenoptera the mandibular shape is typically crescent-shaped in lateral view and triangular in dorsal view. Ant mandibles, as in most insects, are dicondylate and this constrains mandibular movement along a transverse (laterally) oriented plane (Staniczek, 2000; Blanke et al., 2014). The abduction and adduction is produced by abductor and adductor muscles originating on the dorsal and lateral internal surface of the head capsule (Snodgrass, 1935; Grimaldi & Engels, 2005). Given the overwhelming dominance of the trian-

gular – subtriangular mandible variants, it can be assumed this is a plesiomorphic and conserved general shape and an inversion of the mandibular apex from downturned to up-turned should be rare. Deviations from this are the specialized linear mandibles of genera such as *Acanthognathus* Mayr, 1887; *Anochetus* Mayr, 1861; *Daceton* Perty, 1833; *Mystrium* Roger, 1862; *Myrmoteras* Forel, 1893; *Odonotomachus*, and *Strumigenys*, which are straight when seen laterally (Larabee & Suarez, 2014). Even rarer are the instances of “up-turned” (and always more or less elongated) mandibles.

Ants in the ponerine genus *Harpegnathos* Jerdon, 1851 have elongate upturned mandibles convergently shaped with those of *Protalaridris*. Both genera also share the presence of a large crescent-shaped basal ventral tooth with a convex anterior margin in lateral view. The monotypic genus *Talaridris* has an elongate scooped-shaped mandible but with a distinct ventral denticle that has a concave posterior margin when seen laterally. Besides these extant groups the extinct sphecomyrmecine genera *Ceratomyrmex* Perrichot, Wang & Engel, 2016 and *Haidomyrmex* Dlussky, 1996 also bear elongate mandibles with an upturned apical part and ventral tooth at the base (Perrichot et al., 2016). Long-mandibulate *Strumigenys* of the *gundlachi* group have relatively slender, tapering mandibles that in profile may be linear to weakly concave (Bolton, 2000: 176). Their mandibles differ from the aforementioned genera in lacking a basal ventral tooth and the dorsal concavity, when present, is feeble at best.

The masticatory margin of triangular mandibles generally bear variously shaped teeth that lie in the same plane as the dorsal mandibular surface. This configuration is different in the *ascrobicula* group of *Octostruma* (see Longino, 2013a) and *Protalaridris leponcei* sp. n. Their mandibles are triangular but the masticatory margin bears a series of relatively large, irregularly sized teeth that protrude dorso-medially, clearly visible in lateral view. One of the preapical teeth of *P. leponcei* sp. n. is particularly large compared with the others (Fig. 6a), and further enlargement may lead to the situation found in the remaining species of the genus. Such enlargement may be exemplified by an undescribed species *Rhopalothrix* UFV sp. 1 imaged in Antweb (2017; specimen UFV-LABECOL-000326). In the latter, the mandible bears a very large preapical tooth that rivals the mandibular shaft in size. If the mandibles in *P. leponcei* sp. n. represent the plesiomorphic state within the genus, further enlargement of a dorsomedially projecting tooth might have proved advantageous for certain tasks, such as prey securement (Ohkawara et al., 2016). A tooth or denticle projecting from the basal mandibular angle is known in some species of *Neivamyrmex* Borgmeier, 1940 (Borgmeier, 1955). Thus, the “upturned” part of the mandibles in the *armata* group could be derived from a preapical mandibular projection. That possibility is supported by the presence of a large incurved ventral tooth close to the mandibular base of in all these ants; this tooth may actually represent the original apical part of the mandible. Additionally, in the long mandible, only the part distal to the ventral tooth



**Fig. 11.** Comparative morphology of some elongate-mandibled ants with a convex dorsal margin in lateral view. The grey filled area represents the main mandibular shaft. A – *Protalaridris*; B – *Talaridris*; C – *Harpegnathos*; D – *Haidomyrmex*; E – *Ceratomyrmex*. Artwork by A. Ferreira.

is distinctly upturned in *Protalaridris*, *Talaridris*, and *Harpegnathos*. The trap-jaw mandible in the genus *Acanthognathus* bears a slender and curved basal tooth or process (Gronenberg et al., 1998) that is anteriorly convex and with apical denticles, suggesting the possibility it may be the original mandible, but the morphology is much different than of the previously mentioned genera.

Our interpretation may also be useful for addressing enigmatic mandibular morphology in non-extant ants. What Barden & Grimaldi (2012: 8) interpret as the apical tooth of *Haidomyrmex scimitarus* Barden & Grimaldi, 2012 may actually represent a hypertrophied preapical tooth whilst the apex of the so-called ventrobasal mandibular tooth (the posteriormost member of the basal teeth) is most probably the original apical mandibular tooth. Likewise, what is labelled as the basal tooth in *Ceratomyrmex ellenbergeri* Perrichot, Wang & Engel, 2016 (Fig. 1C in Perrichot et al., 2016) would be the principal mandibular shaft and the apical portion of the mandible would be a hypertrophied preapical tooth or projection. As in extant taxa, the upturned part of the mandibles in these early ants begins close to the “basal mandibular tooth”. Fig. 11 depicts our idea of what is the main mandibular shaft and what is the extension of the preapical dentition or margin.

The mandibles of *Haidomyrmex* and *Ceratomyrmex* were interpreted as being unlike anything present in modern ants (Barden & Grimaldi, 2016; Perrichot et al., 2016; Barden 2017) and even implying a vertical movement (Perrichot et al., 2016). In our interpretation, the mandibles of Haidomyrmecini possess analogues in extant genera and it is not necessary to postulate vertical mandibular movement which would imply a 90 degree twist of the mandibular condyles and associated radical structural modifications of the head capsule, mandibular apodemes, and muscles. Haidomyrmecine and *Talaridris* mandibles correspond to the planar type (sensu Keller, 2011), with the external surface facing laterally and the external margin facing ventrally, whilst mandibles in *Protalaridris* and *Harpegnathos* are torqued, with their external surface facing dorsally and the external margin facing laterally (Keller, 2011). What still makes haidomyrmecine mandibles remarkable is the length and the angle at which the dorsal tooth projects, almost perpendicular to the longitudinal axis of the body, something unseen in extant taxa. Hopefully, detailed phylogenies and careful comparative studies of closely related taxa with different mandibular morphology will help elucidate the developmental pathways of such transformations.

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