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A taxonomic revision of the dirt ants, *Basiceros* Schulz, 1906 (Hymenoptera, Formicidae)

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RODOLFO DA SILVA PROBST & CARLOS ROBERTO FERREIRA BRANDÃO A taxonomic revision of the dirt ants, *Basiceros* Schulz, 1906 (Hymenoptera, Formicidae)

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Abstract

The ant genus *Basiceros* is an exclusively Neotropical group known for its cryptic habits. Based on a recent molecular phylogenetic framework, a comprehensive revisionary study of the genus is presented. Nine species are recognized, two of which are described as new (*Basiceros browni sp. nov.* and *Basiceros tumucumaquensis sp. nov.*). *Basiceros redux* (Donisthorpe 1939) is transferred to the genus *Octostruma* (*O. reducta comb. nov.*). As part of this revisionary work, taxonomic keys and images to all species and castes are provided. Castes and sexes (including larvae, males, and intercastes) are described for the first time for several *Basiceros* species. New records considerably expand the distributional range for most species. Natural history data and comments on character plasticity and convergence are also included.

Key words: Attini, systematics, morphology, mouthparts, ant larva, identification, Basiceros-genus group

Introduction

The genus *Basiceros* Schulz, 1906 (Myrmicinae, Attini) is a distinctive group of medium-sized Neotropical ants, considered "masters of camouflage". These ants share a cryptobiotic life habit (Wilson & Brown 1986), having a double layer of specialized hairs that aid with the capture and adherence of soil and litter particles to their integument, giving them an extreme degree of cryptic coloration (Hölldobler & Wilson 1986; Probst *et al.* 2019).

Historically, *Basiceros* has faced significant nomenclatural changes, reflected by the discordance regarding its generic boundaries and phylogenetic relationships. Based on an extensive morphological analysis, Baroni Urbani & de Andrade (2007) proposed the synonymy of the whole "Basicerotini" tribe under Dacetini and all Basicerotini genera under *Basiceros*. More recently, the molecular phylogeny of Ward *et al.* (2015) resulted in a rearrangement and the reduction on the number of tribes within Myrmicinae; one of such changes occurred in "Basicerotini" by being synonymized under the tribe Attini, and it is now referred to as the *Basiceros* genus-group. In contrast to the progress on clarifying higher-level relationships, species-level phylogenies for myrmicine ants have been produced at a considerably slower pace, in most cases due to taxonomic impediments. Fortunately, that is not the case for *Basiceros*, the focus of a recently molecular phylogeny (Probst *et al.* 2019).

Here, we follow the taxonomic classification of Bolton (2022), supported by the molecular study of Probst et

al. (2019), rather than the classification of *Basiceros* proposed by Baroni Urbani & de Andrade (2007). Nevertheless, it is clear that both molecular and morphological data should be incorporated to better understand the generic boundaries within the *Basiceros* genus-group (or *Rhopalothrix* genus-group, as *Rhopalothrix* Mayr 1870 has priority over *Basiceros* Schulz 1906).

Alpha taxonomy

Since its description, the classification of the genus *Basiceros* (Latin *basis*: surface, Greek *keras*: horn, antenna; probably in reference to the peculiar dorsoventrally flattened antennae) has experienced several changes. In 1860, Smith described the monotypic genus *Ceratobasis* and its sole species, *C. singularis*. However, a homonym cerambycid genus had already been described by Lacordaire in 1848. Schulz (1906) proposed the name *Basiceros* to correct the homonym. Later, two genera, *Aspididris* Weber and *Creightonidris* Brown, were synonymized under *Basiceros* by Brown (1974) and Feitosa *et al.* (2007), respectively. Before the present study, eight species can be recognized for the genus: *B. conjugans* Brown, 1974, *B. convexiceps* (Mayr 1887), *B. disciger* (Mayr 1887), *B. manni* Brown e Kempf, 1960, *B. militaris* (Weber 1950), *B. redux* (Donisthorpe 1939), *B. scambognathus* (Brown 1949) and *B. singularis* (Smith 1858).

Phylogenetic relationships

Probst *et al.* (2019) shed light on the evolutionary history of the genus *Basiceros*, recognizing two well-resolved (and diagnosable) internal clades: the *disciger* (four species) and the *singularis* (four species) clades. For the *disciger* clade, Probst *et al.* (2019) recovered *Basiceros scambognathus* as sister to the remaining species in that clade, with *B. conjugans* sister to *B. disciger* + *B. militaris*. For the *singularis* clade, Probst *et al.* (2019) recovered *Basiceros* sp. n. A (=*Basiceros browni* sp. nov. proposed here) sister to *B. convexiceps* and that clade sister to *B. manni* + *B. singularis*.

2. Material and methods

2.1 Relevant literature

This study builds upon the global "Basicerotini" review from Brown & Kempf (1960); a Ph.D. dissertation on the taxonomy and phylogenetic relationships of the "dacetine" tribes based on morphological characters (Dietz 2004); Baroni Urbani & de Andrade (2007), with a proposal similar to Dietz but employing a more extensive number of morphological characters; and more recently, a multi-locus molecular phylogeny (Probst *et al.* 2019).

2.2 Specimens & Depositories

This taxonomic revision is based on material borrowed from several institutions. Around 950 *Basiceros* specimens and 400 additional specimens of related genera were examined, including at least part of the type-series for all described *Basiceros* species. Castes for all taxa were examined when available.

The material examined is listed for every species, with label information (except for type material, which is listed after the taxonomic history). Label data were reinterpreted as necessary (i.e., for localities with name changes, potential label typos, and georeferencing mistakes). Some specimens included in the 'examined material' section were not physically examined but represented by high-resolution stacked macrophotographs either available on AntWeb (AntWeb 2022) or sent to us by curators, thus allowing comparisons with other specimens.

2.3 Terminology

Bolton (1994, 1998, 1999), Baroni Urbani & de Andrade (2007), and Keller (2011) were used as primary sources for external morphology of the adult female castes. Male morphology extensively follows Boudinot (2015). Brown & Nutting (1949) and Boudinot & Fisher (2013) were used for wing venation; additionally, two distinct forewing types for *Basiceros* were added as a shortcut to species descriptions/redescriptions. The "type 1" refers to the forewing in

which the transversal 1m-cu vein is integrally present, completely closing the discal cell; the "type 2" refers to the forewing in which the transversal 1m-cu vein is present either as obsolete (like an appendage of Rs+M) or absent, thus never closing the discal cell (Fig 1). Other veins are present in similar fashion for all species. Terminology for the immature stages followed Wheeler & Wheeler (1955, 1976). Integumental sculpture followed the glossary present in Harris (1979). Pilosity morphology and orientation followed Wilson (1955), with minor modifications for "basicerotines" after Brown & Kempf (1960), Baroni Urbani & de Andrade (2007), and Longino (2013).

The term "gyne" is employed for the caste of reproductive females, replacing "queen" as suggested by de Andrade & Baroni Urbani (1999). The term "intercaste" (*sensu* Peeters 2012) is used when mentioning workers with a mosaic of traits usually restricted to gynes (e.g., the presence of wing buds or rudimentary wing formation (i.e., brachyptery), presence of ocelli, and some degree of mesoscutal/mesoscutellar development).

2.4 Measurements & Indices

This work employs measures and proportions traditionally used in myrmecological studies, with additions considered pertinent (some following Probst *et al.* 2015) (Fig 2). The number of individuals measured and measurements are presented before the descriptions. Measurements were taken with a micrometric reticulum attached to a 10x ocular lens coupled with a Leica MZ95 stereomicroscope (60x) or with a Leica MZ12 (120X), both using a PLANAPO 1.0 as the main objective.

Measurements

- HL: Head Length. All castes. In full face view, the maximum length of head from anterior clypeal margin to posterior margin along head midline.
- HL2: Head Length 2. All castes. In full face view, the maximum length of head from anterolateral clypeal margin to vertexal corner as a virtual line.
- HW1: Head Width 1. All castes. In full face view, the maximum width of head excluding eyes.
- HW2: Head Width 2. Male only. In full face view, the maximum width of head including eyes in full-face view.
- MdL: Mandible length. Mandible Length. Female castes. With head in full face view, length of mandible measured in its outer margin as the chord distance from lateral insertion to mandible apex. Note: this measurement suffers from the degree of clypeal extension over the mandibles and the degree of mandibular curvature
- SL1: Scape Length 1. Female castes. In dorsal view, maximum distance from basal portion to apical portion of scape, traced as a diagonal line.
- SL2: Scape Length 2. All castes. In dorsal view, distance from anterior angle of basal scape lobe to scape apex. In the case of males, length in medial view from scape base middle to scape apex.
- PDL: Pedicel Length. All castes. Maximum length of pedicel from virtual line drawn from dorsal and ventral basal curves to pedicel apex.
- A3L: Antennomere 3 Length. All castes. In dorsal view, the maximum length of antennomere 3 in dorsal view.
- AFL: Apical Flagellomere Length. All castes. In medial view, the maximum length of distal segment of antenna, in medial view.
- FuL: Funiculus Length. Female castes. Length of antennal funiculus, including the pedicel, with flagellomeres in same plane of focus.
- EL: Eye Length. All castes. Maximum diameter of eye with head positioned in lateral view such that anterior and posterior eye margins are in same plane of focus.
- EW: Eye Width. All castes. Maximum width of eye at an axis orthogonal to Eye Length with head oriented as above.
- LOD: Lateral Ocellus Length. Male/Gyne. Maximum diameter of lateral ocellus with head oriented such that anterior and posterior lateral ocellus margins are in same plane of focus.
- MOD: Median Ocellus Length. Male/Gyne. Maximum diameter of median ocellus in full-face view.
- OOD: Oculo-ocellar distance. Male/Gyne. Minimum distance between lateral ocellus and compound eye.
- ML: Mesosoma Length (= Weber's Length). All castes. Maximum diagonal length of mesosoma from vertex

of pronotal inflection to posterior basal angle of metapleuron.

MSL: Mesoscutum Length. Male/Gyne. Maximum length of mesoscutum from anterior apex to transscutal line in dorsal view.

MSW: Mesoscutum Width. Male/Gyne. Maximum width of mesoscutum in dorsal view.

MLL: Mesoscutellum Length. Male/Gyne. Maximum length of mesoscutellum from posterior limit of the transscutal line to posterior apex of mesoscutellum in dorsal view.

MLW: Mesoscutellum Width. Male/Gyne. Maximum width of mesoscutellum posterior to scutelloscutellar line in dorsal view

MFL: Metafemur Length. All castes. Maximum distance of the metafemur in dorsal view, measured from the distal margin of the trochanter to the metafemur apex.

MTL: Metatibia Length. All castes. Maximum length of the metatibia in dorsal view, just before the basitarsal condyle to the metatibial apex.

PTH: Petiole Height. All castes. Height of petiole from apex of node to shallowest point of ventral petiolar margin as close as possible to longest axis of petiole and excluding ventral processes.

PTL: Petiole Length. All castes. Length of petiole from anterior inflection point of petiolar node to posterior-most point of petiolar margin in lateral view.

PTW: Petiole Width. All castes. Maximum distance of petiole measured from its lateral margins in dorsal view.

PPL: Postpetiole Length. All castes. Length of postpetiole from anterior inflection point of postpetiole to posteriormost point of postpetiole margin in lateral view.

PPW: Postpetiole Width. In dorsal view, maximum distance of postpetiolar node.

GL: Length of gaster. All castes. Maximum length of gaster in dorsal view from the anteriormost point of first gastral segment (abdominal segment IV) to the posteriormost point of terminal (visible) gastral segment. Note: this measurement suffers from variation on the projection of gastral segments.

GW: Width of gaster. All castes. Maximum transversal distance of abdominal segment IV in dorsal view.

TL: Total Length. All castes. Axial length of body, including closed mandibles; summed MdL + HL + ML + PTL + PPL + GL.

Indices

CI: Cephalic Index. All castes. HW1/HL*100 CS: Cephalic Size. All castes. (HW1+HL)/2

MCI: Mandibulo-cephalic Index. Female castes. MdL*100/HL

SI: Scape Index. All castes. SL2/HW1*100 ESI: Eye-scape index. All castes. EL/SL2*100

SAI: Scape-antennomere-3 index. Male. SL2/A3L*100

EI1: Eye Index 1. All castes. (EL+EW)/CS

EI2: Eye Index 2. Gyne/Male. HW1/HW2*100

MTI: Mesoscutum Index. Gyne/Male. MTW/MTL*100

MLI: Mesoscutellum Index. Gyne/Male. MLW/MLL*100

MFI: Metafemur index. All castes. HW/HFL*100 PTI: Petiole Index. All castes. PTL/PTH*100

2.5 Identification keys

Two dichotomous keys are provided, one for the females (workers and gynes) and one for males of *Basiceros*. Given the absence of male specimens for some species, the male identification key has gaps, but potential couplets in which these unknown males would fall are discussed. Additionally, since some species are broadly sympatric, a summarized geographical distribution is provided at each final key step to facilitate species identification.

2.6 Images & Distribution maps

All species described in the present study are illustrated with stacked photomicrographs. Source images were obtained with a Leica M205C® stereomicroscope coupled with a Leica DFC 295® or a DFC 450® camera and 1.0 or 2.0 PLANAPO main objectives, respectively. Most images were combined using the Leica Application Suite®

program, versions 3.8 and 4.1, with some images stacked with Zerene Image Stacker© v1.04. PhotoShop CS6® was used to minor touches of brightness, contrast, and background uniformity. Larvae observations were carried out in finer detail using a scanning electron microscope (SEM). Larval specimens were critically point-dried, sputter-coated with gold dust, and imaged using a Philips XL-30 in the Biology Department at the University of São Paulo. Species photographs are included after the respective taxon, followed by distribution maps. Geographic coordinates for *Basiceros* specimens were obtained from the labels of these specimens and checked with Google Earth 7.1.8®.

2.7 List of Repositories

Acronyms for institutions largely follow Evenhuis (2021). For private collections, acronyms are presented by the initials of the curator responsible, followed by PC (Personal Collection):

- ANIC—CSIRO Australian National Insect Collection, Australian Capital Territory, Canberra City, Australia;
- AMNH—American Museum of Natural History, New York, New York, USA;
- AWPC—Dr. Alex Wild Personal Collection, Austin, Texas, USA;
- CAS—California Academy of Sciences, San Francisco, California, USA;
- CEPEC—Centro de Pesquisas do Cacau, Itabuna, Bahia, Brazil;
- DZUP—Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil;
- EcoFoG—The Joint Research Unit (UMR) for the Ecology of Guianan Forests, Campus Agronomique, Kourou, French Guiana.
- FMNH—Field Museum of Natural History, Chicago, Illinois, USA;
- GUPC—Dr. Gary Umphrey Personal Collection, University of Guelph, Ontario, Canada;
- JCPC—Júlio M. C. Chaul Personal Collection, Viçosa, Minas Gerais, Brazil;
- JTL—Dr. John T. Longino Collection, University of Utah, Salt Lake City, Utah, USA;
- INBio—Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Heredia, Costa Rica;
- ICNC—Instituto de Ciencias Naturales de la Universidad Nacional de Colombia,

Santafé de Bogotá, Colombia;

• IFML—Instituto Fundación Miguel Lillo, Universidad Nacional de Tucumán,

Tucumán, Argentina;

• IAVH—Instituto de Investigación de Recursos Biológicos Alexander von

Humboldt, Santafé de Bogotá, Colombia;

- INPA—Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil;
- LACM—Los Angeles County Museum of Natural History, Los Angeles, California, USA;
- MBPC—Dr. Michael G. Branstetter Personal Collection, USDA-ARS Pollinating Insects Research Unit—Utah State University, Logan, Utah, USA;
- MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA;
- MHNG—Muséum d'Histoire Naturelle, Geneva, Switzerland;
- MPEG—Museu Paraense "Emílio Goeldi", Belém, Pará, Brazil;
- MuBio—Museu da Biodiversidade—Universidade Federal da Grande Dourados, Dourados, Mato Grosso do Sul, Brazil:
- MZSP—Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil;
- NHMB—Naturhistorisches Museum, Basel, Switzerland;
- NHM—The Natural History Museum, London, United Kingdom;
- NHMW—Naturhistorisches Museum, Vienna, Austria;
- QCAZ—Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador;
- RSPPC—Rodolfo da Silva Probst Personal Collection, Salt Lake City, Utah, USA;
- UCDC—University of California, Davis, California, USA;
- UFLA—Instituto de Ecologia, Universidade Federal de Lavras, Lavras, Minas Gerais, Brazil;
- UFMG—Departamento de Biologia, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil;
- UFU—Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil;
- UFV—Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil;
- USNM—National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

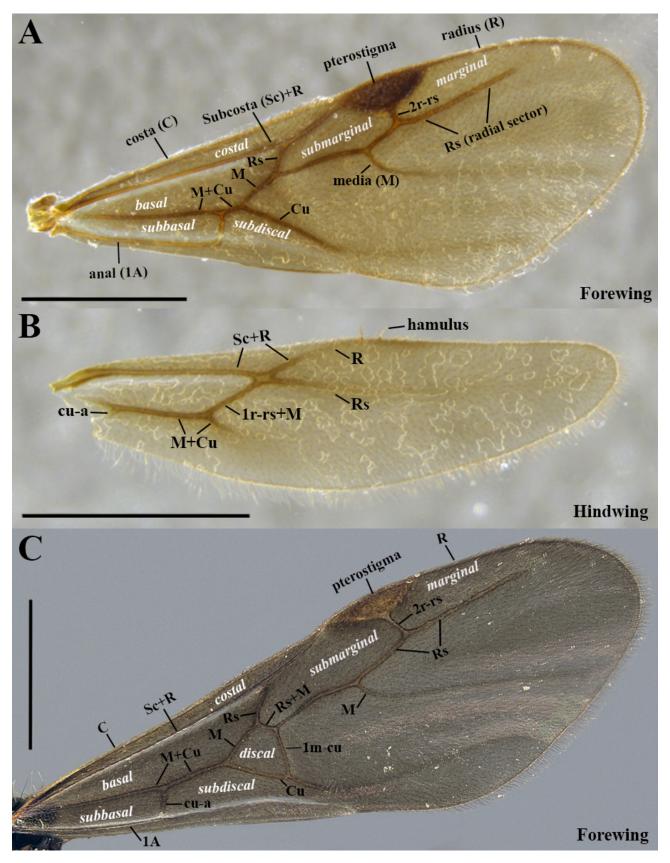


FIGURE 1. Wing venation of *Basiceros* males. A. forewing and B. hindwing of *B. conjugans* (RSPPC, Peru). C. forewing of *B. manni* male (MCZ, Costa Rica: Heredia). Fused veins are indicated with a plus sign and crossveins by a dash. Cell names (in white) are indicated in italics. Scale bars: 1 mm.

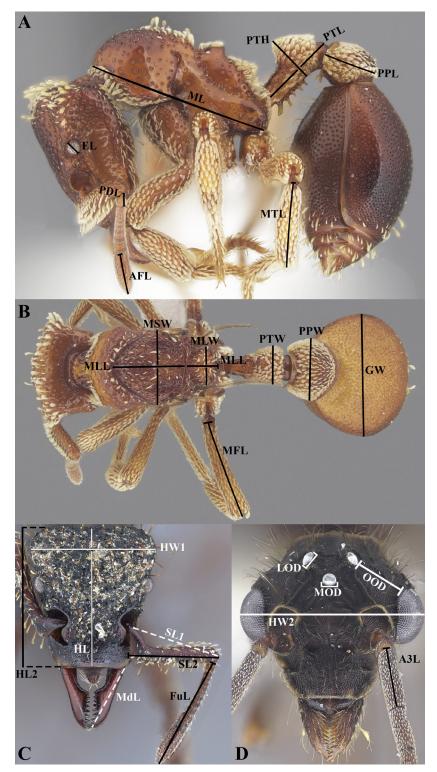


FIGURE 2. Morphological measurements of *Basiceros* species; A. lateral view of worker and B. dorsal view of alate gyne of *B. conjugans* (MCZ546461, Peru: 15 km NE Puerto Maldonado), EL: Eye Length, PDL: Pedicel Length, AFL: Apical Flagellomere Length, ML: Mesosoma Length (= Weber's Length), MTL: Metatibia Length, PTH: Petiole Height, PTL: Petiole Length, PPL: Postpetiole Length, MSL: Mesoscutum Length, MSW: Mesoscutum Width, MLL: Mesoscutellum Length, MLW: Mesoscutellum Width, MFL: Metafemur Length, PTW: Petiole Width, PPW: Postpetiole Width, GW: Width of gaster. C. full-face view of *Basiceros browni* **sp. nov.**, paratype worker (MZSP, Ecuador: Pichincha, Otongachi), HL: Head Length, HL2: Head Length 2, HW1: Head Width 1, MdL: Mandible length, SL1: Scape Length 1, SL2: Scape Length 2, FuL: Funiculus Length. D. full-face view of male of *B. manni* (MCZ, Costa Rica: Heredia), HW2: Head Width 2, LOD: Lateral Ocellus Length, MOD: Median Ocellus Length, OOD: Oculo-ocellar distance, A3L: Antennomere 3 Length. Figures not to scale.

3. Results

Taxonomic history

Basiceros Schulz 1906

Meranoplus (in part) Smith 1858: 195.

Ceratobasis Smith 1860: 78 (junior homonymous of Ceratobasis Lacordaire 1848: 362, Cerambycidae, Coleoptera).

Basiceros Schulz 1906: 156 (name replacing Ceratobasis; Meranoplus singularis, type species by monotypy).

Basiceros in Myrmicinae, Dacetini: Emery 1914: 42; Forel 1917: 246; Wheeler 1922: 666; Emery 1924: 327; Donisthorpe 1943: 627; Brown 1948: 102; Baroni Urbani & de Andrade 1994: 30; Baroni Urbani & de Andrade 2007: 81.

Basiceros in Myrmicinae, Basicerotini: Brown 1949: 87; Brown & Kempf, 1960: 171; Bolton 1994: 105; Bolton 1998: 67; Bolton 2003: 53, 183.

Basiceros in Myrmicinae, Attini: Ward et al. 2015: 17.

Wheeler & Wheeler 1955: 112–113 (larva description); Brown & Kempf 1960: 171–172 (description of the worker and gyne diagnosis); Brown 1974: 132 (worker, gyne, and larva diagnosis; male description; distribution and biology); Bolton 2003: 183–184 (taxonomic background).

Aspididris Weber 1950: 3 (A. militaris, type species by monotypy), junior synonym of Basiceros Schulz: Brown 1974: 132. Creightonidris Brown 1949: 89 (C. scambognatha, type species by monotypy), junior synonym of Basiceros Schulz: Feitosa et al. 2007: 33.

Diagnosis: The workers and gynes of *Basiceros* are differentiated from the other members of the *Basiceros*-genus group by the combination of body size (the largest within this group), antennae with 12 segments, presence of hairs on the postpetiolar sternite, basimandibular seta, and body pilosity (usually composed of a double layer of specialized hairs). Males can be distinguished by the combination of the twisted antennae, mandible shape, petiole and postpetiole shape in dorsal view, pattern of wing venation, and mesopleuron sculpture. The most important morphological characters to distinguish between workers/gynes of different *Basiceros* species are the head and labrum shapes, mesosoma profile in lateral view, and the pattern of specialized pilosity. For males, head and mandible shape, mesosoma in anterior view, shape of petiolar node in lateral view, and mesopleuron sculpture are important.

Caste diagnosis. Worker. Comparatively medium-sized ants (TL: 4.5 to 8.7 mm). Color amber-yellow to black. Integument thick, usually densely sculptured: punctuate/foveate (or a combination of both) or rugose. Pilosity conspicuous and generally specialized; erect setae from sparse to abundant, usually clavate; subdecumbent pilosity sparse to abundant, squamiform, spatulate-clavate or plumose. Labrum shape variable, either long and cuneiform and bilobed apically or somewhat lunate with a rounded distal margin (see Probst et al. 2019, Figs 2-3), labral surfaces with specialized setae (probably with sensorial role) along its distal margin and sometimes in the ventral margin. Head trapezoidal, oblong or posteriorly disc-shaped; lateral and vertexal margins distinctly visible: rounded, angulate or as a continuously or medially emarginated crest along the posterior margin. Mandibles triangular or subtriangular, usually elongated; multidentate, with masticatory margin entirely opposite; apical portion straight to strongly curved ventrally; basal margin from slightly curved to conspicuously concave, clypeomandibular space absent to present in varying degrees (see Probst et al. 2019, Fig 4). Compound eyes relatively developed. Antennae with 12 segments; scape dorsoventrally flattened, with external margin forming biangulate basal lobe followed by a crenulated lamella; antennal club moderate to conspicuous, with last two funicular segments usually distinct. Mesosoma robust or elongate; in lateral view, promesonotum continuously convex to strongly projected caudad; metanotal suture present, broad. Dorsal margin of propodeum slightly sloping upwards at its posterior portion; slope margin from slightly to abruptly oblique. Propodeum armed with triangular or tapered projections, slightly lamelliform and connected by a transverse carina usually slightly curved upwards. Petiole pedunculate; dorsal margin with rounded, low or weakly bulged node; subpetiolar process with different configurations, from absent to multidentate.

Gyne. Similar to conspecific workers, with modifications peculiar to that caste. Ocelli present. In dorsal view, mesoscutum slightly elongated, anterior portion cuneiform; notauli inconspicuous to weakly marked; parapsides generally oval, shallow to deep impressed; parapsidal lines somewhat shiny and slightly conspicuous to obsolete, involved by integumental sculpture; scutoscutellar sulcus from strongly to lightly impressed; pre-scutellum narrow, central portion relatively indistinct; axillae projecting posteroventrally, curved and hook-shaped; mesoscutellum transversely subrectangular to ellipsoid, posteriorly inclined, posterior margin concave. Metanotum visible, slightly projected. Wings usually light brown; pterostigma present in the forewing, distinct and brown to dark brown. Fore-

wing with longitudinal veins C (costa), Sc (subcosta)+R, M+Cu, 1A (anal), Rs+M, Rs (radial sector) and R1 (radius); the Sc+R vein extends from its posterior half to near the front of the pterostigma in tubular form; M+Cu with spectral basal portion and anterior half tubular; anal vein usually with anterior portion tubular; Cu usually tubular, extending posteriorly nebulously; radial sector with nebulous apical portion, not meeting R1; R1 usually reaching the most distal point of the wing margin; anterior portion of the radial sector varying in size. Vein M tubular and oblique, length variable; Rs+M straight or moderately curved, usually tubular, M (media) usually tubular in its anterior half, extending nebulously to the wing margin; Cu similar to M. Transverse veins: cu-a generally tubular, connecting the anal vein with M+Cu just after half of the anal vein, near or right after the branching point; 2r-rs tubular connecting the pterostigma near its median region to the radial sector; Rs connecting the Sc+R veins to the M and Rs+M veins and marking the breakpoint of the latter two, varied 1m-cu vein; absent as an appendage of the Rs+M vein or reaching Cu, closing the discal cell. Hindwing with longitudinal veins Sc+R, M+Cu and 1A; Sc+R briefly extends into a tubular shape after the point of connection with the M+Cu vein as the Sc+R1 vein and extends in the spectral shape to near the distal margin of the wing; anal vein usually tubular; Cu as a tubular appendage either partially or entirely spectral; Rs+M as short tubular appendix and other spectral length or absent; cu-a and 1r-rs+M transverse veins present: the first connecting the anal and M+Cu veins near the median portion of this first; the second connecting Sc+R and M+Cu near the distal portion of these veins. Five to eight submedian hamuli present.

Male. Known Basiceros males are slightly smaller than conspecific gynes. Dark in color, with lighter appendages, from brown to dark brown. Integument mostly punctuate, punctuate-reticulate or foveate; some portions subopaque and slightly granulate, like the appendages; rugulae present near the head vertex, behind the compound eyes and with variable presence on the interocular space; sparse rugulae in the posterior half of the mesonotum and on the propodeum sides; mesopleuron differentially shining: either just at the mesoanepisternum with rest of the mesopleuron granulate, or much of the mesoanepisternum plus part of the mesokatepisternum shiny. Pilosity largely fine, filiform; suberect to subdecumbent, from yellow to brown. Head with maximum width close to the eye insertion; vertexal margin convex; cephalic capsule projected posteriorly, forming a variable conspicuous neck; occipital margin lamelliform and longitudinally costulate, varying in relation to the shape of the head (piriform or subpiriform). Compound eyes convex and prominent, ocelli protruding forming a cephalic crest in different degrees. Mandibles developed, triangular; external margins convex, curving apically; masticatory margins with 9-14 subtriangular teeth; basal margins with morphology similar to that of conspecific females, more or less concave with mandibles closed, leaving or not a clypeomandibular space. Clypeus ample, frontoclypeal portion slightly truncated or bulged, extending to the level of the frontal lobes; anterolateral portion depressed, concave; anterior margin lamellar, yellowish or slightly translucent, straight or medially concave medium, laterally rounded. Frontal area variably distinct, semicircular or transverse; slightly rugose or with a frons carina which extends more or less posteriorly towards the median ocellus. Frontal lobes salient, free margins sharply rounded in front; antennae inserted into their ventral face. Antennal scrobes deep and ellipsoid, delimited by a crenulate border and advancing to the lateral clypeal area. Postgenal carina continuous or almost continuous, irregular, extending from the posterolateral corner of the head to the mandibular insertion. Antennae long and filiform, with 13 segments. Scape short, about twice as long as wide; basal margin oblique and sharply rounded to the external margin, obtuse angle in the inner margin; apex truncated. Antennomeres 2 and 3 approximately half the length of scape; other funicular segments longer than wide; apical segment longer; antennal segments 8 and 9 slightly or conspicuously twisted, causing the antenna to appear to be twisted around its axis to varying degrees. Mesosoma robust, more or less elongated; pronotum anteriorly divided or not in two distinct portions; mesoscutum like conspecific gynes, presenting a longitudinal carina anteromedially, more or less distinct. Notauli complete, shallow or deeply impressed, extending after their converging point in variable fashion towards the scutoscutellar sulcus. Parapsides generally deeply marked, more or less oval; parapsidal lines shiny and distinct. Axillae projected as in the conspecific gynes, hook-shaped. Mesoscutellum in dorsal view shaped like an inverted "U", posterior margin concave. Propodeum with posterior angles projected, projections either obtuse or slightly triangular, divided by strong transversal carina. Propodeal lobes auriculate. Metanotum narrow, medially projected. Petiole with morphology similar to conspecific females; petiolar spiracles projected laterad in the median portion of peduncle. Gaster in dorsal view with five visible segments. Genitalia (after Feitosa et al. 2007): genital capsule slender; parameres slightly enlarged, strongly rounded and with tips curved inward; in lateral view, abruptly narrowed toward the apex, volsella with the general pattern observed in Myrmicinae males; pygidium and subgenital segments with apical portion slightly narrow and rounded. Legs slender; calcar of strigil short and pectinate, present only on prolegs. Brownish wings; forewings with venation similar to conspecific gynes (varying regarding the length of transversal vein 1m-cu, that can be present as a short appendage on males and absent on gynes), with the following configuration: absent, obsolete (as a short appendage to Rs+M) or complete, closing the discal cell. Hindwings with tubular longitudinal veins Sc+R; M+Cu and 1A (anal), the former branching to short vein SC+R1 after the abscissa of Sc+R and M+Cu; Rs+M present as a short appendage after the abscissa of Sc+R and M+Cu. Anal vein short, apex slightly curved upwards, meeting cu-a; 4–8 submedian hamuli present.

Distribution. The genus has a restricted Neotropical distribution. The northernmost record comes from Honduras for *B. manni*, the southernmost record from the State of Rio Grande do Sul, Brazil, for *B. disciger*. In terms of elevation, collection information of examined specimens suggests that *Basiceros* might peak its abundance at low and medium elevation—supported by the absence of specimens in collections from high-elevation forests (>1500m) and studies focusing on ant diversity along altitudinal gradients (e.g., Scott-Santos 2008).

Natural History. The scarce information from the literature (Weber 1950, Brown 1974, Hölldobler & Wilson, 1986) mention the dirt ants as being cryptic, with slow-moving habits, and presenting thanatosis when disturbed. Apparently, no recruitment has been recorded, and workers forage solitarily. As far as it is known, *Basiceros* do not excavate nests, and their colonies are usually found in leaf litter interstices, occupying soil cavities, hollow or rotten logs, seedpods, or preferably in areas with superficial root system or close to the base of large trees.

Little is known about its colonial structure (nests usually have \sim 50–100 individuals); collection records suggested that some species may be polygynic. Intercastes are reported for the first time in the present study. The unique morphology and the usually dense layer of soil and litter particles covering the integument of some species suggest that the dirt ants have a dietary preference—situation reinforced by an impressive morphological variation on the mouthparts across the genus (Probst *et al.* 2019).

Taxonomic synopsis

Basiceros browni Probst & Brandão sp. nov.

- B. conjugans Brown 1974
- B. convexiceps (Mayr 1887)
- B. disciger (Mayr 1887)
- B. manni Brown & Kempf 1960
- B. militaris (Weber 1950)
- B. redux (Donisthorpe 1939) = Octostruma reducta comb. n.
- B. scambognathus (Brown 1949)
- B. singularis (Smith 1858)
- B. tumucumaquensis Probst & Brandão sp. nov.

Identification key for female castes of Basiceros

| 1. | Head with round vertexal margin, either presenting a medially emarginate or continuous crest (Figs 11A and 17A) |
|----|---|
| - | Vertexal margin continuously or moderately concave, crest absent (Fig 13A) |
| 2. | In full-face view, crest converging medially, emarginate. Sulcus interrupted by median vertexal convexity (South America, widely distributed) (Figs 11–12) |
| - | In full-face view, vertexal crest continuous, separated by a broad uninterrupted sulcus (Central and N South America) (Figs 17–20) |
| 3. | Mandibles triangular, apices not abruptly curved ventrally, external margins convex in their basal portion (Figs 8A and 23A); basidorsal sulcus absent |
| - | Mandibles subtriangular, apices strongly curved ventrally (Figs 21C, 27E), external margins subparallel in their basal portion; basidorsal sulcus present (Figs 21A, 26A–B) |
| 4. | Head pilosity majorly composed of decumbent and squamiform hairs. Mandibles with basal portion covered with squamiform hairs; basal angle of mandibles right-angled, region indistinctly translucent. Surface of antennal scrobes completely sculptured, rugo-punctuate (South America, mainly Brazil) (Figs 21–22) |
| - | Squamiform pilosity on head restricted to clypeal surface. Basal angle of mandibles broadly round, strongly translucent. Antennal scrobes matte, finely strigulate (N and NW Brazil) (Figs 26–27) |
| 5. | In dorsal view, vertexal corners round; vertexal margin with short and clavate hairs. In full-face view, clypeomandibular space narrow, much shorter than half the maximum length of the clypeus (Fig 5A). Specialized pilosity on mesosoma and gaster sparse (Fig 5B) |
| - | In dorsal view, vertex corners angulate; vertexal margin with long and clubber hairs in its apical portion. In full-face view, |

clypeomandibular space wide, longer than half the maximum length of the clypeus (Fig 3A). Specialized pilosity on mesosoma Pilosity on petiolar node, postpetiole, and lateral margin of propodeum dense, whitish, and squamiform. Subpetiolar process 6. Pilosity on the petiolar node, postpetiole, and lateral margin of the propodeum sparse. Subpetiolar process consisting of a single ventral process located in the anterior portion of the peduncle (Brazilian Atlantic Forest, Santa Catarina to Bahia) (Figs 8-9) B. convexiceps In full face view, external margins of mandibles continuously curved from base to apex. Frontoclypeal surface smooth and 7. shiny or slightly shagreened. Labrum lunate, anterior margin rounded (see Probst et al. 2019, Figs 2-3), lacking cleft 8 In full face view, external margin of mandibles slightly sinuous. Frontoclypeal surface finely foveate-reticulate. Labrum acute and bilobed apically, lobes separated by very narrow cleft (Probst et al. 2019, Figs 2H and 4G) (Ecuador) (Figs 3-4) B. browni sp. nov. Mandible dorsum with dense squamiform hairs or irregular fovea. Clypeus with decumbent and squamiform pilosity. Distal 8 margin of labrum convex (Probst et al. 2019, Fig 2F). Base of sternite of first gastral segment bearing median longitudinal Basal portion of mandibles smooth and shiny. Clypeus covered with piligerous punctures. Distal margin of labrum with medially protruding knob (Probst et al. 2019, Fig 2G). Base of sternite of first gastral segment lacking longitudinal carina or median

Identification key for Basiceros males

1. 1m-cu complete, always closing the discal cell (Figs 1C, 14E); clypeomandibular space wide (Fig 14D); pronotum divided into 1m-cu absent or obsolete, discal cell absent (Fig 1A); clypeomandibular space narrow or absent (Fig 12D); pronotum undivided 2. Mandibles subtriangular, external margin strongly convex, apical tooth projected; head subhexagonal (Fig 22D-F) B. scambognathus 3. Mesosoma shagreened, matte; mesopleuron costulate; antennal torsion exaggerated (Fig 28) . . B. tumucumaquensis sp. nov. Mesokatepisternum covered with irregular rugulae; contrasting with the reticulate sculpture of mesoanepisternum; anterior face 4 Mesopleuron (mesokatepisternum + mesoanepisternum) reticulate; anterior face of pronotum conspicuously keeled (Fig 14D-F) B. manni 5. Subpetiolar process present as anterior projection, curved anterad, followed by 1-4 teeth, a lamella, or both. Mesoanepisternum with at least half of its surface smooth and shiny, mesokatepisternum smooth and shiny on about half of its length (Fig 6D-F) B. conjugans Subpetiolar process absent; mesoanepisternum smooth and shiny on about 2/3 of its length; mesokatepisternum fully punctu-6. Subpetiolar process present as an anterior spiniform projection, with apex slightly curved anteriorly; mesoanepisternum smooth

Notes: Overall, not many males were available for most *Basiceros* species; therefore, male key should be interpreted as tentative. It is likely that the male of *Basiceros browni* **sp. nov.** keys out on step 4, given the size of worker and mandibular morphology, similar to the other species in this dichotomy. Step 1 should be read with caution, as the male of *B. convexiceps* was not examined, and its inclusion in the key is supported only by the diagnosis and forewing illustration provided by Emery (1924). *Basiceros conjugans* males can sometimes present the transversal vein 1m-cu in one of the forewings, so that the discal cell can be present and absent on the same individual.

Basiceros browni Probst & Brandão sp. nov.

(Figs 2C, 3, 4, 30)

Type material. *Holotype worker*: ECUADOR: Los Ríos (spelled as "Pichincha"): 47km N from Quevedo, Rio Palenque Research Station, 29.vii.1978, G.J. Umphrey col., N. GJU # 0860 [MCZ]. *Paratype workers*: Same locality, date, and collector as holotype [MCZ, one gold coated worker; GUPC, one worker]; same locality and collector, 30.vii.1978 [NMH, one worker (NHM1014338/CASENT0900941)]; Pichincha: Otongachi, 0°18'49" S 78°57'15" W, 850m, 04.ix.2009, G. Ramón col., KT-1419/LL8-W15 [MZSP, one worker].

Diagnosis (only known from workers). Comparatively medium to large (TL 6.55–7.59 mm); color light brown to dark brown; densely sculptured, rugose to areolar-rugose, procoxae and gaster foveate; petiole tubuliform, without projected node; mandibles triangular, long and pedunculate with twelve teeth on each masticatory margin; clypeomandibular space ample; labrum cuneiform, bilobed apically, lobes separated by a narrow cleft; pilosity consisting of a basal layer of flat and spatulate to subplumose decumbent curved hairs for most of their length, and another layer of long erect and clavate hairs.

Description. *Worker* (n=4, range includes holotype measurements). HL 1.25–1.41, HL2 1.29–1.45, HW1 1.16–1.33, MdL 0.8–0.9, SL1 0.93–1.13, SL2 0.90–1.15, PDL 4.5–6, A3L 0.04–0.05, AFL 0.38–0.45, FuL 1.04–1.21, EL 0.15–0.18, EW 0.14–0.16, ML 1.7–2.0, MfL 1.40–1.68, MtL 1.08–1.25, PH 0.32–0.35, PL 0.87–0.97, PW 0.32–0.38, PPL 0.45–0.52, PPW 0.47–0.55, GL 1.47–1.77, GW 1.06–1.16, TL 6.55–7.59, CI 93–95, CS 1.21–1.37, MCI 62–64.00, SI 76–86, ESI 15–16, SAI2 240–255, EII 0.24–0.25, MFI 77–85, PTI 266–291.

Size comparatively large compared to other *Basiceros* species. Light brown to dark brown, with lighter appendages, yellowish-brown to brown, respectively. Body predominantly covered by two types of hair. White to light brown semi-erect to erect hairs, long and filiform and slightly clavate, present on head dorsum near eye height and extending to occipital region, sparsely present on ventral region of head; on the anterolateral corner and dorsum of pronotum; a pair present on the anterodorsal margin of propodeum; on sides and petiolar dorsum; on the dorsum of postpetiole, two pairs on the anterior margin of postpetiolar sternite; on the dorsal and ventral gastral margins, more abundant dorsally. Length of these hairs varying according to position, notably longer on the dorsal surface of entire body. White to yellowish decumbent hairs, flattened, short and curved, apically spatulate or subplumose, present on the head dorsum, pronotum and propodeum, more densely on the latter. One pair of spatulate hairs on the basal portion of lateroventral region of mandibles and another on the base of stipes, relatively close to the hypostomal margin. Setae sparse, from simple and short to apically spatulate, at the base of mandibles. Long and erect spatulate hairs on the anterior margin of antennal scapes, scape dorsa covered by short spatulate hairs, filiform setae on the inner face of the antennal basal lobe, hair on the scape elbow (anterior region of lobe) with the same morphology as the special hairs present on the rest of the body. Clypeal disc with short and appressed setae. Filiform and apically curved hairs present on the pygidium and hypopygium. Short and subdecumbent spatulate hairs on trochanters and tibiae and on posterior region of tarsi, becoming thinner on the distal segments.

Mandibles smooth over most of its length and shiny, with sparse piligerous punctuations, interdental filiform setae present, surpassing length of the teeth; anterior region striated. Clypeus rugo-reticulate in great part of its central disc; lateral regions predominantly areolar-rugose, anterior region of clypeus laminar, smooth and shiny, with its anteromedial portion weakly covered by longitudinal striate impressions. Head dorsum covered by thick and irregular striae, gaps between them forming foveae of variable size. Internal surface of antennal scrobes. Ventral face of head punctuate-reticulate, changing to rugose near posterior margin and roof of antennal scrobes; extending posteriorly to the vertexal margin, covering this region and the sulcus present near the median region. Vertexal region scrobiculate around the occipital carina. Mesosoma strongly sculptured, dorsum covered with vermicular rugae ranging from strongly irregular in the dorsum of the promesonotum to obliquely longitudinal in the dorsal region of the propodeum; lateral region of the pronotum and central portion of mesopleuron punctate-reticulate; mesopleuron with sinuous lamellar epicnemial carina bordered by sparse scrobiculations; lateral region of propodeum with irregular and transversally vermiculate striae, forming foveae of variable size, varying to punctate-reticulate in its central range and becoming rugose again near the bulla of the metapleural gland; posteropropodeum covered by sparse punctuations, varying to longitudinal rugulae as the sloping face advances to the propodeal lobes. Petiole and postpetiole with oblique to irregular longitudinal rugae. Posterior region of the petiole longitudinally rugulose. First gastral segment densely punctuate-reticulate; punctuations intermediate and distinct, with smooth and shiny space between them; punctuations decreasing near the posterior margin, thinner and more reticulate. Other gastral segments with exposed tergites finely reticulate—same to sternites, but with margins and shinier. Procoxae punctuate-reticulate, meso- and metacoxae punctuate to dotted to irregularly rugulose; legs with inconspicuous rugo-reticulations.

Head subtrapezoidal, with posterior margin slightly convex medially; mandibles long and peduncular, masticatory margins with 12 triangular teeth, apex of basal tooth comparatively more rounded and apical tooth wider; clypeomandibular space present, semi-spherical. Labrum cuneiform, bilobed apically; lobes separated by a very narrow or even slightly inconspicuous cleft. Clypeal disc flat, anterior margin lamellar, slightly convex in its median range. Palps hidden. Antennal scrobes shallow, with indistinct posterior limit. Antennal scapes long (SL 0.90–1.15) and slightly tubular; basal lobe short and trapezoidal; anterior margin crenulated and laminar; funicular segments

gradually increasing in size, two-segmented apical club present with the apical segment being as long as the sum of the five anterior funicular segments and slightly shorter than half the length of scape (AFL: 0.38–0.40; SL1 0.93–1.00). Compound eyes rounded and convex, located just above the posterior half of the head (in frontal view) and at the limit of the anterior margin of the scrobes (lateral view), with about nine ommatidia in the largest diameter. Vertexal margin slightly concave, with a shallow groove in its median portion; posterolateral edges angulate, not protruding. Occipital carina present, not projected.

Lateral profile of mesosoma with promesonotum convex, sloping posteriorly into a broad and deep metanotal suture. Propodeal profile slightly convex posteriorly. In dorsal view, humeral corners projected and rounded; promesonotal suture indistinct to weakly marked; promesonotum slightly wider than twice the propodeum. Sloping face of the propodeum anteriorly delimited by a superior transverse carina that connects to the propodeal spines, those divergent in dorsal view and oriented upwards, presenting a strong carina in the region of convergence with the slope. Propodeal spiracle tubular, opening circular. Metapleural gland bulla prominent; posterolateral region carinate, opening surrounded by cuticular flap. Propodeal lobes short and rounded. Tarsal claws simple. Petiole in lateral view long and tubular; smooth and sloping anterior surface, meeting the dorsal surface obtusely; dorsal face convex, with an anterior portion lower than the median portion; in dorsal view, peduncle long, petiole with anterior face ellipsoid, posterior face slightly narrower and marginally rounded, subpetiolar process composed of an anteroventral oblique and bifid projection, followed by 4–7 spiniform projections of different sizes, the first or second sometimes denticular and the first sometimes protruding from the base of anterior anteroventral process. Postpetiole longer than wide; wider and higher posteriorly; in dorsal view, anterior margin concave. In lateral view, postpetiolar sternite carinate; in ventral view, present a pair of carinae in parallel with the lateral limits of this sclerite. Sting conspicuous.

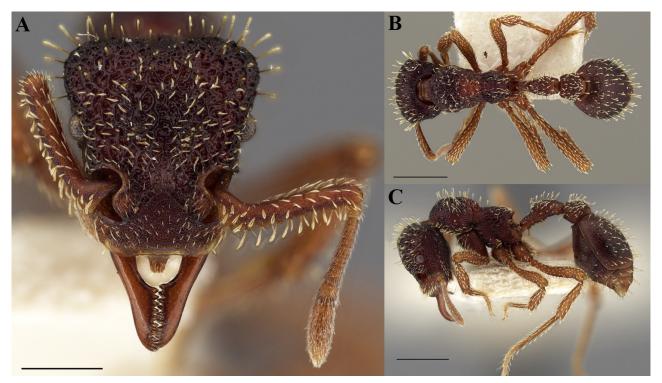


FIGURE 3. Basiceros browni **sp. nov.**, holotype worker (MCZ, Ecuador: Los Ríos); A. full-face view, B. lateral view, and C. dorsal view.

Gyne, male, and larva: unknown.

Etymology, named after Dr. William (Bill) Brown Jr., reference for the taxonomy of "basicerotine" ants.

Comments. *Basiceros browni* **sp. nov.** can be separated from other *Basiceros* by the combination of a tubuliform petiole, without a projected node; long and pedunculate mandibles with a wide clypeomandibular space; labrum shape (cuneiform, lobes separated by narrow cleft); and general pilosity (long, erect, and clavate hairs).

This new taxon was initially recognized from stacked macrophotographs of a worker specimen on AntWeb, deposited at the NHM in London. The label contained a handwritten note indicating it as a paratype (although this

species was yet to be formally described) of the species "*Basiceros browni* sp. nov.". Thanks to the aid of Dr. Brian Fisher (Cal Academy) in identifying the collector origin, the specimen was linked to Dr. Gary J. Umphrey, professor in the Department of Statistics at the University of Guelph, Ontario, Canada. Dr. Umphrey kindly traveled to the FMNH in Chicago with some *Basiceros* specimens. Among the workers of this new taxon that Dr. Umphrey made available for examination, one was coated for SEM and missing the left proleg. For those specimens, considerable variation in size could be noted (in mm: HL 1.25–1.41, ML 1.70–2.00, GL 1.47–1.77, TL 6.55–7.59). Additionally, specimens presented slight variation in the distal margin of labrum, with the cleft in one specimen practically indistinct. The lighter coloration of one of the workers and the absence of particles covering its integument suggest a recently emerged worker, selected to be the holotype.

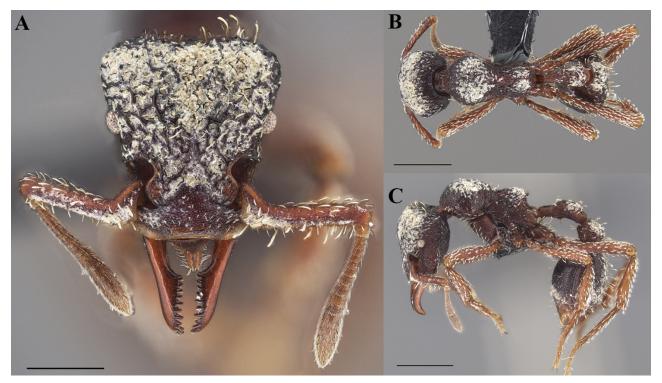


FIGURE 4. *Basiceros browni* **sp. nov.**, paratype worker (GUPC, Ecuador: Los Ríos); A. full-face view, B. lateral view, and C. dorsal view.

Distribution. So far, only known from the provinces of Pichincha and Los Ríos in Ecuador from two collection events (1978 and 2009, respectively). The specimens collected at the Río Palenque Research Station have "Pichincha" as the province; this reserve is instead located in the Province of Los Ríos.

Natural history. Virtually nothing is known about the biology of this species. The first collection resulted in four workers; three workers retrieved on July 29, 1978 from a rotten log at the edge of a trail in the middle of a forest. According to Dr. Umphrey, the nest was not found. The last 1978 specimen was collected the following day while foraging about three meters from the place occupied by that rotten log, suggesting it might have been part of the same colony. The paratype collected in Otongachi came from a Winkler sample.

Basiceros conjugans Brown, 1974

(Figs 2A–B, 5–7, 31)

Basiceros conjugans Brown 1974: 134, Figs 1-2 (worker, gyne, and male), Ecuador.

Type material. ECUADOR: Limoncocha & vic.: IX–XI.1964, H.R. Hermann col., n. (one worker—holotype; 4 workers, 2 males—paratypes) [MCZ 32179] (examined); (one alate gyne, one male—paratypes) [NHMB] (examined). COLOMBIA: Leticia: 7 km North of Leticia, 10–25.ii.1972, Stewart B. Peck & Jarmila Peck cols., (one worker—paratype) [ANIC] (examined).

Diagnosis. Dark amber to black; integument punctuate-foveate; clypeomandibular space narrow; corners of vertexal margin rounded, sulcus present medially and separating posterofrontal tumosity; petiolar node truncate anteriorly; postpetiolar and petiolar nodes usually densely covered by squamiform hairs.

Description. *Worker* (n=4). HL 1.25–1.28, HL2 1.25–1.30, HW1 1.28–1.31, MdL 0.72–0.78, SL1 0.84–0.89, SL2 0.89–0.94, PDL 0.11–0.13, A3L 0.03–0.05, AFL 0.36–0.38, FuL 0.97–1.00, EL 0.16–0.17, EW 0.14–0.16, ML 1.69–1.72, MfL 1.33–1.34, MtL 1.00–1.06, PH 0.38, PL 0.77–.081, PW 0.36–0.38, PPL 0.47–0.50, PPW 0.53–0.61, GL 1.59–1.63, GW 1.13–1.19, TL 6.58–6.61, CI 100–105, CS 1.27–1.28, MCI 56–62, SI 69–73, ESI 17–19, SAI2 247–252, EI1 0.23–0.26, MFI 95–97, PTI 204–216.

Body yellowish-amber to dark brown; appendages slightly lighter, yellowish to dark brown. Mandibles covered by tiny piligerous punctures, apex with short yellowish setae; interdental setae present, yellowish and filiform, subequal to teeth length. Basimandibular seta present, narrow and erect, slightly clavate. Suberect and clavate hairs in the median portion of the stipe dorsa. Frontoclypeal margin covered by spaced piligerous punctuation; lateroclypeal region with short and squamiform, decumbent yellow hairs. Occipital region predominantly covered by coarse (foveolar) piligerous punctuations; pilosity close to the posterolateral region of the head and the vertexal margin composed of whitish to yellowish, short and subdecumbent, squamiform hair. Lateral and vertexal margins of head covered by erect to suberect clavate hairs, yellowish and in the following conformation: one hair above the eyes, at the anterior limit of the antennal scrobe; four hairs on the posterolateral margin of the head, surrounding the meeting point between the posterior limit of the scrobe and the vertexal margin; one hair near the posterolateral corner of the head; four or five hairs on each side of the vertexal margin, separated by the median groove. A pair of yellowish erect and clavate hairs in the frontal region, close to the vertexal margin. Lateroventral head margin covered by whitish and squamiform hairs, subdecumbent; ventral surface of head with curved suberect and subdecumbent filiform setae, length variable. Occipital carina surrounded by four to six long and filiform hairs. Yellowish to whitish plumose pilosity, usually subdecumbent, on the mesosoma and metasoma in the following conformation: surrounding the anterolateral margin of pronotum; on the mesonotum and propodeum dorsa; marginating the sloping face of propodeum; densely on petiolar and postpetiolar node dorsa; three pairs on each side of the anterolateral region of the postpetiolar sternite; on the anterolateral region of procoxae and meso and metacoxae dorsa; on legs, from trochanters to basitarsi dorsum. Clavate hairs in the following conformation: one pair of erect hairs present on mesonotum dorsum close to promesonotal suture; erect to suberect hairs close to gastral sternite and tergite margins. Mesosternum shelf (surrounded by the epicnemial fossa) with short, filiform setae along its length. Long and filiform setae present on the anterior portion of procoxae and median portion of first gastral sternite. Thick and suberect setae present on the ventral margin of basitarsus to apex of distal tarsomere. Antennae pilosity: dorsal surface of the scape primarily covered by short, subdecumbent and squamiform hairs; external margin of scape with long, erect, and squamiform (on its apical half) hairs; funiculus densely covered with short yellowish setae; ventral margin of scape with longitudinal rows of median, curved and subdecumbent setae. Remaining of integument with thick piligerous punctuations.

Body mostly smooth and shiny on glabrous regions. Mandible and clypeus dorsa sparsely covered with punctuations. Anteroventral portion of mandibles and ventral margin of scapes finely alveolate. Head punctuate-foveate, posterolateral surface of antennal scrobe punctuate-rugose. Pronotum sparsely foveate. Dorsum of mesonotum, anterodorsal region of the propodeum, dorsal surface of the meso- and metacoxae, and dorsum of petiolar and post-petiolar node punctuate-rugose. Mesopleuron and lateral of the propodeum smooth and shiny or subopaque. Surface of propodeal declivity punctuate-rugose. Gaster densely punctuate-reticulate; tergite of abdominal segments V, VI, and VII finely and densely punctuate, slightly opaque, tergal margins smooth and shiny; sculpture sparser in the first gastral sternite, especially in the longitudinal axis of median region. Antennal scapes smooth or finely rugulose, usually shiny. Funiculi densely and finely punctuate, usually opaque. Legs smooth or superficially rugose; procoxae punctuate-foveate.

Head subtrapezoidal, sides delimited by raised margin extending from eye height to posterolateral region. Vertexal margin with gently convex corners slightly projected posterad, and with median groove dividing tumosity on the posterofrontal region of the head. Cervical margin carinate. Palp formula 2,2; palps strongly fused, giving the impression of being unsegmented; maxillary palp slightly larger in size and slightly wider than labial; labial palp apically clavate. Stipes subrectangular. Labrum cuneiform; distal margin bilobed, lobes separated by a narrow cleft, basal region canaliculate. Mandibles triangular; in full-face view, external margins slightly concave; basal margin lamellar; basal angle obtuse, followed by a masticatory margin with ten triangular teeth, apical tooth slightly curved;

in lateral view mandibular apex slightly curved ventrally. Clypeomandibular space narrow. Anterior clypeal margin lamellate; anterolateral portion gently convex; anterior margin slightly concave in its median portion. Scape with slightly obtuse basal angle, followed by translucent and crenulated lamellar portion. Antennal fossa deeply impressed. Antennal scrobe comparatively deep in its lower half, posterior limit faintly distinct.

Lateral profile of mesosoma with promesonotal complex subglobular. In dorsal view, promesonotal suture practically indistinct; metanotal suture broad and strongly impressed, longitudinally costulate. Mesopleuron anteriorly marginate, interrupted at the meeting of a conspicuous epicnemial fossa. In dorsal view, propodeum subrectangular. In lateral view, anterior portion of propodeum slightly oblique posteriorly, abruptly followed by the sloping face. Propodeal slope laterally carinate and with transverse carina connecting to short, triangular and acute projections. Opening of propodeal spiracle rounded. Metapleural gland bulla prominent, protruding; opening transversal and covered by cuticular lamella. Petiolar peduncle longitudinally carinate on dorsal surface. In dorsal view, propodeal spiracle projected laterally. In lateral view, petiolar node with anterior face truncate, posterior face covered by pilosity; postpetiole slightly longer than petiolar node. Subpetiolar process highly variable: anterior process, followed by spiniform lamella or anterior process bifid, followed by spines and/or angular lamellar process.

In dorsal view, petiolar node longitudinally subrectangular; postpetiole (pilosity excluded) slightly wider than long; posterior margin convex and widely inserted in the anterior gastral cavity. Calcar of strigil pectinate. Pro-, meso-, and metabasitarsi longer than the sum of other tarsomeres. Tarsal claws simple.

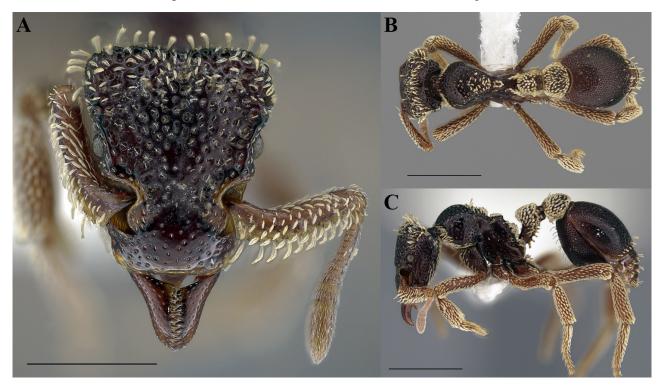


FIGURE 5. *Basiceros conjugans*, holotype worker (MCZ 32179, Ecuador: Limoncocha); A. full-face view, B. lateral view, and C. dorsal view. Scale bars: A = 0.5 mm, B–C = 1 mm.

Gyne (n=3). HL 1.31–1.35, HL2 1.34–1.39, HW1 1.14–1.19, MdL 0.72–0.75, SL1 0.84–0.88, SL2 0.85–0.94, PDL 0.13–0.14, A3L 0.05, AFL 0.38–0.41, FuL 0.97–1.00, EL 0.20–0.23, EW 0.16–0.19, LOD 0.07–0.08, MOD 0.08–0.10, OOD 0.37–0.43, ML 1.70–1.84, MSL 0.75–0.81, MSW 0.82–0.87, MLL 0.30–0.31, MLW 0.45–0.50, MfL 1.23–1.25, MtL 0.97–1.00, PH 0.41–0.44, PL 0.75–0.81, PPL 0.53–0.55, PW 0.21–0.34, PPW 0.5–0.63, GL 1.88–2.03, GW 1.25–1.36, TL 6.91–7.30, CI 84–88, CS 1.23–1.27, MCI 54–55, SI 74–79, ESI 22–26, SAI2 226–232, EII 0.31–0.32, MTI 105–116, MLI 145–160, MFI 92–95, PTI 184–188.

Color and sculpture similar to the worker; size slightly larger. Cephalic dorsum with three ocelli: median ocelli inserted slightly below and lateral ocelli inserted just above a pair of clavate and erect hairs. Head and waist pilosity as in workers. Pilosity of anterolateral margin of pronotum denser and longer than in workers. Whitish and subdecumbent, squamiform hairs close to humeral angles and surrounding the posterior limit of pronotum; short and sparse on the dorsum of mesoscutum; on the scutoscutellar sulcus axillae; on the dorsum of mesoscutellum; a

suberect pair on the metanotal flange. Whitish erect to suberect and clavate hairs on each side of pronotum, one pair close to the pronotal suture; a pair on the metanotal flange; narrower and arranged in eight pairs on the dorsum of mesoscutum; one pair in each parapside; one on each lateral portion of axilla, one on the lateral margin of mesoscutellum. Hairs on gaster more abundant than on workers. In dorsal view, mesoscutum anteriorly rounded, slightly cuneiform, posterior margin slightly convex in the meeting with the scutellar suture; notauli indistinct; parapsidal lines narrow and inconspicuous, involved by the sculpture; shallow, parapsis rudimentary; tegula narrow, apical margin rounded. Prescutellum narrow; axillae projected posteriorly, rounded and slightly depressed. Scutellar sulcus well marked. Mesoscutellum transversely subrectangular, posterior limit concave. Dorsal face of propodeum strongly inclined. In lateral view, anapleural sulcus broader anteriorly at the connection with the epicnemial fossa, narrowing posteriorly. First gastral sternite with median region slightly projecting on its basal half. Forewing mostly conforming to type 2, transversal vein 1m-cu present as an appendage; hindwing with fix submedian hamuli.

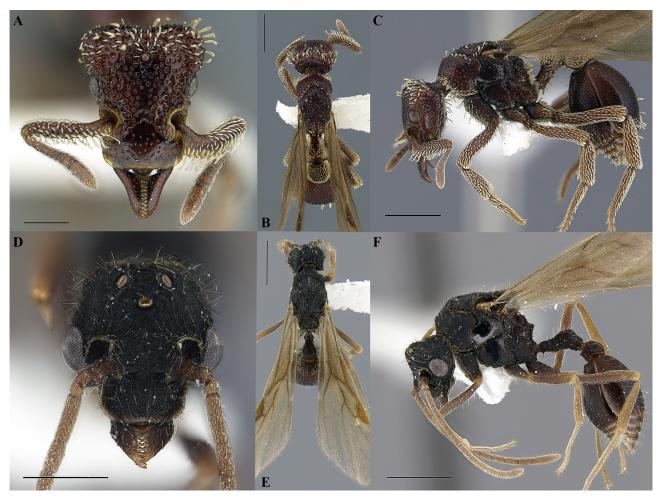


FIGURE 6. *Basiceros conjugans*, paratypes gyne and male (MCZ 546463, Ecuador: Limoncocha), Ecuador: Limoncocha); A and D. full-face view, B and E. dorsal view, C and F. lateral view. Scale bars: A, D = 0.5 mm, B, C, E, F = 1 mm.

Male (n=2). HL 0.85–0.93, HW1 0.77–0.81, HW2 **0.63**–0.95, MdL 0.40–0.43, SL2 0.15–0.21, PDL 0.10–0.13, A3L 0.28–0.31, AFL 0.44–0.48, EL 0.30–0.33, EW 0.23–0.26, LOD 0.09, MOD 0.08–0.09, OOD 0.31–0.34, ML 1.43–1.59, MSL 0.75–0.85, MSW 0.70–0.78, MLL 0.30–0.34, MLW 0.43–0.48, MfL 1.15–1.25, MtL 0.83–0.88, PH 0.25–0.30, PL 0.63–0.70, PW 0.23–0.33, PPL 0.31–0.36, PPW 0.34–0.40, GL 1.36–1.50, GW 0.98–1.10, TL 5.01–5.41, CI 84–91, CS 0.81–0.87, MCI 44–47, SI 19–28, ESI 150–200, SAI 50–70, SAI2 34–50, EI1 0.65–0.71, EI2 80–**124**, MTI 87–98, MLI 136–141, MFI 61–67, PTI 231–250. (In bold: measurements suffered influence of prolegs partially covering compound eyes).

Size slightly smaller than the conspecific gyne. Color black; postpetiole and first gastral tergite disc brown; appendages yellowish to light brown. Apical portion of mandibles smooth and yellowish. Wings yellowish to brown. Mandible dorsa and apex with long and fine yellow hairs, semi-erect to subdecumbent, slightly longer on apical portion of mandibles. Head with two main types of hair: medium and fine, yellow and subdecumbent, primarily on

the frontal disc of clypeus; long and whitish to yellowish (sometimes with a curved apex), present along the genal carina, on the vertexal margin, and the ventral surface. The second hair type widely present throughout the body: on mesosomal dorsum, waist, and gaster, exceptionally long on the ocellar region, on procoxae and dorsum of petiole. Antennomeres with short and yellowish appressed setae. Legs with medium and yellowish decumbent to decumbent setae.

Body uniformly punctuate-reticulate, sculpture varying on diameter and degree of impression. Apical portion of mandibles smooth and shiny. Irregular longitudinal rugae present in the neck to faintly on the vertex margin, close to occipital carina. Irregular transverse rugae on the dorsum of mesoscutellum, on the metakatepisternum and propodeum. Mesoanepisternum slightly darker, smooth and shiny over a little more than half its length; posteromedial portion of mesokatepisternum smooth and shiny. Dorsolateral rugae present on the anterior portion of petiolar node.

Head subpiriform; occipital margin wide and lamellar, medially concave. Palp formula 1,1; palpi slightly swollen and flattened on apical half; maxillary palp appears to be slightly longer and wider than labial. Mentum narrow and triangular. Stipes subrectangular. Labrum elongated, distal margin bilobed; approximately ten long setae present. Mandibles triangular, curved towards their apexes; masticatory margin with nine teeth of similar size. Clypeus with central disc convex, slightly elevated; lateral regions depressed; anterior margin lamellar and slightly concave. Postgenal carina present, shaped like a longitudinal line, smooth and shiny just after the supraclypeal region and extending posteriorly on the head until close to the upper limits of the antennal scrobes. Antennal arch medially expanded as swollen posterolateral lobe, completely hiding the antennal bulb in frontal view. Antenna pedicel longer than wide, third antennomere about three times longer than the pedicel. Eyes large and globular, protruding from the cephalic capsule. Ocelli caramel-colored, projected. Mesoscutum cuneiform in dorsal view, elongated anteriorly. Smooth and shiny carina present on the anteromedial region of mesoscutum, extending as a line near the dorsal margin. Notauli V-shaped, converging at the center of mesoscutellum and extending as a median longitudinal sulcus to the line of the scutellar suture. Parapsidal lines shiny; curved on its anterior portion, subparallel and directed anterolaterally to the parascutal flange. Parapsis oval. Transcutellar sulcus slightly angled medially. Axillae protruded, strongly curved posteriorly; hook-shaped. Anapleural suture broad, strongly impressed and scrobiculate—mesoanepisternum conspicuously elevated relative to mesokatepisternum. Scutoscutellar sutured narrower compared to other Basiceros males; smooth and with a median transverse carina. Mesoscutellum subrectangular; posteromedially depressed; posterior margin strongly concave and depressed. Metanotum with posterior margin lamellar. Propodeum armed with triangular, laminar projections. Propodeal lobes auricular. Calcar of strigil short and pectinate. Tarsal claws simple; short arolia present. Petiole claviform; in lateral view petiolar node low; petiolar spiracle projected in dorsal view. Subpetiolar process with anteriorly curved projection followed by 1-4 teeth or with lamella or both (as Brown (1974) mentioned: "very inconstant"). Postpetiole approximately half the length of petiole in lateral view. In dorsal view, petiolar node rounded. Forewing type 1 or type 2. Hindwing with six submedian hamuli.

Larva (first description, based on three specimens). Approximate length through spiracles: 3.7 mm; profile pogonomyrmecoid: largest diameter near middle of abdominal region, thoracic region slender than abdominal region; curved ventrally. Anus ventral, anal opening weakly convex. Spiracles small. Integument of ventral region densely covered by spinules arranged in transverse rows. Pilosity moderately dense, denser near abdominal apex, sparse on the rest of the body; hairs long (0.10–0.30 mm), flexible and indented; alveolus and articular membrane present or not. Cranium suboctagonal, antennae very small. Clypeus protruded. Labrum bilobed, slightly wider than twice its length; ventral face densely spinulose; anteroventral margin of each lobe with about 4–5 rounded sensilla; anterodorsal border with two isolated short setae resembling trichoid sensilla. Mandibles pogonomyrmecoid, long and narrow, medially curved; apical tooth slightly curved and with rounded apex, separated from other teeth by conspicuous diastema; two protruding teeth projected from the basal margin; anteroventral margin with spiculae in short and arcuate subtransversal lines. Maxillae parabolic, dorsum with 4 setae, apex spinulose; maxillary palps digitiform, elongated and narrow, with three apical encapsulated sensilla and one spinulose lateral sensillum; galea digitiform, with two apical encapsulated sensilla. Labium covered by short transverse rows of spinules; those developed, capillary (about 0.02 mm) and densely covering the rest of labium surface; labial palp papillary, with five apical sensilla (two encapsulated and three with spinules); opening of sericeous gland transversal, bearing a short isolated sensillum on each side. Hypopharynx spinulose.

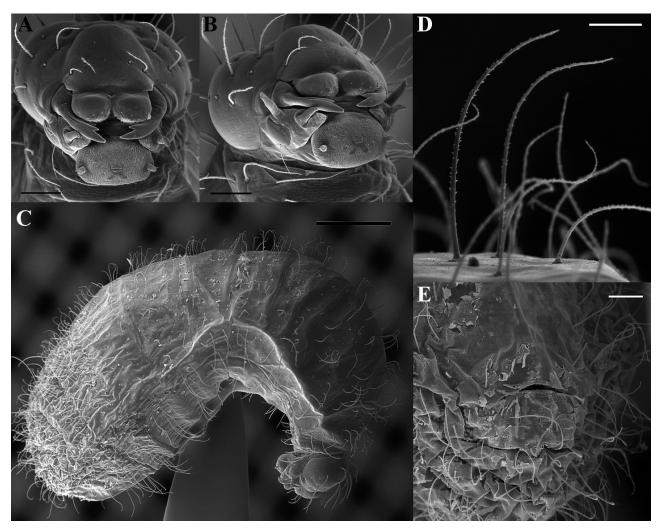


FIGURE 7. *Basiceros conjugans*, larva (MZSP, Peru: Madre de Dios); A. head in anteroventral view; B. head in oblique view; C. lateral view; D. dorsal pilosity; E. anus. Scale bars: A, B, E = 0.1 mm; C = 0.5 mm; E = 0.05 mm.

Etymology. from the Latin *conjugant*- (*conjugans*), present participle of the verb *conjugare*, meaning "connecting", "uniting". Such an epithet is undoubtedly a reference to the intermediate morphology of this species among the other taxa of the then considered separate genera *Aspididris* and *Basiceros*. When describing the species, Brown (1974) refers to *B. conjugans* as the "additional intergradient" and formally synonymizes *Aspididris* under *Basiceros*.

Comments. Brown (1974), based on the shape of the vertexal margin and the clavate hairs distributed along its length, speculates on the intermediate state of *B. conjugans* within the genus when comparing it to *B. disciger* and *B. manni. Basiceros conjugans* presents what Brown categorizes as "an intermediate pattern of transversal ridges on the vertexal margin"; the same for the concentration of clavate hairs in this region. The following could be added to the list of "intermediate" characters: head shape, more elongated than in *B. disciger* and *B. militaris*; the presence of a narrow clypeomandibular space, separating the clypeus from the basal region of the mandibles—absent in *B. disciger* and *B. militaris* and broad in *B. manni* and *B. singularis*; and the specialized pilosity (clavate or subplumose), denser than observed for *B. disciger* and *B. militaris*—what could explain the greater tendency for soil and vegetation particles to adhere to females of *B. conjugans* compared to other taxa from the *disciger* clade. In addition, males of *B. conjugans* may present a complete 1m-cu vein, closing the discal cell. This characteristic is found in *Basiceros* males from the *singularis* clade, but it is absent in other males from the *disciger* clade, confirming that this species might have a combination of characteristics of these two clades.

In terms of variation, workers of *B. conjugans* present variable integumentary and pilosity colorations, depth of the metanotal suture, shape of the petiolar node and subpetiolar process, integumentary sculpture (degree of impression and brightness), and size. However, together with *B. convexiceps*, it is one of the most morphologically

"cohesive" species. The specialized pilosity pattern (with emphasis on the vertexal margin, back of propodeum, petiolar node, and dorsal margin of the postpetiole) and head and mesosoma morphologies are present similarly on all examined specimens. It is important to mention that the pilosity is present as described for specimens in good conditions, but some specimens—probably resultant of abrasion—lack several special hairs, such as those on the vertexal margin and the back of the mesoscutum (in the case of gynes).

The holotype has a reddish-brown color and is probably a young worker, as other examined specimens from Ecuador are darker colored. Other Ecuadorian specimens have a similar reddish-brown color, usually within series containing darker specimens. The most extraordinary integumental coloration comes from Peruvian specimens collected in Napo, close to the border with Ecuador: a clear yellowish-amber and very bright integument. Regarding the morphology of the subpetiolar process, in the case of gynes and workers, it varies from: a set of two spines, composed of an angulate anteroventral "boot"-shaped or spine, followed by a lamella; a process with an anteroventral projection followed by 5–6 spines; or by lamellar processes and/or fused spines. The male subpetiolar process varies from an anterior curved process to a set of several short spines followed by a lamellar process at the end of the peduncle's ventral margin.

In addition, some specimens were partially covered by litter and soil particles, making it difficult to see certain structures, such as the ocelli on the gynes. Males may show variation in the forewing venation, with the length of transversal 1m-cu vein present differentially in the same specimen: it may be absent or present as a short appendix in one wing while present as complete in the other wing.

Distribution. This species is known for the Eastern Amazonian rainforests in South America and from secondary forests in Trinidad—more precisely, at the Arena Forest Reserve, place of a sustainable management system of a tropical forest (Shelterwood System), developed in the 1950s. For the present study, *B. conjugans* distribution is considerably expanded based on new records for the Brazilian states of Pará and Rondônia, Peru, and Guyana. *Basiceros conjugans* was known to Brazil based on a single worker collected in Porto Walter (Delabie 2000), a municipality in the state of Acre close to the Peruvian border. That worker was found in the stomach contents of the amphibian *Bufo typhonius* (Linnaeus, 1758) (= *Rhinella margaritifera* (Laurenti, 1768)). The material examined here indicates that this species possibly occurs in southern Venezuela and the Brazilian states of Roraima and Amazonas.

Natural history. Little is known about the biology of this dirt ant. Specimens were manually collected from rotten logs or leaf litter samples, with most of the examined material collected via Winkler extractors. In 2012, as a student of the Neotropical Ant Course at the Sachavacayoc Center (Peru, Madre de Díos), one of us (RSP) collected part of a colony nesting in a rotten trunk. Next to the collected material (larvae, a pupa, few workers) was an unidentified gastropod shell, the body of a turtle ant worker (*Cephalotes* sp.), and two cephalic capsules: one from an unidentified trap-jaw ant worker (*Odontomachus* sp.) and one from the termite *Uncitermes teevani* (Termitidae, Syntermitinae). These observations, associated with a cryptic life habit, suggest that *B. conjugans* might feed on carcasses of other arthropods. It cannot be ruled out that this species might prey on termites, which has occasionally been observed for other *Basiceros* (see natural history accounts for *Basiceros manni* and *B. singularis*). *Uncitermes teevani* does not build a nest and lives in the interstices of litter (Dr. Maurício Moura, pers. comm.).

Material examined. BRAZIL: Acre: Porto Walter, 08°15'31.2"S 72°46'37.1"W, 05.ii–17.iv.1997, J. Caldwell col. (1 worker) [CEPEC]; Pará: Parauapebas, 6°20'41.34"S 49°58'29.06"W, 08–22.v.2013, C.A.R. Souza et al. col., CARSTE 6040 (1 worker) [MZSP]; Rondônia: Porto Velho, Área Caiçara, 09°26'14.6"S 64°49'58.2"W, 27.iii–09.iv.2011, R.R. Silva & Albuquerque, E.Z. cols. (1 worker) [MZSP], 04–18.ix.2012, Ulysséa, M. A. & Prado, L. P. cols. (1 worker) [MZSP]; Porto Velho, Área Abunã, 09°35'46"S 65°20'56"W, 27.iii–09.iv.2011, R.R. Silva & Albuquerque, E.Z. cols. (2 workers) [MZSP], 09°35'43.7"S 65°20'55.7"W, 27.iii–09.iv.2011, R.R. Silva & Albuquerque, E.Z. cols. (1 worker) [MZSP]. COLOMBIA: Nariño Orito, Territorio Kofan, 00°30'N 77°13'W, 1000m (4 workers) [IAVH]. ECUADOR: Coca: v.1965, La Peña col., n. 546612 (1 male) [MCZ]; Napo: 20km S de Tena, 600m, 11.vii, Stewart B. Peck & Jarmila Peck cols., LACM 326569 (1 worker) [LACM]; Limoncocha, 250 m, 18.vi.1976, Stewart B. Peck & Jarmila Peck cols., n. 546454 (1 worker) [MCZ]; Jatun Sacha, 7km ESE Puerto Misahuallí, Lat. -1.0667 Long. -77.6167, 400m, 05.viii.1991, P. S. Ward col., PSW11365-31 (1 worker) [UCDC]; Puerto Misahuallí, 15.vii.1978, G.J Umphrey col., GJU 0774, (2 workers) [GUPC]; same data (1 worker) [MZSP]; same data (1 worker) [MNH]; same data (1 worker) [RSPPC]. Pichincha: 4 km E Santo Domingo de los Colorados, 08.vii.1976, Stewart B. Peck & Jarmila Peck cols., n. 546456 (1 worker) [MCZ]; 47 km S Santo Domingo, Rio Palenque Station, 700m, 18–30.v.1975, Stewart B. Peck & Jarmila Peck cols., n. 546456 (1 worker) [MCZ]; 47 km S Santo Domingo, Rio Palenque Station, 700m, 18–30.v.1975, Stewart B. Peck & Jarmila Peck cols., n. 546456 (1 worker) [MCZ]; pr. Morona Santiago:

Los Tayos, 3.viii.1976, Tjitte de Vries col. (1 worker) [MZSP]; Zamora: Chichipe, Copalinga, Lat. -4.091222 Long. -78.96069, 1030m, 30.ix.2009, T. Delsinne & Arias-Penna, T. cols. (1 worker) [MZSP]; Jardin Botánico, Estación El Padmi, 18.7km NEE Yantzaza, 835m, 3.74572°S 78.61436°W, 15.vi.2014, T. Delsinne & Arias-Penna, T. cols. (1 worker) [MZSP]; GUYANA: Upper Takutu-Upper Essequibo: Acaraí Mountains, near New Romeo Camp, 1°20'842"N 58°57'496"W, 735m, 16.x.2006, C. J. Marshall, TRS 061016-LS04 (2 workers) [USNM]; 1°20'896"N 58°57'491"W, 753M, J. Sosa-Calvo col., TRS 061016-LS06 (1 worker) [USNM]; 1°23'06"N 58°56'789"W, 294m, T. R. Schultz & J. Sosa-Calvo cols., JSC061010-LS09 (1 worker) [USNM]; 1°23'191"N 58°56'808"W, 303m, T. R. Schultz & J. Sosa-Calvo cols., JSC061010-LS03 (1 worker) [USNM]; 1°23'137"N 58°56'787"W, 314m, T. R. Schultz & J. Sosa-Calvo cols., JSC061010-LS06 (2 workers) [USNM]; 1°23'122"N 58°56'761"W, 273m, T. R. Schultz & J. Sosa-Calvo cols., JSC061010-LS08 (1 gyne) [USNM]. PERU: Cusco: Estación Biológica Villa Carmen, Lat. -12.863717 Long. -71.400528, 590m, 6.viii.2013, Corrie S. Moreau col., CSM 2987 (5 workers, brood) [MZSP, RSPPC]; Loreto: Jenaro Herrera, 04°53'55"S 73°39'00"W, 121m, 13–23.i.2011, Neotropical Ant Course (1 worker) [MZSP]; Madre de Díos: Sachavacayoc Center, 12°49'36.5"S 69°22'14.4"W, 209m, 19–31.vii.2012, R. Feitosa & R. Probst cols. (7 workers, brood) [MZSP]; Sachayacayoc Center (Castanhal), 12°51'21"S 69°21'43"W, 210m, 19–31.vii.2012, R. Feitosa col. (1 worker) [JCPC], Tambopata: 15 km NE Puerto Maldonado, 22.vi.1989, S. P. Cover & J. Tobin cols., LACM 326568 (2 workers) [LACM]. Tambopata Research Center: Lat. -13.14048 Long -69.62108, 318m, viii.2001, D. Feener col., TRC-S05-R1C09/CASENT0637530 (1 gyne) [JTL); Lat. -13.1381 Long. -69.62767, 289m, ix.2001, D. Feener col., TRC-S10-R1C01/CASENT0637518 (1 worker) [JTL). TRINI-DAD & TOBAGO: Arena Forest Reserve: 1.05km SSE de San Rafael, 10°57'N 61°26'W, R. R. Snelling col., LACM 326570 (1 worker) e LACM 326571 (1 worker) [LACM].

Basiceros convexiceps (Mayr 1887)

(Figs 8–10, 30)

Ceratobasis convexiceps Mayr 1887: 581 (worker). Brazil: Santa Catarina.

Borgmeier 1937: 245, Figs 30-33 (worker, gyne, larva diagnosis).

Emery 1924: Plate 6, Fig 9 (male diagnosis, figure corresponds to forewing).

Combination in Basiceros: Emery 1924: 328.

Basiceros squamifer Borgmeier 1937: 245. Brazil: Rio de Janeiro, Jussaral (next to Angra dos Reis).

Basiceros squamifer as junior synonym of Basiceros convexiceps: Brown & Kempf 1960: 172.

Type material. BRAZIL: Santa Catarina: no locality, no date, Hecko (?) col., (one worker—holotype of *Ceratobasis convexiceps*) [NHMW] (examined). Rio de Janeiro: Angra dos Reis, Jussaral, 30.x.1935, M. S. Lopes & H. Lent cols. (60 workers, three gynes and larvae of different instars—cotypes/syntypes of *Basiceros squamifer*), n. 5510—Coleção Borgmeier (41 workers, two gynes—cotypes/syntypes of *Basiceros squamifer*) [MZSP]; same data (three workers—cotypes/syntypes of *Basiceros squamifer*) [IFLM]; same data, MZC-Cotype n. 28512/Cotype n. 5540 (three workers and two gynes—cotypes/syntypes of *Basiceros squamifer*) [MCZ]; USNM-Cotype n. 58766 (two workers—cotypes/syntypes of *Basiceros squamifer*) [USNM], USNM-Cotype n. 5561 (one worker—cotype/syntype of *Basiceros squamifer*) [GUPC] (examined); same data (one worker—cotype/syntype of *Basiceros squamifer*) [MNHN-Muséum National d'Histoire Naturelle] (not examined); same data (one worker—cotype/syntype of *Basiceros squamifer*) [MSNG-Museo Civico di Storia Naturale 'Giacomo Doria'] (not examined); other type material (9 workers) not located and not examined.

Diagnosis. Color reddish, ferruginous. Head trapezoidal; vertexal margin continuously convex in both directions, except for the presence of a median longitudinal groove. Subpetiolar process composed of single projection, anteroventral to the peduncle and curved anteriorly—posterior margin rarely presenting a small dentiform projection.

Description. *Worker* (n=3). HL 1.25–1.28, HL2 1.25–1.30, HW1 1.28–1.31, MdL 0.72–0.78, SL1 0.84–0.89, SL2 0.89–0.94, PDL 0.11–0.13, A3L 0.03–0.05, AFL 0.36–0.38, FuL 0.97–1.00, EL 0.16–0.17, EW 0.14–0.16, ML 1.69–1.72, MfL 1.33–1.34, MtL 1.00–1.06, PH 0.38, PL 0.77–.081, PW 0.36–0.38, PPL 0.47–0.50, PPW 0.53–0.61, GL 1.59–1.63, GW 1.13–1.19, TL 6.58–6.61, CI 100–105, CS 1.27–1.28, MCI 56–62, SI 69–73, ESI 17–19, SAI2 247–252, EI1 0.23–0.26, MFI 95–97, PTI 204–216.

Color reddish, ferruginous; appendages slightly lighter, reddish-brown. Mandibles covered with tiny piligerous

punctuations, apex with short yellowish setae; interdental setae present, yellowish and filiform, subequal to teeth length. Basimandibular seta present, narrow and erect, slightly clavate. Suberect and clavate hair on the dorsomedial region of each stipe. Frontoclypeal margin covered by spaced piligerous punctuations; lateral limits of clypeus with decumbent, short and squamiform yellowish hairs. Head dorsum predominantly covered by coarse (foveate) piligerous punctuations; pilosity close to posterolateral region of head and vertexal margin composed of whitish to yellowish, short and subdecumbent squamiform hairs. Head lateral and vertexal margins covered by clavate yellowish hairs, erect to suberect in the following conformation: one hair above the eyes, at the anterior limit of the antennal scrobe; four hairs on the posterolateral margin, bordering the meeting of upper limit of scrobe and vertexal margin; a hair near the posterolateral corner of the head; four or five hairs on each side of the vertexal margin, separated by the median sulcus. A pair of yellowish hairs erect and clavate on the frontal region, close to the vertexal margin. Sides of head ventral margin covered by whitish and squamiform subdecumbent hairs; ventral head surface with suberect and subdecumbent curved filiform setae, length variable. Four to six long fine setae bordering the occipital carina. Yellowish to whitish subplumose hairs, usually subdecumbent, on the meso- and metasoma, in the following conformation: surrounding the anterolateral margin of pronotum; on the dorsum of mesonotum and propodeum; on the side of the sloping margin of propodeum; densely on the dorsum of petiolar and postpetiolar nodes; three pairs on each side of the anterolateral region of the postpetiolar sternite; on the anterolateral region of the procoxae and dorsum of meso- and metacoxae; on legs, from trochanters to basitarsus dorsum. Clavate hairs in the following conformation: one pair, erect, present on the dorsum of mesonotum, close to the promesonotal suture; erect to suberect, close to the margins of the sternites and gastral tergites. Mesosternum shelf (surrounded by epicnemial carina) with short, filiform setae along its length. Long, filiform setae present in the anterior portion of procoxa and median portion of the first gastral sternite. Thick and suberect setae present from the ventral margin of basitarsus to the apex of the apical tarsomere. Antennae pilosity: dorsal surface of scape primarily covered by short subdecumbent and squamiform hairs; external margin of scape with long and erect hairs, clavate on apical half; funiculus densely covered with short appressed yellowish setae; ventral margin of scape with longitudinal rows of medium setae, curved and subdecumbent. Remaining of integument with coarse piligerous punctuations.

Body mostly smooth and shiny on glabrous regions. Mandibles and clypeus dorsa sparsely covered by punctuations. Anteroventral portion of mandibles and ventral margin of scapes finely alveolate. Head punctuate-foveate, posterolateral surface of antennal scrobe punctuate-rugose. Pronotum sparsely foveate. Dorsum of mesonotum, anterodorsal region of the propodeum, dorsal surface of the meso- and metacoxae, and dorsum of the petiolar postpetiole nodes punctuate-rugose. Mesopleuron and lateral of the propodeum smooth and shiny or subopaque. Surface of propodeal declivity punctuate-rugose. Gaster densely punctuate-reticulate; tergite surface of abdominal segments V, VI, and VII finely and densely punctuate, slightly opaque, tergal margins smooth and shiny; more sparse sculpture in the first gastral sternite, especially in the longitudinal axis of median region. Antennal scapes smooth or finely rugulose, usually shiny. Funiculi densely and finely punctuate, usually opaque. Legs smooth or superficially rugose; procoxae punctuate-foveate.

Head trapezoidal, narrower anteriorly. Vertexal margin continuously convex in both directions, except for the presence of a shallow longitudinal sulcus that extends downwards into the posterofrontal region of the head; posterolateral angles rounded. Cervical margin carinate. Stipes subrectangular. Labrum cuneiform, long; distal margin bilobed, lobes tapered and separated by narrow cleft. Mandibles triangular; in full-face view, lateral margins of mandibles slightly concave in its apical half; basal angle usually indented, followed by 12–13 triangular teeth on the masticatory margin; in lateral view, mandibular apex slightly curved ventrally. Clypeomandibular space semielliptical. Clypeus anteriorly lamellated; anterolateral portion gently convex; anterior margin subrectilinear. Scape with obtuse basal angle ranging from slightly convex to slightly concave before the beginning of a translucent and crenulate lamellar portion. Antennal fossa deeply impressed. Antennal scrobe comparatively deep in its anterior half.

In lateral view, mesosoma profile with promesonotal complex subglobular. In dorsal view, promesonotal suture practically indistinct; metanotal suture broad and deeply inserted, longitudinally costulate. Mesopleuron anteriorly marginate, interrupted at the meeting with a conspicuous epicnemial fossa. In dorsal view, propodeum subrectangular. In lateral view, anterior portion of propodeum slightly oblique posteriorly, abruptly followed by the sloping face. Propodeal declivity laterally carinate and with transverse carina connecting to short, sharp and triangular propodeal projections. Opening of the propodeal spiracle rounded. Metapleural gland bulla protruding, prominent; opening transversal and covered by cuticular lamella. Petiolar peduncle longitudinally carinate on its dorsal surface. In dorsal view, propodeal spiracle weakly projected laterally. In lateral view, petiolar node with truncated anterior face,

sloping posterodorsally; postpetiole slightly longer than the petiolar node. Subpetiolar process consisting of an anterior process curved anteriorly. In dorsal view, petiolar node longitudinally elliptical; postpetiole (excluding pilosity) slightly wider than long, posterior margin convex and widely inserted into the anterior concavity of gaster. Calcar of strigil pectinate. Pro-, meso- and metabasitarsi longer than the sum of other tarsomeres. Tarsal claws simple.

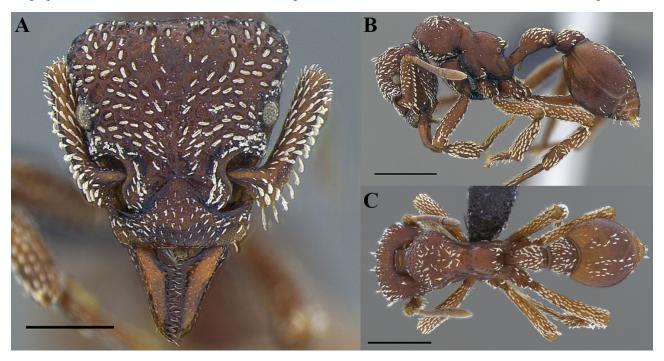


FIGURE 8. *Basiceros convexiceps*, worker (MZSP, Brazil: São Paulo); A. full-face view, B. lateral view; C. dorsal view. Scale bars: A = 0.5 mm, B–C = 1 mm.

Gyne (n=2). HL 1.34–1.36, HL2 1.31–1.34, HW1 1.34–1.41, MdL 0.80–0.81, SL1 0.94–1.00, SL2 0.91–0.97, PDL 0.13, A3L 0.03–0.05, AFL 0.39, FuL 1.00–1.08, EL 0.25–0.30, EW 0.22–0.25, LOD 0.09, MOD 0.09–0.13, OOD 0.41–0.44, ML 2.03, MSL 1.00–1.06, MSW 1.03, MLL 0.34–0.36, MLW 0.56–0.59, MfL 1.34–1.38, MtL 1.08–1.09, PH 0.44, PL 0.97, PW 0.47, PPL 0.56, PPW 0.72, GL 1.94, GW 1.41–1.44, TL 7.64–7.67, CI 100–103, CS 1.34–1.38, MCI 59–59, SI 67–68, ESI 25–32, SAI2 232–248, EI1 0.34–0.41, MTI 97–103, MLI 163–165, MFI 97–104, PTI 221.

Color and sculpture similar to worker; body size ranging from equal to slightly larger. Cephalic dorsum with three ocelli: median ocelli inserted slightly below and lateral ocelli inserted just above a pair of clavated and erect hairs. Head pilosity as in workers. Pilosity of the anterolateral pronotal margin denser and longer than in workers. Whitish subdecumbent and squamiform hairs near the humeral angles and surrounding the posterior limit of pronotum; short and sparse on the dorsum of mesoscutum; on the scutoscutellar sulcus; on the dorsum of mesoscutellum; a pair on the metanotal flange, suberect. Whitish erect to suberect and clavate hairs on each side of pronotum, one pair close to pronotal suture; a pair on the metanotal flange; narrower and present as eight pairs on mesoscutum dorsum; one pair on each parapsis; one on each axilla, laterally; one on the lateral margin of mesoscutellum. Hairs on the gaster more abundant than on workers. In dorsal view, mesoscutum anteriorly rounded, slightly cuneiform, posterior margin slightly convex, medially in the meeting with the scutoscutellar suture; notauli indistinct; parapsidal lines narrow and inconspicuous, involved by the sculpture; parapsis shallow, rudimentary; tegulae narrow, apical margin rounded. Pre-scutellum narrow; axillae projected posteriorly, rounded and slightly depressed. Scutoscutellar suture well-defined. Mesoscutellum transversely subrectangular, posterior limit concave. Dorsal face of propodeum strongly inclined. In lateral view, anapleural sulcus broader anteriorly at the connection with the epicnemial fossa, narrowing posteriorly. Median region of first gastral sternite slightly projected on its basal half. Wing venation unknown (only dealate gynes were examined).

Male. Only known from diagnosis (Emery 1924), translated below: "Epistoma (= clypeus) projected anteriorly. Frontal margin (= frontal carina) short, auricular. Mandibles long, advancing beyond the clypeus and disc-shaped, lateral margin (= external margin) rounded and medial margin (= masticatory margin) straight, armed with numerous sharp, serrated teeth. Antennae long, 1st funicular segment very short. (In the forewing) Portion of the wing anterior

to the pterostigma large and well developed, radial (=1st marginal) cell open; cubital cell *Solenopsis*-type; inconstant discal cell". According to Emery's description, the forewing fits in part the type 1 adopted for the present work.

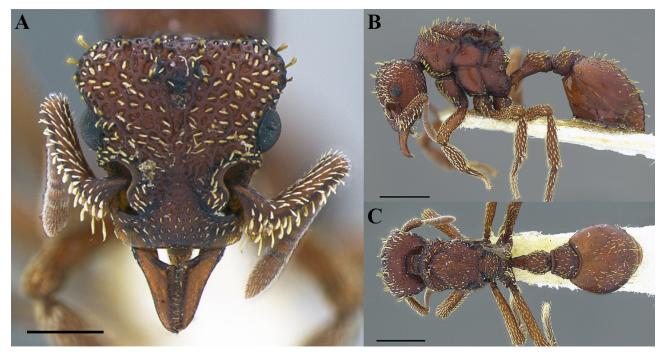


FIGURE 9. *Basiceros convexiceps*, gyne (MZSP, Brazil: São Paulo). A. full-face view, B. lateral view; C. dorsal view. Scale bars: A = 0.5 mm, B–C = 1 mm.

Larva (first description, based on several specimens from the type-series of *B. squamifer*). Approximate length through spiracles: 4.4 mm (Borgmeier 1937, 246: "larger larvae measure about 4 mm"); profile pogonomyrmecoid: larger diameter near the middle of the abdominal region, thorax markedly narrower than the abdominal region, forming a neck; curved ventrally. Anus ventral; anal opening moderately convex, anal lobe present. Spiracles small. Integument of the ventral region densely covered by spinules arranged in transverse rows. Due to the state of the larvae, pilosity was lost in most of the body surface. Still, it was possible to notice sparse broken setae on the head, alveolar and with articular membrane, and on the ventral margin of the thorax (about 0.10–0.20 mm), flexible and denticulate (Borgmeier 1937, 246: "{the larvae} have a fine erect pilosity and in each segment there is a transverse row of isolated, longer and anteriorly curved hairs"). Cranium subhexagonal, median impression present, antennae very small and inserted in the anterior half of the cephalic capsule. Clypeus protruding. Labrum strongly bilobed; ventral surface spinulose. Mandibles pogonomyrmecoid, long and narrow, medially curved; apical tooth curved and with a rounded apex; two protruding teeth projecting into the masticatory margin. Maxillae parabolic, apex spinulose; maxillary palps and galeae digitiform, subequal, elongated and narrow. Labium covered by subtransverse rows of spinules; spinules developed, capillary (about 0.02 mm) and densely covering the labium surface; labial palp papillary; opening of sericeous gland transverse. Hypopharynx densely spinulose.

Etymology. From Latin "convexus", arched, curved; "ceps", combinative form of "caput", head. Mayr probably named this species based on the shape of the vertexal and occipital margins, which, except for a shallow groove in the median region of the vertexal margin, are continuously and uniformly convex in both directions. Also from Latin "squama", scale; "fer", radical of "ferre", infinitive present of the irregular verb "ferô", to carry, to bring. Borgmeier probably named the junior synonym B. squamifer based on the squamiform pilosity. It is interesting to mention that the term "squama"—possibly originated from the Latin "squalidus" (rough, coated with dirt, dirty), could also be associated with the epithet of this species.

Comments. Brown & Kempf (1960) refer to this species as having the most generalized morphology within the then Basicerotini tribe, arguing that the group's adaptive radiation probably came from an ancestral stock similar to *B. convexiceps*.

Based on all the specimens available for examination for the present study, the morphological uniformity presented by this taxon is remarkable. Considering the current geographical distribution of *B. convexiceps*, there is practically no variation between specimens from different locations, except for minor differences in cephalic rugos-

ity and pilosity—the latter probably associated with abrasion. In his description of *B. squamifer*, Borgmeier (1937, p. 245) distinguishes it from *B. convexiceps* mainly by the different postpetiolar proportions. According to Mayr (1887: 581) "der zweite Knoten ist kürzer als hinten breit, aber so lang als vorne breit" (the second node [=postpetiole] is shorter than wide posteriorly, but as long as wide anteriorly) and Borgmeier cites it as distinctly longer than wide for *B. squamifer*. Brown & Kempf (1960), when examining the type-series of both species, claimed that Mayr's original description failed to approximate the correct proportions of the postpetiole and synonymized *B. squamifer* under *B. convexiceps*.

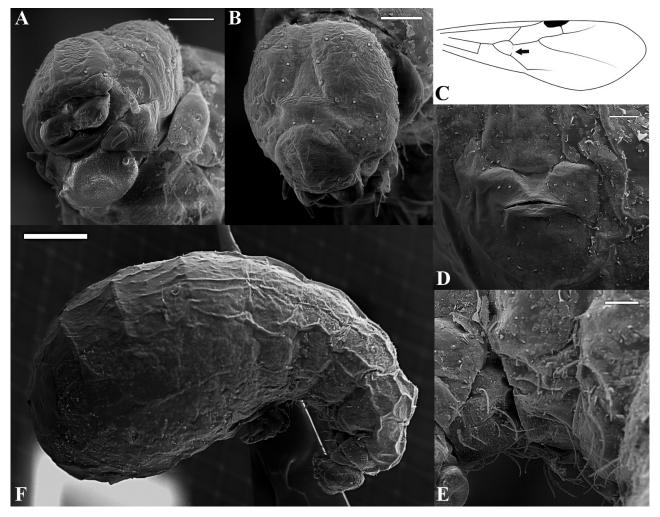


FIGURE 10. *Basiceros convexiceps*, larva (from type-series of *Basiceros squamifer*) (MZSP, Brazil: Rio de Janeiro) and male forewing diagram (adapted from Emery, 1924) (Brazil: Santa Catarina); A. Head in ventro-oblique view, B. head in oblique view, C. male forewing (black arrow highlights transversal 1m-cu vein), D. anus, E. thorax in lateroventral view, highlighting the spinose pilosity, F. lateral view. Scale bars: A, B–E = 0.1 mm; F = 0.5 mm.

The male described by Emery (1924) could not be located. Several attempts to examine that specimen were made, initially by contacting the NHMW, since the type-material of *B. convexiceps* collected by Dr. Gustav Mayr is supposedly deposited in that Institution. Additionally, the online database of the MHNG—where Emery's collection is located—does not inform that male specimen to be deposited there and our correspondence with the MHNG curator has yet to be returned. Other communications made with different European Museums also resulted in none locating that specimen.

The description of the larvae is based on several specimens found with the type-series material of *B. squamifer*. The original vial was located in the wet (alcohol) collection of the Hymenoptera Laboratory at the MZSP, along with Borgmeier's original labels with the same collection codes—including a label citing the microenvironment in which the specimens were collected. Although sample conservation was not ideal, one of the immatures was cleaned and submitted to the SEM. In addition, the vial contained fourteen workers; this material has been sorted, pin mounted, and incorporated into the MZSP collection.

Borgmeier (1937: 246) mentions that the description of *B. squamifer* was based on 60 workers and three wingless gynes, all collected in the same nest. However, relying on the material from the original collection, 49 workers deposited in different institutions were examined. One worker deposited at the MNHN and another one deposited at the Museo Civico di Storia Naturale "Giacomo Doria" (MSNG) were not examined, and it was not possible to locate the other nine workers mentioned by Borgmeier (1937). Considering the material available, the worker in the best state of conservation will be designated as the lectotype, aiming for the nomenclatural stability of the group.

In the present study, the worker deposited at the NHMW and examined by stacked macrophotographs is considered the holotype described by Dr. Mayr, although AntWeb treats the same specimen as a syntype of *B. convexiceps*. However, Mayr mentioned in his original description (1887) the monotypic status of *B. convexiceps*, which reinforces that specimen as being the holotype.

Two workers collected in Blumenau and deposited at the NHMB lack any mention of collection date, with labels only referring to the collector (spelling refers to "Müller"). This material was not mentioned in any publication referring to *Basiceros*, possibly due to difficulty obtaining material from the NHMB. Considering the age and calligraphy of the labels and comparing them with other ants collected in Santa Catarina, both by William Müller and Dr. Arth. Müller, these two workers were probably collected by the latter. It is interesting to mention that there is a second label (in German) on those specimens. The label data suggest that specimens were deposited in Dr. Félix Santschi's collection during the time Dr. Santschi was established in Tunisia—more precisely in the city of Kairouan.

Mariano & Delabie (2013) studied the karyotype of two populations of B. convexiceps (one in Bahia and one in Minas Gerais) and registered for both 2n = 20, with meta and submetacentric chromosomes.

Distribution. This species is restricted to areas of the Brazilian Atlantic Forest biome, with records from the State of Santa Catarina to Bahia. Interestingly, it has not yet been collected in the State of Espírito Santo.

Natural history. Virtually nothing is known about the natural history of this species, and few are the collection events in which this species was found. For example, considering the entire length covered by the BIOTA Project, spanning the whole distribution of the Atlantic Forest and hundreds of 1m² leaf litter samples, only four specimens were collected: one in the State of Santa Catarina, one in Paraná, and two in São Paulo. According to field notes from Borgmeier, the nest series from Jussaral (60 workers and three gynes) was collected from a wide, rotted trunk, under the bark and inside it. The presence of three wingless gynes suggests that the colony was polygynic (Borgmeier, 1937). Some specimens were collected from litter samples, indicating that *B. convexiceps* also nests or forages in the leaf litter.

Material examined. BRAZIL: Bahia: Itororó, 14°57'81"S 40°02'33"W, 08.viii.2000, J. R. M. dos Santos col. (1 worker) [CEPEC]; Minas Gerais: Viçosa, Mata do Paraíso, 20°45'S 42°52'W, 13.xi.2000, I. C. Nascimento col. (2 workers) [CEPEC], 20°48'S 42°51'W, 12.ii.2015, J. Chaul, A. P. Alves cols. (1 worker) [MZSP]; Paraná: Morretes, Parque Estadual do Pau-Ôco, 25°34'33.5 "S 43°53'19.5" W, 06–11.v.2002, Silva, R. R. & Dietz, B. H. cols. col., (1 worker) [MZSP]; Santa Catarina: Blumenau, undated, Müller (?) Col. (2 workers) [NHMB]; São Bento do Sul, APA Rio Vermelho, 26°21'51"S 49°16'16"W, 30.iii–04.iv.2001, Silva, RR & Eberhardt, F. cols., (1 worker) [MZSP]; without locality, without date, Carlo Emery col., (1 worker), donation by W. M. Wheeler [MCZ]; São Paulo: Ilha dos Búzios, 19.x.1963, Expedition of the Department of Zoology col., N. 2804 (1 gyne), n. 2835 (1 worker) [MZSP]; Picinguaba, Parque Estadual da Serra do Mar, 23°20'10"S 44°50'15.3" W, 30.ii–04.iv.2001, C. R. F. Brandão & Equip. cols. (2 workers) [MZSP]; no date, no locality (1 gyne) [USNM].

Basiceros disciger (Mayr 1887)

(Figs 11–12, 31)

Ceratobasis disciger Mayr 1887: 581 (worker) Brazil.

Brown & Kempf 1960: 180 (gyne). Brown 1974: 140 (male diagnosis).

Combination in Basiceros: Emery 1924: 328.

Combination in Aspididris: A. discigera Brown & Kempf 1960: 179.

Combination in Basiceros: Brown 1974: 140.

Type material. BRAZIL: Santa Catarina: no locality, no date, Hecko (?) col., (one worker—holotype of *Ceratobasis disciger*) [NHMW] (examined); no locality, no date, Goeldi col. (one worker—paratype [?]) [AMNH] (examined).

Diagnosis. Head in frontal view with vertexal margin crested, medially emarginate and confluent at this point with the central convexity of head dorsum.

Description. *Worker* (n=5). HL 1.13–1.39, HL2 1.14–1.41, HW1 1.03–1.27, MdL 0.56–0.64, SL1 0.66–0.75, SL2 0.73–0.84, PDL 0.09–0.11, A3L 0.03, AFL 0.33–0.36, FuL 0.78–0.89, EL 0.09–0.16, EW 0.09–0.13, ML 1.34–1.55, MfL 0.91–1.11, MtL 0.75–0.88, PH 0.28–0.31, PL 0.53–0.69, PW 0.25–0.31, PPL 0.38–0.48, PPW 0.50–0.53, GL 1.34–1.63, GW 1.00–1.09, TL 5.20–6.34, CI 91–94, CS 1.08–1.31, MCI 47–50, SI 66–72, ESI 12–18, SAI2 223–236, EII 0.17–0.21, MFI 112–114, PTI 180–188.

Size small to medium, comparatively. Color yellowish-brown to dark brown; appendages lighter, yellowish to dark brown. Mandibles generally lighter than the predominant body coloration; covered by sparse and minute piligerous punctures, apex with short yellowish setae; interdental setae present, yellowish and filiform, subequal to teeth length. Basimandibular setae present, fine and erect. Suberect and clavate hair on the dorsomedial region of each stipe. Frontoclypeal margin covered with spaced piligerous punctuations. Pilosity on head dorsum restricted to a pair of clavate hairs on the posteromedian region, close to the median emargination of vertexal crest.

Head lateral and vertexal margins covered by yellowish clavate or subclavate hairs, erect to suberect in the following configuration: seven clavate hairs on the side of head, starting from the region above the eyes and bordering the anterior limit of scrobe and the posterior limit of vertexal crest; four hairs on each side of the dorsal (anterior) edge of vertexal crest; three hairs on each side (before median emargination) on vertexal margin. Ventral head surface densely covered by suberect and clavate hairs. Mesosoma and metasoma with subdecumbent pilosity surrounding the anterolateral margin of pronotum; on dorsum of mesonotum and propodeum; on lateral of propodeal declivitous margin; densely on the dorsum of petiolar and postpetiole nodes; one to two pairs on each side of the anterolateral region of postpetiolar sternite; on the laterodorsal regions of gaster; on the anterolateral region of procoxae and on the dorsum of meso- and metacoxae; on the legs, from trochanters to basitarsus dorsa. Erect and clavate hairs in the following configuration: two pairs on each margin of humeral angle, two pairs on the dorsum of mesonotum; two pairs on the dorsum of petiolar node: one pair at the anterior limit and one pair at the posterior limit; two to three pairs on the dorsum of postpetiole; one pair close to the median region and another pair at the posterior limit; five to eight pairs on each side of the first gastral tergite; row of six hairs in the visible portion of the second, third and fourth gastral tergites; similar configuration of gastral dorsum also on the ventral region of this somite. Mesosternum shelf (surrounded by epicnemial carina) with short, filiform setae along its length. Long and filiform setae present in the anterior portion of the procoxa and on the median portion of the first gastral sternite. Thick and suberect setae present from the ventral margin of basitarsus to apical tarsomere. Antenna pilosity: dorsal surface of scape primarily covered by short, subdecumbent, subclavate hairs; external margin of scape with long erect hairs; funiculus densely covered with short yellowish setae; ventral margin of scape with longitudinal rows of curved and subdecumbent medium setae.

Body mostly smooth and shiny on glabrous regions. Head punctuate-rugose; irregular rugae present on the posterior portion of the frontal tumosity; surface of antennal scrobe predominantly punctuate-foveate, posterolateral portion punctuate-rugose; ventral margin rugose. Pronotum laterally foveate; anterior margin with irregular transverse rugae. Dorsum of mesonotum, anterodorsal region of propodeum, dorsal surface of meso- and metacoxae and dorsum of petiolar and postpetiolar nodes punctuate-rugose. Anterior portion of mesopleuron punctuate-rugose. Side of propodeum with oblique and irregular rugae. Surface of propodeal slope sparsely punctuate-rugose. Gaster densely punctuate-reticulate; tergite of abdominal segments V, VI, and VII finely and densely punctuate, slightly opaque, tergal margins smooth and shiny; sculpture of first gastral sternite limited to the lateral limits and posterior portion of this sclerite; remaining surface smooth, from subopaque to shiny. Antennal scapes smooth or finely rugose, usually shiny. Funiculi densely and finely punctuate, usually opaque. Legs smooth or rugose; procoxae punctuate-foveate.

Head disc-shaped, laterally convex; sides of head bordered by a raised margin that extends from the eye height to posterolateral region and behind the head, forming a crest. Face with central tumosity from the frontoclypeal portion to vertex margin, resembling the shape of a bowling pin (narrower in its central portion). Frontal sulcus present along the tumosity. Vertexal margin with convex corners, slightly projected backward; vertexal crest conspicuous and moderately emarginated. Cervical margin carinate. Palp formula 2,2; palps strongly fused, giving the impression of being unsegmented. Stipes subrectangular. Labrum cuneiform; distal margin bilobed, lobes tapered and sep-

arated by narrow cleft. Mandibular triangular; in full-face view, lateral margins of mandibles slightly concave; basal margin lamellar close to basal angle, which is obtuse; masticatory margin with 11–13 triangular teeth, apical tooth slightly curved; in lateral view mandibular apex slightly curved ventrally. Clypeus anteriorly lamellate; anterolateral portion gently convex; anterior margin slightly concave in its median portion. Scape with slightly obtuse basal angle and concave margin before the beginning of a translucent and crenulate lamellar portion. Deep antennal fossa.

Lateral profile mesosoma with a bulging promesonotal complex, obliquely inclined on its posterior portion, propodeum oblique, anterior margin raised and abruptly followed by the sloping face. In dorsal view, promesonotal suture practically indistinct; metanotal suture broad and strongly impressed, longitudinally costulate. Mesopleuron anteriorly emarginate, interrupted at the meeting with a conspicuous epicnemial fossa. In dorsal view, propodeum dorsum anteriorly narrow, slightly triangular. Propodeal slope laterally carinate and with transverse carina connecting to short, triangular, and slightly upward curved propodeal projections. Opening of the propodeal spiracle rounded. Metapleural gland bulla protruding, prominent; opening transversal and covered by cuticular lamella. Petiolar peduncle longitudinally carinate on the dorsal surface. In lateral view, petiole claviform; petiolar node with anterior surface slightly concave, dorsal margin dome-shaped to convex; postpetiole convex. Subpetiolar process highly variable: from absent to composed of bifid anterior process followed by spines and/or angular lamellar processes. In dorsal view, petiolar node longitudinally trapezoid, anterior margin narrower and rounded, posterior margin straight; postpetiole slightly wider than long; anterior margin emarginate; posterior margin convex and widely inserted to the anterior concavity of gaster. Gaster anteriorly emarginate; median gastral sulcus present, practically obsolete and extending over the entire dorsum of the first tergite, slightly narrower posteriorly. Calcar of strigil pectinate. Tarsal claws simple.

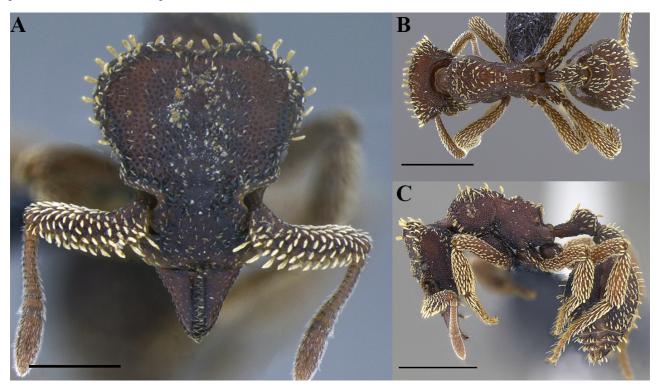


FIGURE 11. *Basiceros disciger*, worker (MZSP, Brazil: São Paulo); A. full-face view, B. lateral view. C. dorsal view. Scale bars: A = 0.5 mm, B–C = 1 mm.

Gyne (n=4). HL 1.25–1.44, HL2 1.28–1.47, HW1 1.25–1.41, MdL 0.59–0.69, SL1 0.75–0.78, SL2 0.81–0.91, PDL 0.11, A3L 0.03, AFL 0.34–0.41, FuL 0.88–1.03, EL 0.19–0.22, EW 0.19, LOD 0.06–0.08, MOD 0.06–0.09, OOD 0.44–0.55, ML 1.59–1.89, MSL 0.75–0.91, MSW 0.78–0.94, MLL 0.28–0.38, MLW 0.42–0.50, MfL 1.06–1.19, MtL 0.84–0.95, PH 0.38–0.41, PL 0.72–0.81, PW 0.31–0.38, PPL 0.47–0.53, PPW 0.56–0.61, GL 1.72–1.97, GW 1.25–1.38, TL 6.38–7.33, CI 97–100, CS 1.25–1.42, MCI 47–53, SI 64–67, ESI 22–25, SAI2 223–236, EI1 0.27–0.33, MTI 103–104, MLI 133–155, MFI 115–118, PTI 191–200.

Color similar to workers; sizer slightly larger; mesosomal sculpture more developed. Pronotum with irregular foveae close to anterior margin of mesoscutum; dorsum of mesoscutum with coarse and irregular longitudinal rugae,

forming fovea of different sizes. In lateral view, pronotum, mesoanepisternum and mesokatepisternum with coarse and/or foveal punctuations, both sparse; surface of metanepisternum and metakatepisternum slightly granulate, subopaque; dorsum of the propodeum declivitous face covered by transversal rugae. Cephalic dorsum with three ocelli: median ocelli inserted slightly below and lateral ocelli inserted just above the pair of clavate and erect hairs. Head pilosity as in workers. Pilosity of anterolateral margin of pronotum denser and longer than in workers. Clavate and erect hairs on mesosoma in the following conformation: three pairs close to humeral angles and surrounding the posterior limit of pronotum; about eight pairs on the dorsum of mesoscutum; three hairs on the lateral margin, just above wing insertions; one pair on each parapsis; one pair on the lateral region of axillae; two pairs on the dorsum of mesoscutellum; a pair on the metanotal flange, suberect. Pilosity of petiole same as for workers; hairs on postpetiolar dorsum more abundant; postpetiolar sternite with four pairs of curved and subdecumbent clavate hairs. Hairs on gaster more abundant than on workers. In dorsal view, mesoscutum anteriorly rounded, slightly cuneiform and with smooth and shiny median carina; posterior margin slightly convex medially at the meeting with scutoscutellar suture; notauli indistinct; parapsidal lines narrow and inconspicuous, involved by the sculpture, slightly curved; parapsis shallow; tegulae subrectangular, apically rounded. Pre-scutellum narrow; axillae projected posteriorly, rounded and slightly depressed. Scutoscutellar suture well-marked, sulcus broad and semicircular, relatively shallow. Mesoscutellum transversely subrectangular, anterior limit concave. Dorsal face of propodeum strongly inclined; in lateral view, declivitous margin emarginate; propodeal projections obtuse and angled. In lateral view, anapleural sulcus broader anteriorly at the connection with the epicnemial fossa, narrowing posteriorly. First gastral sternite with median region slightly projected on basal half. Wing venation unknown (only dealate gynes were examined).



FIGURE 12. *Basiceros disciger*, gyne and male (MZSP, Brazil: São Paulo); A and D. full-face view, B and E. dorsal view, C and F. lateral view. Scale bars: A, D = 0.5 mm, B, C, E, F = 1 mm.

Male (first description) (n=3). HL 0.81–0.90, HW1 0.75–0.84, HW2 0.88–0.95, MdL 0.37–0.39, SL2 0.19–0.22, PDL 0.11–0.13, A3L 0.33–0.38, AFL 0.59–0.63, EL 0.28–0.31, EW 0.25–0.27, LOD 0.08–0.09, MOD 0.08–0.09, OOD 0.34–0.37, ML 1.45–1.58, MSL 0.72–0.81, MSW 0.72–0.75, MLL 0.250–0.28, MLW 0.41–0.44, MfL 1.16–1.19, MtL 0.86–0.92, PH 0.23–0.28, PL 0.63–0.69, PW 0.25–0.28, PPL 0.31–0.37, PPW 0.40–0.47, GL 1.40–1.65, GW 0.90–0.98, TL 4.98–5.59, CI 892–931, CS 0.78–0.88, MCI 43–46, SI 25–26, ESI 142–150, SAI 57–58, SAI2 31–35, EI1 0.66–0.71, EI2 85–88, MTI 92–100, MLI 155–162, MFI 64–71, PTI 244–266. (In bold, measurement from a male with dilated gaster).

Size slightly smaller than conspecific gyne. Color dark brown to black; shiny portion of mesoanepisternum dark brown; yellowish to brown appendages, coxae brown. Distal portion of mandibles amber. Wings dark brown. Mandibles with long fine semierect to subdecumbent yellow hairs on dorsum and apex, slightly longer on the latter. Head with two main types of hair: medium, yellow and fine, subdecumbent; primarily on the frontal disc of clypeus; and long and whitish to yellowish, sometimes with a curved apex along the genal carina, on the vertexal margin and ventral surface. The second hair type is widely present throughout the body: on the dorsum of the mesosoma, waist and gaster, ocellar region, procoxae and petiolar dorsum. Antennomeres with short yellowish appressed setae. Legs with medium yellowish decumbent to decumbent setae. White and short hairs from subdecumbent to decumbent on anterior half of the mesokatepisternum and on procoxae dorsa.

Body uniformly punctuate-reticulate, minor changes on diameter and degree of sculpture impression. Apical portion of mandibles smooth and shiny. Irregular longitudinal rugae sometimes present above compound eyes, reaching posterolateral corner of postgenal carina, on neck, and weakly on vertexal margin close to the occipital carina. Mesoscutellum dorsum, metakatepisternum, and propodeum strongly rugose. Mesoanepisternum slightly darker, smooth and very shiny in just over half or 2/3 of its length; mesokatepisternum fully punctuate-reticulate. Oblique rugae present or not on the lateral region of propodeum, near the edge of declivitous face. Dorsolateral rugae present on the anterior portion of the petiolar node.

Head subpiriform; in full-face view, median triangular crest on its top, just above the ocelli; occipital carina wide and lamellar, medially concave. Palp formula 1,1; palps slightly compressed on its apical half; maxillary palp slightly larger in size and slightly wider than labial. Stipes subrectangular. Mandibles triangular, apically curved; masticatory margin with 11 triangular teeth of similar size. Clypeus with central disc convex, slightly elevated; anterior margin lamellar, ranging from distinct to slightly inconspicuous; slightly concave. Postgenal carina present and well-marked, extending to the vertexal margin. Narrow and linear carina, smooth, just after the supraclypeal region and extending posteriorly into the head until just above the antennal fossae. Antennal arch expanded as a swollen posterolateral lobe, completely hiding the antennal bulb in full-face view. Pedicel longer than wide, third antennomere about twice as long as pedicel. Compound eyes large and globular, protruding from the cephalic capsule. Ocelli projected, caramel-colored; transversal rugae present or not between the lateral ocelli.

In dorsal view, mesoscutum cuneiform, elongated anteriorly. Smooth and shiny carina present on the anteromedial region of mesoscutum, variably extending as a line near the dorsal margin. Notauli V-shaped, broad and extending close to posterior limit of parapsides—from there, converging as a single, indistinct line until the transscutal suture. Parapsidal lines smooth and shiny; slightly depressed, curved on anterior portion, subparallel and slightly sinuous on its median portion; apex wider. Parapsides narrow, slightly elliptical. Transscutal suture slightly angled medially, median portion from distinct to relatively indistinct. Axillae protruding, strongly curved posteriorly; hookshaped and with rounded apexes. Anapleural sulcus broad and scrobiculate, strongly impressed—mesoanepisternum raised above mesokatepisternum. Scutoscutellar sulcus smooth and deep, with transversal carinae. Mesoscutellum subrectangular; depressed on posteromedian region; posterior margin strongly concave and depressed. Posterior margin of metanotum lamellar. Propodeal projections short, laminar, and obtuse; slightly projected upwards or not. Propodeal lobes auricular. Calcar of strigil short and pectinate. Tarsal claws simple; arolia present, short and narrow. In lateral view petiole claviform; dorsal face from bulging to strongly convex; ventral margin without subpetiolar process. Postpetiole approximately half the length of petiole in lateral view. In dorsal view, petiolar node longitudinally elliptical; petiolar spiracle projected. Forewing type 2; hindwing with 4–5 submedian hamuli.

Larva. unknown.

Etymology. from the Greek, "disci", variant of "diskos": disco; "Gerous" = "ger", a derivative of the Latin "gerere" which means to possess, to carry + "ous", a Latin suffix that forms adjectives that in general mean "to possess, full of" certain quality. Dr. Gustav Mayr must have named this species based on the shape of the vertexal margin, whose rounded corners form a distinct cephalic disc.

Comments. Brown & Kempf (1960: 179) mention the transitional form of *Aspididris discigera* within the genus *Basiceros* when comparing the head shape between *B. convexiceps* and *Aspididris militaris*. The authors conclude that "while the generic split seems almost academic, the distinction can still be drawn rather clearly on a practical basis, and there seems to be no good reason to synonymize *Aspididris* (under *Basiceros*) unless further intergradient species are found" (what eventually happened after Brown's 1974 description of *B. conjugans*).

Among all *Basiceros* species, *B. disciger* presents the greatest morphological variation, associated with its wide geographic distribution (see below). Features in adult workers and gynes, such as size, sculpture (especially head,

mesopleuron, and gaster), body coloration, impression of the metanotal suture, shape of petiolar node, and the amplitude of the median convergence of the vertexal crest appear in different combinations and gradations, making it difficult to distinguish a specific obvious pattern on the geographic scale covered by this species. Regardless, head shape (with a median emarginated vertexal crest), promesonotum profile, and specialized pilosity (when not lost to abrasion) are considerably uniform characters in all specimens examined. After examining a significant number of specimens from different geographic regions, a more comprehensive concept regarding species boundaries for *B. disciger* is adopted for the present study. Nevertheless, it cannot be disregarded for this taxon to be an assemblage of cryptic species, situation that a phylogeography study could potentially address.

The examination of AntWeb photographs of specimens collected in Misiones, northeastern Argentina (CASENT0006143) and Itapuá, southern Paraguay (CASENT0173734) revealed that they are intercastes. In fullface view, the Argentinian specimen shows a frontal sulcus (generally narrow and restricted to the frontal region of the head) wide and surrounded by piligerous punctuations, extending to the widest point of the head, a little above the median ocellus. The lateral ocelli are located just above the posterior limit of this sulcus. In the Paraguayan specimen, although the frontal sulcus is not as conspicuous, it is present surrounded by piligerous punctuations. The median ocellus is partially hidden under the integument, and the lateral ocelli are present as integumentary impressions bearing a clavate hair. Although the frontal sulcus is present in the true gynes of B. disciger, the ocelli are inserted close to the median convergence of the vertex crest, contrary to what was observed in these two intercastes. In addition to the presence of this sulcus and the ocelli, the mesosoma has clavate hairs surrounding what would be the mesoscutal impression; in dorsal view, it is possible to distinguish the impression of the scutellar sulcus and a wider and more marked metanotal suture than in workers. Since it is only possible to establish the presence of ovaries by dissecting the specimen before fixing it, there is no way to attribute a reproductive role to these two specimens. However, these specimens are not considered the result of teratology, as other B. disciger specimens either had similar characteristics of these intercastes, contrasting to specimens that showed defective formations of appendages, especially the head—probable failures during their development.

Of all specimens examined during the dissertation project, about 45% were of *B. disciger*. Many projects developed under the guidance of the senior author of the present study were developed in points located across the Atlantic Forest biome, especially in the Serra do Mar mountain chain. For this reason, the MZSP has impressive material from the Southeast region of Brazil. For example, for the present study, several specimens from the Picinguaba region within the Serra do Mar State Park were examined, from distinct sites.

Distribution. Basiceros disciger displays the widest geographic distribution in Basiceros. For the present study, new records are presented for Argentina (first record), Bolivia (first records), Colombia, Ecuador (first records), Paraguay (new records), Peru, and Venezuela. For the Brazilian territory, specimens were collected across a large extension of the Atlantic Forest, from the States of Rio Grande do Sul to Alagoas. When considering the records for Western Amazon, Atlantic Forest, State of Mato Grosso, Bolivia, and Paraguay, the "V-shaped" distribution of B. disciger can probably be explained by old connections (mid to late Miocene) between modern Cerrado and southern Mato Grosso to the Chaco and savannas of Bolivia and Paraguay; those connecting the Atlantic and Amazon forests in the past.

Natural history. *Basiceros disciger* debunks the myth that *Basiceros* species are rarely collected. The advent of extensive collections and the use of Winkler extractors reveal that, at least for *B. disciger*, this genus is a common inhabitant of litter and topsoil layers. For example, Scott-Santos (2008) studied six different elevation ranges in the Picinguaba region of Serra do Mar State Park, collecting 20 1m² litter samples in each elevation range, submitted to Winkler extractors for 48 hours. Scott-Santos found *B. disciger* in 14 and 12 samples at altitudinal quotas of 400 and 600m, respectively. This species is also found in areas with a relative degree of anthropization. One specimen was collected in a trail edge area, in the Xixová-Japuí State Park (southwest of the state of São Paulo) with tertiary vegetation in a medium degree of regeneration (Probst *et al.*, in review).

Material examined. ARGENTINA: Misiones: 20km SE de Puerto Iguazú, 31.xii.1990, Stewart B. Peck & Jarmila Peck cols., CASENT0006143 (1 intercaste) [CAS]; BOLIVIA: Cochabamba: 109km E of Cochabamba, 17°08'52"S 65°42'64"W, 1400m, 03.ii.1999, R. Anderson, n. 18627 (1 worker); Caranavi: near Radio (not identified), 800 m (GPS refers to town at 960m *a.s.l.*), 24–26.vi.1981, Kugler & Lambert cols., MCZ 546465 (1 worker) [MCZ]; Santa Cruz: Buena Vista, Lat. -17.45 Long. 63.66667, 18.xii.1993, 350m, P.S.Ward#12438-19/CASENT0914887 (1 worker) [UCDC]; BRAZIL: Alagoas: Quebrângulo, Reserva Pedra Talhada, 05.viii.1999, K. A. Santos col. (5 workers) [CEPEC]; Quebrângulo—WF, 09°19'S 36°28'W, Carmo, J. C. S. do col. (1 worker)

[MZSP]; Bahia: Ilheus, Pimenteira, 14°32.72'S 39°25.39'W, 06.x.1997, Santos, J. R. M. & Carmo, J. C. S. cols., n. 928 (?) (1 gyne) [CEPEC]; Vitória da Conquista, Poço Escuro, 14°50'28"S 40°50'20"W, 09–17.i.2001, Carmo, J. C. S. col. (3 workers) [CEPEC]; Espírito Santo: Reserva Biológica Nova Lombardia; 4 km N de Santa Teresa, 24.ii.1967, 900m, W.L. Brown col., MCZ 546466 (2 workers, 1 male) [MCZ]; Santa Teresa, Estação Biológica Santa Lúcia 19°58'09"S 40°32'15"W, 20–24.i.2001, Schoereder, J. H. & Ribas, C. R. cols. (1 gyne) [MZSP]; Goiás: Campo Limpo, Fazenda Conceição, 16°19'51.0"S 49°09'49.2"W, 02-07.vii.2005, Silva R. R. col. (1 worker) [MZSP]; Mato Grosso do Sul: Bonito, R.P.P.N. Brasil Bonito, 21°06'27"S 56°38'14"W, xi. 2009, Silvestre, R. et al. cols. (2 workers) [MuBio]; Minas Gerais: Conceição do Mato Dentro, Serra da Serpentina, 19.03394°S 43.33678°W, Área 3, 18–28.iii.2008, R. R. Silva col. (2 workers); same data, 18–28.iii.2009, Silva, R. R. col. (1 worker); same locality, 17–27, v. 2011, R. R. Silva & E. Z. Albuquerque cols. (9 workers, 4 gynes) [MZSP]; Lima Duarte, P.E. do Ibitipoca, Mata Grande, 14.x.2011, Pigello Queiroz col. (1 gyne) [MZSP]; Serra do Brigadeiro (PESB), 20°39'16"S 42°24'58"W, 1300-1800m, i.2007, R. Solar col. (1 worker) [UFV]; Viçosa, Mata do Paraíso, 20°48'28.3"S 42°51'01.4"W, 750m, 1.v.2013, J. Chaul, R. Jesus, F. Rezende, L. Ribeiro cols., H11-E11 (1 teratological worker) [JCPC]; 20°48'11.5"S 42°51'25.9"W, 725m, i.v.2013, J. Chaul, R. Jesus, T. Vargas, L. Ribeiro e F. Rezende cols., E12-H12 (2 workers) [JCPC]; Nico, 20°47'42.9"S 42°50'51"W, 733m, 08.v.2013, J. Chaul & R. Jesus, H16 (3 workers) [JCPC]; Paraná: Bocaiúva, 25°08'S 49°04'W, v.1963, F. Plaumann col., WWK 3991 (13 workers, 3 gynes) [MZSP]; same locality, 1000m, v.1963, F. Plaumann col., n. 4544 (1 worker) [MZSP]; Guaragi, 25°16'S 50°14'W, 1000m, F. Plaumann col., n. 4582 (1 worker, 1 gyne) [MZSP]; Iguazú (probably Foz do Iguaçu), iv.1965, Fritz Plaumann col., MCZ 546468 (3 workers) [MCZ]; Morretes, P. E. do Pau Ôco, 25°34'33.5"S 48°53'19.5"W, 06-12.v.2002, R. R. Silva & B. H. Dietz cols. (14 workers) [MZSP]; Rio Azul, 1000m, x.1959, F. Plaumann col, n. 3155 (3 workers) [MZSP]; same data (2 workers) [USMN]; Rondon, iv.1965, F. Plaumann col., n. 4545 (1 worker) [MZSP]; Tibagi, P.E. do Guartelá, Trilho do Rio, 24°33'49.61"S 50°15'32.36"W, 20–25.ix.2015, W.Franco, R.M. Feitosa, A. Machado col. (3 workers) [DZUP]; Tunas, Parque das Lauráceas, 24°51'16"S 48°43'00.4"W, 21-29.ii.2001, Silva & Eberhardt cols. (9 workers, 3 gynes) [MZSP]; Rio de Janeiro: Nova Iguaçú, ReBio Tinguá, 22°34'14"S 43°24'51"W, 2.ii.2002, Mayhé A. & Veiga-Ferreira S. cols. (4 workers) [MZSP]; Santa Maria Madalena, P.E. do Desengano, 21°58'41"S 41°57'00"W, Mayhé A. & Veiga-Ferreira S. cols. (3 workers) [MZSP]; Teresópolis, P.N. da Serra dos Órgãos, 23–28.xi.1999, Rocha, Dietz & Rosa cols. (1 worker, 1 gyne) [MZSP]; Rio Grande do Sul: 5km N de Progresso, Linha Araçá—near Rio Fão, 29°10'S 52°20'W, 300-400m, 06.v.1999, J. Bihn col. (5 workers) [MZSP]; Barão de Cotegipe, vii.1960 F. Plaumann col., n. 3763 (1 intercaste) [MZSP]; Barros Cassal, 700m, ix.1960, F. Plaumann col., n. 3597 (1 worker, 1 gyne) [MZSP]; Bom Jesus, 1000m, xii.1962, F. Plaumann col., n. 3479 (1 worker) [MZSP]; Morro Reuter, xii.1964, F. Plaumann col., n. 4106 (1 worker) [MZSP]; Nova Petrópolis, ix.1959, F. Plaumann, n. 3230 (7 workers) [MZSP]; Sapiranga, 31.iii.2006, F. Schmidt col. (1 worker) [MZSP]; same locality, 10.iv.2006, same collector (1 worker) [MZSP]; Sinimbu 29°30'S 52°30'W, 200m, ix.1960, F. Plaumann col., WWK 3282 (23 workers) [MZSP]; Santa Catarina: BR470, between Navegantes e Indaial, 02.v.2009, M. A. Ulysséa col. (1 worker) [MZSP]; Blumenau: no data, Raichansperger (Reichensperger?) col. (1 worker) [NHMB]; Blumenau, P.E. das Nascentes, 27°06'15"S 49°09'14"W, 20–27.x.2000, Silva R. R. & Eberhardt F. cols. (5 workers) [MZSP]; same locality, 27°01–06'S 49°01–10"W, 10.ii.2001, Eberhardt F. col. (1 headless worker) [MZSP]; Campo Alegre, Morro do Serro, xii.1958, F. Plaumann col., n. 3019 (1 worker); same data, WWK 3007 (1 worker) [MZSP]; Chapecó, v.1957, Fritz Plaumann col., MCZ 546472 (1 worker) [MCZ]; same locality, 600m, viii.1960, F. Plaumann col. (7 workers, 1 gyne) [MZSP]; Chapecó, Rio Irani, 04.xii.1998, R. R. Silva col. (2 workers) [MZSP]; Florianópolis, Parque Estadual da Serra do Tabuleiro, i.2013, 27°49'27"S 48°33'50"W, J. Chaul col. (1 worker) [JCPC]; Nova Teutônia (Seara), 27°11'S 52°23'W, 300–500m, no collector, MCZ 546470 (2 workers, 1 gyne) [MCZ]; Nova Teutônia, 27°11'S 52° 23'W, 300–500m, several collections from Fritz Plaumann: x.1954 (17 workers) [MZSP]; vi.1960 (1 worker) [MHNG], (22 workers, 2 gynes) [MZSP]; vi.1967 (1 worker), ix.1955, vii.1958 (2 worker), iv.1972 (1 worker), vi.1963 (1 worker), xi.1972 (1 worker), iv.1976 (1 worker), vii.1961 (1 worker), v.1959 (2 workers) [all deposited at MZSP]; Seara, 24°07'S 52°18'W, 05.xii.1998, R. R Silva cols. (2 workers) [MZSP]; Seara, L. Sta Lúcia, mata ciliar, 9.xi.1998, R. R. Silva (3 workers, 1 gyne) [MZSP]; Palhoça, P. E. da Serra do Tabuleiro, 27°44'28"S 48°41'50"W, 02-10.vi.2003, Silva R. R., Dietz B. H. & Tavares A. cols. (6 workers) [MZSP]; São Bento do Sul, APA do Rio Vermelho, 26°21'51"S 49°16'16"W, 30.iii-04.iv.2001, Silva R. R. & Eberhardt F. cols. (21 workers—1 without gaster, 3 gynes) [MZSP]; São Bonifácio, P.E. Serra do Tabuleiro, 27°49'06"S 48°54'41"W, 08–13.iii.2004, Silva R. R., Dietz B. H. & Albuquerque N. cols. (9 workers) [MZSP]; São Paulo: Agudos, vii.1959. C. Gilbert (3 workers) [MZSP]; Cananeia, Ilha do Cardoso, 25°05'48.7"S 47°55'47.3"W,

24–28.xi.2002, Silva R. R. col. (1 worker) [MZSP]; Cunha, P.E. da Serra do Mar, Núcleo Cunha-Indaiá, 23°15'03"S 45°00'26"W, 21–22.iv.2001, A. A. Tavares & R. R. Silva cols. (10 workers, 1 gyne) [MZSP]; Itu, Fazenda Serra de Itu, Projeto Serra, 1980, no collector (2 workers); P.E. da Cantareira, Núcleo Engordador, 23°21'-27'S 46°29'-42'W, 12-22.v.2003, R. Feitosa & A. Oliva cols. (1 gyne) [MZSP]; Piedade, "Cobrinha", xii.2018 (probably 2008), Gabriela Bieber col. (2 workers) [MZSP]; Praia Grande, P.E. da Serra do Mar, Núcleo Pilões-Cubatão, 25°38'31"S 46°32'24"W, 26–27.i.2001, A. Tavares & R. R. Silva cols. (6 workers, 2 gynes) [MZSP]; Ribeirão Grande. P.E. Intervales, Base Barra Grande, 02.ii. 1999, A. A. Tavares col. (2 workers) [MZSP], Salesópolis, E. B. B. São Vicente, P.E. Xixová-Japuí, 23°59'S 46°23'W, 15.v.2011, Rodolfo Probst col. (1 worker) [MZSP]; Tapiraí, 24°01'55"S 47°27'56"W, 08-14.i.2001, Silva & Eberhardt cols. (8 workers, 2 gynes) [MZSP]; Ubatuba: P.E.S.M. Núcleo Picinguaba, 23°17'54.4" a 23°18'21.6"S 44°47'13.2"S a 44°49'4.8"W, 200m 400m, 600m, 800m e 1000m, several collections from 26.i.2006 to 18–21.ii.2007, E. F. Santos & C. P. Scott-Santos cols. (69 workers, 9 gynes, 17 males) [MZSP]. COLOMBIA: Meta: Quebrada Susumuco (label as Susamuko), 23 km NW de Villavicencio, 1000m, 5.iii.1972, Stewart B. Peck & Jarmila Peck cols. (1 worker) [MCZ]; Villavicencio, 4.14516 -73.63239 +- 5km, 1-4.iii.1972, Stewart B. Peck & Jarmila Kukalova-Peck cols., FMHD 72-146/FMNH-INS 0000095861 (1 worker) [FMNH]; same data, 500m, 1-4.iii.1972, Stewart B. Peck & Jarmila Kukalova-Peck cols., FMHD 72-146/FMNH-INS 0000095861 (1 worker), [FMNH]; Norte de Santander: P.N.N. Tamá Alto de Herrera, Vda. Diamante, 07°07'N 72°13'W, 1000m, 26.xi.1999, E. González col. (2 workers) [MZSP]. ECUADOR: Napo: 20 km S de Tena, 600m, 11.vii, Stewart B. Peck & Jarmila Peck col., MCZ 5464471 (1 gyne) [MCZ]; same data, MCZ 546473 (1 worker) [MCZ]. PARAGUAY: Alto Paraná: Puerto Presidente Stroessner, 6.xi.1974.x-14.xi.1979, Geneva Museum Paraguay Expedition, Baud, Dlouhy, etc. cols. (1 worker) [ANIC]; Puerto Bertoni, 11.xi.1982, V. Mahnert (2 workers) [MHNG]; Canendíyu: ao Sul de Salto d. Guaíra, 1.xi.1976, Geneva Museum Paraguay Expedition, 4.x-14.xi.1979, Baud, Dlouhy, etc. cols., ANIC ant vial 30.226 (1 worker, 1 gyne), label mistake (1976 collection from a 1979 expedition?) [ANIC]; Junção entre os Rios Carapá & Alto Paraná, 2.xi.1979, Geneva Museum Paraguay Expedition, 4.x-14.xi.1979 Baud, Dlouhy, etc. col. (1 worker) [ANIC]; Itapuá: San Benito, 29.x.1982, V. Mahnert col. (2 workers, 1 gyne) [MHNG]; San Rafael, 6.xi.1982, C. Dlouhy col., CASENT0173734 (1 intercaste); same data, CASENT0173735 (1 gyne) [AWPC]. PERU: Huánuco: Leoncio Prado, P.N. Tingo María, vic. Cueva de las Lechuzas Lat. -9.31666 Long. -76.03333, 660m, 08-13.i.1983, A. F. Newton & M. K. Thayer cols., FMNH 83-924/FMNH 0000095854 (1 worker) [FMNH]; Departamento Pasco: Chontilla, 22 km a SE do Vale de Iscozazin (Iscocacín), 26.vii.1961, Fred S. Truxal col., MCZ 546464 (1 worker) [MCZ]; Tambopata, 3.v.2001, TRC-S14-104-R2C04 (2 dealate gynes) [DZUP]; VENEZUELA: Portuguesa: Vía Biscucuy, Concepción, 1000m, 18.viii.1983, J. E. Lattke col., MIZA 437 (2 workers) [MZSP]; same data, MIZA 437/MCZ. 546469 (2 workers) [MCZ].

Basiceros manni Brown & Kempf 1960

(Figs 13–15, 30)

Basiceros manni Brown & Kempf 1960: 177, Figs 3, 11 (worker, gyne): Costa Rica.

Wheeler & Wheeler 1955: 112, Plate 10, Figs 16–17 (immature of *Basiceros manni* identified as prepupa of *Basiceros* sp. Hamburg Farm, Costa Rica; collected with the type-series of what would be described as *B. manni*). Wheeler & Wheeler 1983: 607 (larva).

Type material. COSTA RICA: Limón ("Santa Clara"): Hamburg Farm, 1924, F. Nevermann col., n. 65065 (one worker—holotype) [USNM] (examined); same data, n. 65065 (five workers, one gyne) [USNM] (examined); same data, n. 30878 (three workers—paratypes) [MCZ] (examined); same data (fours workers, one gyne—paratypes) [MZSP] (examined); (eight workers—paratypes) (not examined, location unknown); Colombiana Farm, iii.1920, W. M. Mann col. (three workers) [MZSP] (examined); same data (three workers—paratypes) (not examined, location unknown). HONDURAS: Colón: Sangrelaya, v.1924, W.M. Mann col., n. 546483 (one worker—paratype) [MCZ] (examined); same data (one worker—paratype) (not examined, location unknown).

Diagnosis. Comparatively large size; color light to dark brown coloration. Specialized pilosity distributed in a double layer: a basal subdecumbent plumose, and a fine erect and clavate layers. Clypeomandibular space broad; dorsum of mandibles and clypeus with piligerous punctuations. Petiole claviform, elongated and with a depressed node. Anterior margin of first gastral sternite continuous, without longitudinal projection in the form of carina or prominence. Additionally, adult workers and gynes are usually densely covered with soil and litter particles, which adhere to the double layer of specialized hairs (see Fig1A from Probst *et al.*, 2019).

Description. *Worker* (n=4). HL 1.50–1.53, HL2 1.56–1.62, HW1 1.31–1.39, MdL 0.97–1.00, SL1 1.18–1.22, SL2 1.19–1.20, PDL 0.14–0.15, A3L 0.04–0.06, AFL 0.47–0.50, FuL 1.30–1.34, EL 0.22–0.25, EW 0.19–0.22, ML 2.28–2.40, MfL 1.87–2.03, MtL 1.51–1.62, PH 0.37–0.40, PL 1.03–1.12, PW 0.36–0.39, PPL 0.59–0.65, PPW 0.56–0.65, GL 2.00–**2.09**, GW 1.31–1.40, TL 8.43–8.68, CI 88–92, CS 1.42–1.44, MCI 64–66, SI 85–90, ESI 18–20, SAI2 237–253, EI1 0.28–0.33, MFI 65–70, PTI 264–283. (In bold, measurement for worker presenting slightly dilated gaster).

Size large compared to other Basiceros species. Color (when integument is visible and not densely covered with particles) brown to reddish-brown; appendices slightly lighter. Mandibles and appendages slightly reddish-brown; mandibular dorsa covered with minute piligerous punctuations; apex with short yellowish setae; interdental setae present, yellowish and brush-shaped, slightly longer than teeth. Basimandibular setae present, narrow and erect, located at the anteroventral limit of mandibular peduncle. Sparse squamiform hairs on the anterodorsal margin of the mandibular peduncle, close to the basimandibular setae. Stipes covered by fine, medium, and subdecumbent pilosity; each dorsum with a suberect hair close to its anterior margin. Labrum densely covered with piligerous punctuations bearing short and decumbent setae. Median frontoclypeal portion covered by coarse piligerous punctuations; lateral limits of clypeus with decumbent, short and squamiform yellowish hairs. Head dorsum predominantly covered by piligerous fovea bearing either squamiform or plumose-like hairs, subdecumbent; sparse long erect to suberect hairs on the anterior portion of head, more abundant near the posterolateral region of head and vertexal margin. Ventral surface of head covered by piligerous punctuations; long, erect hairs near the sides of head and squamiform hairs marginating the ventral limit of antennal scrobe. Pilosity on meso- and metasoma present as a double layer of specialized hairs. The "basal" layer is composed of yellowish and subdecumbent plumose-like hairs, present on meso- and metasoma in the following conformation: dense, surrounding the anterior margin of pronotum; slightly sparse on the dorsum of pronotum and mesonotum, dorsum and lateral of propodeum, mesopleuron near the epicnemial fossa, upper portion of mesopleuron, dorsal surface of petiolar node and postpetiole; sides of petiolar peduncle with plumose hairs, following the petiolar node; dorsum of gaster with plumose and squamiform hairs, relatively sparse, on the anterior face and anterolateral portion of procoxae and sparser on the dorsum of metacoxae. The second layer is composed of erect to suberect hairs, long and slightly clavate, present in the meso- and metasoma in the following conformation: dense on the dorsal surface of pronotum, petiolar node, postpetiole, and gaster (relatively sparse on the anterior region of first gastral sternite); one pair present on metanotal suture; 4–5 pairs on the back and sides of propodeum; slightly thinner and sparse on petiolar peduncle; two pairs on each side of anterior margin of postpetiolar sternite; present on the anterior face and anterolateral portion of procoxae; two to three pairs on the dorsum of meso- and metacoxae. Femora and tibiae covered by short, subdecumbent hairs (on tibiae, with a flatter aspect); minute appressed and clavate hairs also present on legs, more easily recognized on ventral surface of femora, tibiae (dorsum of meso- and metatibia as well) and basitarsi. Antennal pilosity unique: subdecumbent squamiform hairs on the basal lobe of scape, dense hairs, erect to suberect on scape dorsum; external margin with long erect hairs, slightly swollen on its median portion and distributed along the crenulation; short clavate and apically curved hairs also following the external margin; ventral face with short, subdecumbent setae; funicles densely covered with short, decumbent setae.

Body mostly smooth and shiny on glabrous regions. Dorsum of mandibles and clypeus covered with punctuations. Anteroventral portion of mandibles slightly alveolate. Anterior margin of labrum finely reticulate. Head dorsally rugose-foveate, irregular rugae forming fovea of different sizes; antennal fossa reticulate; antennal scrobe surface punctuate-foveate on its posterior half; head ventral face coarse and sparse punctuations. Pronotum foveate on anterior margin and sides. Mesonotum with lateral costulae, extending to the anterior face of propodeum. Gaster densely punctuate-reticulate; tergite of abdominal segments V, VI, and VII finely and densely punctate, slightly opaque, tergal margins smooth and shiny, slightly yellowish; more sparse sculpture on the first gastral sternite, especially in the anteromedial portion. Scapes finely reticulate. Legs smooth.

Head oblong, sides emarginate from the eye insertion to posterolateral region and behind the head; posterior portion of head slightly depressed, projected posteriorly; vertexal margin with rounded corners, median portion broadly concave. Cervical margin strongly carinate. Palp formula 2,2; palps strongly fused; maxillary palp slightly larger and wider than labial, with one sensillum; labial palp apically clavate, with two sensilla. Stipes subrectangular. Labrum lunate, laterally curved (apex 0.07 mm); distal margin rounded, medial knob present. Mandibles triangular; in full-face view, lateral margins slightly concave; basal margin conspicuously concave, clypeomandibular space wide; basal angle rounded, followed by about 20 slightly rounded denticles and gradually decreasing in size

along the masticatory margin; in lateral view mandibular apex slightly curved ventrally. Clypeus lamellated laterally and on the anterolateral portion; anterior margin concave medially. Short frontal sulcus present separating the dorsal convexity into two parts. Compound eyes large. Carina-like rugae below eyes, projecting from the middle of the antennal fossa margin and extending to the side of the head, like an arc. Scape with lamellar basal angle slightly rounded, external margin crenulate and lamellar. Antennal fossa deep. Antennal scrobe deep on the anterior half, posterior and ventral limits weakly distinct.

Mesosoma slender; lateral profile of promesonotal complex continuously convex, strongly sloping caudad; metanotal suture wide. Mesopleuron bordered anteriorly, interrupted at the meeting of a narrow epicnemial fossa. In lateral view, anterior portion of the propodeum short and slightly oblique posteriorly, dorsal surface of propodeum slightly sloping posteriorly. Propodeal slope laterally carinate and with strong transverse lamellar carina connecting to sharp and tapered, slightly curved upwards propodeal projection. Opening of propodeal spiracle round. Bulb of metapleural gland prominent, projected and slightly narrowed; opening transversal and covered by cuticular lamella. Dorsal surface of petiolar peduncle careened longitudinally. In dorsal view, propodeal spiracle slightly projected dorsally. In lateral view, petiole long and claviform; postpetiole subcircular, subequal to the length of petiolar node. Subpetiolar process variable: from anterior process slightly curved anteriorly, followed by 4–8 spines of various sizes to slightly bifid process followed by simple or double spines and vestigial processes on the posterior portion of peduncle. In dorsal view, petiolar node ogive-shape; posterior margin of postpetiole convex and widely inserted to anterior concavity of gaster. Postpetiolar sternite conspicuously carinate anteromedially, prora present, lamellar and slightly darkened. Anterodorsal lamellar margin of gaster yellowish; median longitudinal sulcus present on first tergite, shallow and glabrous. Calcar of strigil pectinate. Meso- and metabasitarsi conspicuously long, about ¾ of tibial length. Tarsal claws simple.

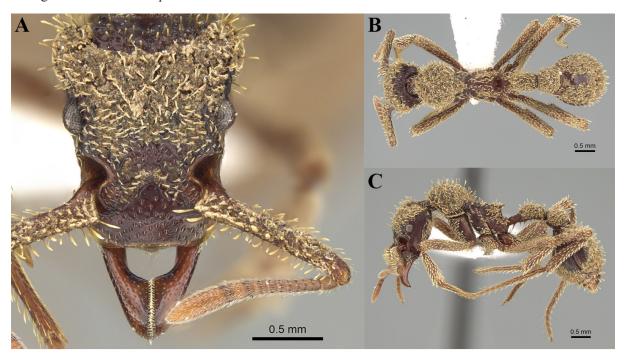


FIGURE 13. *Basiceros manni*, worker (CASENT0914888, Costa Rica: Heredia); A. full-face view, B. lateral view, C. dorsal view. Images by Michele Esposito (CAS).

Gyne (n=3). HL 1.48–155, HL2 1.53–1.62, HW1 1.33–1.40, MdL 1.00, SL1 1.19–1.22, SL2 1.18–1.20, PDL 0.15–0.16, A3L 0.05–0.06, AFL 0.48–0.50, FuL 1.31–1.36, EL 0.31–0.33, EW 0.25–0.28, LOD 0.06–0.09, MOD 0.08–0.09, OOD 0.30–0.37, ML 2.34–2.47, MSL 1.06–1.15, MSW 0.93–1.00, MLL 0.28–0.34, MLW 0.44–0.45, MfL 1.95–2.00, MtL 1.50–1.60, PH 0.35–0.40, PL 1.03–1.15, PW 0.40–0.48, PPL 0.65–0.69, PPW 0.67–0.70, GL 2.11–2.28, GW 1.50–1.53, TL 8.75–9.08, CI 89–91, CS 1.40–1.47, MCI 64–67, SI 85–92, ESI 21–27, SAI2 240–245, EII 0.37–0.41, MTI 80–94, MLI 127–163, MFI 67–70, PTI 284–292.

Coloration and sculpture similar to conspecific workers; size slightly larger. Cephalic dorsum with three ocelli: median ocelli inserted at the top of the frontal sulcus and lateral ocelli inserted slightly above. Head pilosity as in conspecific workers. Double layer of specialized pilosity on pronotum denser than in workers. Mesoscutum almost

lacking basal pilosity, only two subdecumbent hairs present, with a plumose aspect, anteriorly to each parapsis, and four hairs close to the margin of the scutoscutellar suture; erect pilosity relatively sparse, present primarily on lateral margins of mesoscutum; central portion of mesoscutum nearly glabrous. Mesoscutellum with double-layer of pilosity. Median region of metanotum with a pair of long, clavate and suberect hairs and four hairs from the basal layer with a plumose appearance. Posterior corner of mesoanepisternum, just below forewing insertion, with basal pilosity. Ventral and posterior limits of mesokatepisternum with basal pilosity, as well as the ventral portion of metakatepisternum. Dorsum of meso- and metacoxa with specialized pilosity. Remaining regions with pilosity shape and configuration similar to conspecific workers. Mesoscutum with irregular longitudinal rugae, interspersed with rugulae forming fovea of different sizes. Mesoscutellum irregularly rugo-foveate. Mesopleuron smooth, subopaque (weakly granular aspect) on most of its extension, except for foveate posterolateral portion of mesoanepisternum. Anapleural sulcus smooth. Anterior portion of petiolar peduncle finely reticulate. Gastral sculpture deeper than on workers. Other regions of the body ornamented as conspecific workers. In dorsal view, humeral angles strongly projected, dividing pronotum into two portions. Mesoscutum anteriorly rounded and slightly wedge-shaped; anteromedial carina present, short and longitudinal; posterior margin broadly convex at the meeting with the scutoscutellar suture; notauli indistinct; parapsidal lines obsolete, involved by the sculpture; parapsis subreniform, slightly deep, tegulae narrow, elongated, apical margin rounded. Pre-scutellum narrow; axillae projected posteriorly, rounded and slightly depressed. Scutoscutellar suture well-marked, transversally costulate. Mesoscutellum trapezoidal, posterior limit concave. First gastral sternite with a slightly projecting median region on basal half. Forewing type 1; hindwing with five submedian hamuli.



FIGURE 14. *Basiceros manni*, gyne (MCZ 546486, Costa Rica: Heredia) and male (MCZ, Costa Rica: Heredia); A and D. full-face view, B and E. dorsal view, C and F. lateral view. Scale bars: A, D = 0.5 mm, B, C, E, F = 1 mm.

 $\label{eq:male} \textit{Male} \ (n=2). \ \text{HL} \ 0.93-0.96, \ \text{HW}1 \ 0.95, \ \text{HW}2 \ 1.10, \ \text{MdL} \ 0.55-0.56, \ \text{SL}2 \ 0.20-0.23, \ \text{PDL} \ 0.13-0.15, \ \text{A3L} \ 0.48, \ \text{AFL} \ 0.61-0.63, \ \text{EL} \ 0.35-0.38, \ \text{EW} \ 0.28-0.31, \ \text{LOD} \ 0.09-0.10, \ \text{MOD} \ 0.09, \ \text{OOD} \ 0.32-0.37, \ \text{ML} \ 1.88, \ \text{MSL} \ 0.93-1.05, \ \text{MSW} \ 0.78-0.80, \ \text{MLL} \ 0.33-0.38, \ \text{MLW} \ 0.45-0.46, \ \text{MfL} \ 1.80-1.85, \ \text{MtL} \ 1.29-1.33, \ \text{PH} \ 0.25-0.30, \ \text{PL} \ 0.88-0.90, \ \text{PW} \ 0.35-0.38, \ \text{PPL} \ 0.43, \ \text{PPW} \ 0.43-\textbf{0.50}, \ \text{GL} \ 1.63-1.80, \ \text{GW} \ 1.15-1.25, \ \text{TL} \ 6.35-6.45, \ \text{CI} \ 98-102, \ \text{CS} \ 0.94-0.96, \ \text{MCI} \ 58-59, \ \text{SI} \ 21-23, \ \text{ESI} \ 166-175, \ \text{SAI} \ 42-47, \ \text{SAI2} \ 32-36, \ \text{EII} \ 42-47, \ \text{EI2} \ 120-123, \ \text{MTI} \ 78-81, \ \text{MLI} \ 123-138, \ \text{MFI} \ 51-52, \ \text{PTI} \ 300-350. \ \text{(In bold: for one male, wings partially covered the lateral margin of postpetiole)}.$

Slightly smaller than conspecific gyne. Coloration dark brown to black, with sides of pronotum and mesoscutum, posterodorsal region of scutellum and portion of dorsum of petiole brown; postpetiole and anterior to anterolateral region of gaster testaceous; appendages brown to light brown; antennas with opaque appearance. Wings whitish to yellowish. Mandibles with long yellow hairs close to their apexes; dorsum with fine yellowish hairs and subdecumbent, slightly shorter. Head with two main types of hair: medium to short, yellow and fine, erect to suberect, sparse; and long and yellowish, generally with a curved apex and primarily on frons, vertexal, and ventral regions. The second hair type widely present throughout the body: on the dorsum of mesosoma, waist and gaster, coxae and mesokatepisternum suture. Filiform subdecumbent and short hairs present on the first gastral tergite and sternite. Antennomeres with short appressed whitish setae. Legs with suberect setae sparsely distributed among short decumbent to decumbent setae.

Body uniformly punctuate-reticulate (sculpture changing diameter and degree of impression). Distal half of mandibles smooth and shiny. Irregular longitudinal rugae on the central disc of clypeus, on head dorsum, and neck. Irregular transverse rugae near the occipital carina; on the dorsum of mesosoma; on pronotum sides, and propodeum. Mesoanepisternum shiny on its anterodorsal portion.

Head piriform; occipital margin wide and lamellar. Palp formula 1,1; palps apically subclavate and subequal; maxillary palp slightly wider than labial; apexes of palpi with long, filiform sensillum. In ventral view, mentum arrow-shaped. Labrum trapezoidal; basal region transversely striate; distal margin weakly concave; corners angled; 10–12 long and erect setae present. Mandibles triangular, elongated and gently curved apically; masticatory margin with 12–14 conical teeth, the basal and the subbasal sometimes extremely short and apical tooth slightly falcate. Clypeus with convex central disc and lateral regions depressed; anterior margin lamellar and moderately flat; frontoclypeal region excavated. Carina genal present on head side, extending posteriorly to occipital carina. Frons with arc-shaped carina above the antennal insertions and connected to frontal lobes. Antennal scrobes deep and marginally lamellar. Antennal arch expanded to posterolateral lobe, hiding the antennal bulb in full-face view. Pedicel longer than wide, third antennomere about five times longer than pedicel. Eyes large, globular, protruding from cephalic capsule; posterior margin emarginated. Ocelli pearl-shaped, projected on carinate crests.

In dorsal view, mesoscutum keel-shaped; pronotum transversally projected anterodorsad by a carinate conical or rounded process. This carina extends laterally through the pronotum, dividing it into a lower and an upper portion and producing triangular lateral flaps. Broad and partially shiny carina present on the anteromedial region of mesoscutum, extending to the dorsal region. Anterior portion of notauli separating the mesoscutum into two distinct regions: an anterior, narrow and slightly higher and obliquely convex in profile, delimited by the notauli lateroposterad and forming a projection at this region; and one posterior region, subquadrate. Notauli broad and somewhat deep, converging posteriorly on a sinuous longitudinal carina almost continuously covering mesoscutal surface. Parapsidal lines shiny; curved on anterior portion, subparallel and directed anterolaterally to the parascutal flange; posteriorly reaching the notauli. Parapsides broad, deep and reniform. Transscutal articulation convex. Axillae strongly curved posteriorly, projected and hook-shaped. Anapleural sulcus broad, deep-mesoanepisternum considerably elevated above the mesokatepisternum; scrobiculate and slit-shaped; posterior limit oblique. Scutoscutellar sulcus wide and longitudinally scrobiculate. Mesoscutellum subquadrate; posterior margin concave, crenulate and moderately depressed. In dorsal view, metanotum distinct, posterior margin projected, lateral margins lamellar. Propodeal spines short and triangular; carinate as in conspecific females. Propodeal lobes auricular. Calcar of strigil pectinate. Tarsal claws simple; short arolia present. Shape of petiole similar to conspecific females, claviform; in dorsal view, petiolar spiracle projected; anteroventral process followed by minute triangular spines. Postpetiole short; in lateral view, dorsally convex; spiracle projected; sternite with transverse lamellar prora near the anterior margin. Forewing type 1; hindwing with five to six submedian hamuli (four in one specimen, probably due to loss)

Larva. Approximate length through spiracles: 5.1 mm; profile pogonomyrmecoid: larger diameter near the middle of abdominal region, slender thorax; curved ventrally. Anus ventral, anal opening weakly convex, anal flap present. Spiracles minute. Integument of ventral region densely covered by spinules arranged in transverse rows. Pilosity moderate, denser on abdominal dorsum and ventral margin, sparse on rest of the body; long hairs—especially on part of head and ventral margin of thorax—(0.15–0.30 mm) flexuous and denticulate; alveolus and articular membrane present or not. Cranium slightly suboctagonal, occipital margin with median impression; antenna extremely minute. Clypeus protruding. Labrum bilobed, approximately three times wider than long; ventral surface densely spinous; anteroventral margin of each lobe with about six rounded sensilla; anterodorsal border with four isolated short setae resembling trichoid sensilla. Mandibles pogonomyrmecoid, long and narrow, curved; subapical

tooth slightly forward to the plane of apical tooth; basal tooth strongly projected into the inner margin; anteroventral margin densely covered by subtransverse lines of short and arcuate spinules. Maxillae parabolic, dorsum with five setae, apex spinose; maxillary palps and galeae digitiform, subequal in diameter; maxillary palp with five sensilla: two apical, encapsulated, two lateral with one spinule, and one subapical spinulate; galeae with two apical spinulate sensilla. Labium covered by short transverse rows of spinules; spinules developed, capillary (about 0.02 mm) and densely covering the area surrounding the opening of the sericeous gland, shorter spinules on the rest of labium surface; labial palp papillary, with five apical sensilla (two encapsulated and three with spinules); three trichoid sensilla isolated under the labial palp, in triangular configuration. Opening of sericeous gland transversal, each side with a short and isolated sensillum. Hypopharynx densely spinous; spinules arranged in short subtransverse rows.

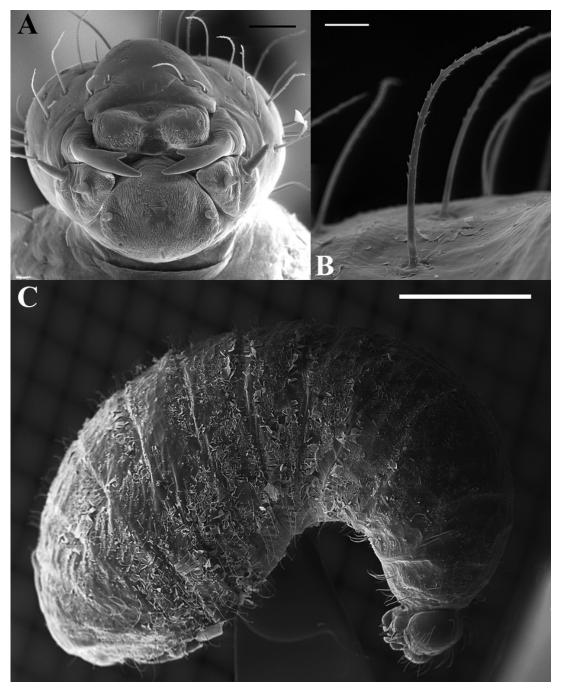


FIGURE 15. *Basiceros manni*, larva (MZSP, Nicaragua: Boaco); A. head in anteroventral view, B. dorsal pilosity, C. lateral view. Scale bars: A = 0.1 mm, C = 1 mm, B = 0.05 mm.

Etymology. This species was named after Dr. William M. Mann (1886–1960), a prominent American entomologist and myrmecologist. Dr. Mann was a doctoral student of William Morton Wheeler at Harvard University and

worked at the United States Department of Agriculture (USDA) as an entomologist, conducting several expeditions, mainly in Central and South America. According to Brown & Kempf (1960: 178), Dr. Mann was the first to discover this taxon (he collected much of the type-series on expeditions in Costa Rica and Honduras) and to recognize it as a new species (Mann 1922).

Comments. *Basiceros manni* is very similar to *B. singularis* in several characteristics, such as size, general morphology, and pilosity. Specimens of both species are easily mistaken when covered with litter and soil particles. In terms of variation, there are differences in the shape of the subpetiolar process, sculpture, and in a lesser degree in pilosity for the female castes. For males, the variation observed is mainly in the sculpture (especially in the mesosoma) and shape of the transverse keel of the anterior margin of the pronotum, whose apex ranges from conical to slightly rounded. Dietz (2004) mentions that in dorsal view it is impossible to visualize the metanotal flange on the male of *B. manni*, however part of the metanotum is present on specimens examined for the present study.

Most males examined here are part of nest series collected by E.O. Wilson and B. Hölldobler at La Selva Biological Station, in Costa Rica, with three specimens obtained by Wilson & Hölldobler (1986) from lab colonies during an ethological project involving those nest series.

A brachypterous intercaste have been collected for this species in Nicaragua (Dr. Michael Branstetter, pers. comm.). However, this specimen was not examined.

Distribution. This species is recorded from low elevations, in primary or low anthropogenically disturbed forests, in Costa Rica, Honduras, and Nicaragua and is likely restricted to this geographic distribution. Records for this species for Ecuador, Panama, Trinidad and Tobago, and islands in the Western Caribbean Sea (case of St. Vincent and the Grenadines) are not supported in the present study. Based on the specimens examined during this study, *B. manni* does not occur in Ecuador or Trinidad and Tobago, and some specimens of *B. singularis* examined from these two points were wrongly identified as belonging to *B. manni*. It was not possible to access material from the other locations mentioned and there is no way to ensure that this species occurs there. The MCZ online database highlights that those Trinidad & Tobago specimens might have unmatched specimen label information in terms of locality. Additionally, a worker collected at French Guiana by The Joint Research Unit Ecology of Guianan Forests (EcoFoG) (AntWeb specimen code ECOFOG-IT14-0106-61) and identified as *B. manni* by Franco *et al.* (2019) is actually a worker of *B. singularis*.

Natural History: *Basiceros manni* is the species of the genus with the greatest amount of behavioral ecology data, thanks largely to the work of Wilson & Hölldobler (1986) and Hölldobler & Wilson (1986) and to the information recorded on the page http://ants.biology.utah.edu/genera/basiceros/species/manni/manni.html, maintained by Dr. John Longino. Foraging workers of this species are usually covered by a thick layer of particles, as mentioned in the diagnosis. Hölldobler & Wilson (1986) speculate that the specialized double-layer pilosity acts with the layer of erect and clavate hairs capturing soil and litter particles from the environment and the layer of subdecumbent plumose hairs adhering them to the ant's body. Individuals of *B. manni* present thanatosis and this behavior, added to the cryptic coloration presented by this species—a result of the already mentioned dense cover of soil particles and litter adhered to its integument—makes field observation of this dirt ant an ungrateful task.

Colonies of *B. manni* are usually found nesting in decayed trunks at different levels of composition, in the leaf-litter located at the base of trees. Wilson & Hölldobler (1986) mention the collection of a colony nesting in a rotten fava bean of *Pentaclethra macroloba* partially buried in the leaf-litter. Ronald Garcia, field biologist at La Selva Biological Station in Costa Rica, share the following data on a colony nesting in an abandoned nest of what appears to be a Meliponini bee (Fig 16), with the following report: "The nest was in a tree fork of a living tree, to more or less, 40 cm from the ground. The nest got my attention because the entrance looks like some stingless bees, this entrance is unbelievable! It is in the Aerial Tram, in the foothill of the Braulio Carrillo Mountain, 500m a.s.l. The size of the nest is a little more than a fist".

Wilson & Hölldobler (1986), studying three colonies in the laboratory for about a month, report that ovaries are maximally developed in younger workers, associated with the laying of trophic eggs. In contrast, the venom gland reservoir reaches its maximum size in older workers, associated with an increase in predatory activity. These ants exhibit an exceptionally simple behavioral repertoire (Wilson & Hölldobler *op. cit.*). There is a temporal division of labor, with young workers acting as nurses and older workers leaving the nest in search of food. Dr. Jack Longino reports on his website (see address above) that he found this species in lowland forests of Costa Rica, usually with workers foraging alone at night or collected from litter samples submitted to a Winkler extractor. In addition, he observed a nest in a primary forest at Los Patos area in the Corcovado National Park, also in Costa Rica. The colony

was on a trunk in an advanced state of decomposition at the base of a small tree, and the workers were scattered in several chambers. One chamber had almost all the immatures, in another some larvae and four empty shells of gastropods of the same species, with a long and pointed spiral (also see the natural history topic under *Basiceros singularis*). Dr. Longino comments that Dr. Ted Schultz (USNM) collected a colony in a primary forest area of humid tropical forest at La Selva Station. The contents of the nest included (in addition to workers, gynes, males and immatures) a variety of empty gastropod shells, various termite abdomens and other unidentified objects reminiscent of *Camponotus* (Formicidae: Formicinae) gasters. Unfortunately, Wilson & Hölldobler's (1986) "cafeteria" experiments did not include land snails, and their captive colonies of *B. manni* accepted beetle larvae, centipedes, termites, and freshly killed *Drosophila* adults. Prey was offered directly to the larvae. The workers foraged alone and did not recruit.



FIGURE 16. *Basiceros manni* colony in abandoned Meliponini nest at La Selva Biological Station, Costa Rica: Heredia; A. Exterior view of nest entrance, B. Detail of chamber with immatures below nest entrance, C. Brood chamber. Images: courtesy of Ronald Garcia.

This scenario of likely specialized predation on land snails was reinforced by Dr. Michael Branstetter. According to him, all colonies collected in Nicaragua had empty gastropod shells. The shells appear to belong to a "pulmonated" zonitid mollusk (Zonitidae), probably from the genus *Glyphyalinia* (Dr. Jaime Jardim pers. comm.).

Material examined. COSTA RICA: Cartago: Turrialba, summer of 1988, I. Perfecto col., n. 17—n. 326567 (2 workers) [LACM]; Heredia: La Selva Biological Station, 4.II.1974, Talbot & VanDeVender cols., n. 326565 (3 workers) [LACM]; 24.iii.1985, E. O. Wilson col., n. 546485 (2 workers) [MCZ]; same data, 26.iii.1985, B. Hölldobler & E. O. Wilson cols. (2 workers, 1 male) [MCZ]; same data, 29.iii.1985, B. Hölldobler & E.O. Wilson col., n. 546486 (3 workers, 1 gyne) [MCZ]; same data, 29.iii.1985, B. Hölldobler & E.O. Wilson cols. (2 workers) [MCZ]; same data, 19.xi.1985, E.O. Wilson col., (1 worker, 1 male) [MCZ]; same data, iii.1987, E.O. Wilson col. (3 workers) [MCZ]; same data, 14.iii.1987, E.O. Wilson col., (1 worker, 1 male) [MCZ]; same data, 23.iii.1988, S.P. Cover col., n. 546463 (2 workers) [MCZ]; same data, 10°26'N 84°00'W, 14.x.1991, J. T. Longino col., n. J.Longino#3078-5, INBIO-CRI001237650 (1 worker), [JTL]; same data, 02.vii.1992, T. R. Schultz col., n. TRS920702-08, 538640 e 538643 (1 worker, 1 gyne, 1 male) [USNM]; Puerto Viejo, 3.viii.1965, R.J. Hamton col., (3 workers) [ANIC]; same data, n. 326566 (2 workers, 1 gyne) [LACM]; Lat 10.4333 Long. -83.9833, 50m, 2.iii.1987, D. Olson col., DM029/CASENT0914888 (1 worker) [UCDC]; La Selva Biological Station-AntCourse 2004, 10°26'N 84°0'W, 50m, 4-14.viii.2004, B. L. Fisher, BLF10423/CASENT0052769 (1 worker) [CAS]. Limón ("Santa Clara"): Colombiana Farm: iii.1924, W.M. Mann col., n. 546484 (2 workers) [MCZ]; same data (11 workers, 1 gyne) [USNM]; Hamburg Farm: 1924, F. Nevermann col., n. 546487 (1 worker) [MCZ] (type?); Around Guapiles, Rio Toro Amarillo, 25.ii–9.iii.1966, W.L. Brown col., n. 546481 (3 workers) [MCZ]; same data, n. 546480 (3 workers) [MCZ]; same data (2 workers) [MZSP]; same data, n. 326564 (1 worker) [LACM]; Península Osa: Corcovado: Los Patos, 01.iii.1981, J. Longino col., n. 546482 (1 worker) [MCZ]; Puntarenas: 15 km SSW Puerto Jimenez, Lat. 8.407665 Long. -83.32788, 07.iii.2010, J. T. Longino col., n. J. Longino#6901.45/CASENT0634078 (1 worker) [JTL]; No label (according to Gary Umphrey: COSTA RICA: La Selva/III-14-87, E. O. Wilson col. (1 worker, 1 male) [MCZ]. NICARAGUA: Boaco: 8km LSE de El Porton, Lat. 12.58465 Long. -85.4656, 750m, n. MGB1723 (3 workers, 1 pupa, 1 larva) [MBPC]; Chontales: 4km NE de Cuapa, 20.iv.2011, Lat. 12.2903 Long. -85.35436, 740m, 17.iv.2011, n. MGB1735 (5 workers, a pupa, some larvae) [MBPC]; RAAN: Parque Nacional Cerro Saslaya, Lat. 13.77065 Long. -08498018, 310m, 7.v.2011, LLAMA#Wa-D-02-44, CASENT0628761 (1 worker) [JTL].

Basiceros militaris (Weber 1950)

(Figs 17–20, 31)

Aspididris militaris Weber 1950: 3, Fig 1 (worker*, gyne*). Trinidad & Tobago.

Wheeler & Wheeler 1955: 114, Plate 6, Figs 11-15 (larva).

Combination in Basiceros: Brown 1974, 134.

Type material. *Holotype.* TRINIDAD & TOBAGO: Trinidad, Nariva Swamp: 23.iv.1935. Weber#140 [AMNH] and two paratypes (one paratype, same locality, same data, Weber#140.1, MCZ 28746; one paratype, same locality, 22.iv.1935, Weber#139, MCZ 28476;) [MCZ] (all intercastes) (examined).

Diagnosis. In full-face view, head with vertical margin in the form of a continuous crest, anteriorly separated from the central head convexity by a wide and uninterrupted sulcus.

Description. *Worker* (first description (see Type Material above and Comments section)) (n=5). HL 1.40–1.50, HL2 1.39–1.51, HW1 1.37–1.40, MdL 0.62–0.65, SL1 0.78–0.84, SL2 0.84–0.87, PDL 0.09–0.12, A3L 0.03, AFL 0.33–0.34, FuL 0.90, EL 0.13, EW 0.09–0.11, ML 1.43–1.62, MfL 1.05–1.13, MtL 0.89, PH 0.37, PL 0.59–0.65, PW 0.31–0.34, PPL 0.43–0.48, PPW 0.56, GL 1.54–1.65, GW 1.19–1.25, TL 6.04–6.58, CI 93–97, CS 1.39–1.45, MCI 43–44, SI 61–62, ESI 14–14, SAI2 245–266, EII 0.15–0.16, MFI 125–131, PTI 158–175.

Size small compared to other *Basiceros*. Coloration dark brown to black; appendages lighter, brown to light brown. Mandibles slightly lighter than the predominant integument coloration; dorsa covered by sparse and minute piligerous punctures, apex with short yellowish setae; interdental setae present, yellowish and filiform, subequal to length of teeth. Suberect clavate hair on the dorsum of each stipe, on its median region. Dorsal surface of head covered by piligerous punctuations; pilosity on head dorsum restricted to a pair of clavate hairs in the posteromedian region, close to the posterior limit of central tumosity. Head lateral and vertexal margins covered by whitish to yellowish erect and clavate hairs, in the following configuration: 10 hairs on the lateral, starting from the region above the eyes and bordering the anterior limit of antennal scrobe and the posterior limit of vertexal crest; five hairs on either side of the dorsal (anterior) edge of vertexal crest; ten hairs on vertexal margin. Ventral surface of head densely covered by filiform suberect hairs, of two sizes: at the center, long hairs arranged in pairs, medium hairs on head sides, densely distributed. Mesosoma and metasoma with slightly clavate subdecumbent pilosity surrounding the anterolateral margin of pronotum and on the sides of propodeal slope. Dorsum of the meso- and metasoma with erect clavate hairs as follows: a pair close to the promesonotal suture; a pair on metanotal flange; a pair on the center of postpetiolar dorsum; 2–3 pairs on the dorsum of first gastral tergite; row of six hairs on the visible portion of the second, third and fourth gastral tergites (similar conformation of gastral dorsum also present on ventral region of this somite, in this case, hairs are slightly clavate). Posterior margin of petiole and dorsum of postpetiole with whitish decumbent and squamiform hairs. Filiform and long hairs on propleura, on the anterior portion of procoxae, and gastral sternites. Squamiform hairs on the anterolateral portion of procoxae and dorsum of meso- and metacoxae. Remaining leg surface densely covered by decumbent hairs from clavate to squamiform. Other pilosity appressed and short, part of thin or thick piligerous punctuations.

Glabrous regions of body ranging from mostly smooth and shiny to subopaque and slightly grainy. Head evenly punctuate; punctuations denser on the cephalic sulcus; surface of antennal scrobe predominantly punctuate-fove-ate, anterior portion sometimes smooth, posterolateral portion punctuate-rugose; ventral margin rugose. Pronotum punctuate-foveate. Dorsum of mesonotum, anterodorsal region of the propodeum, dorsal surface of meso- and meta-coxae and dorsum of petiolar and postpetiolar nodes punctuate-rugose. Mesopleuron and metapleuron predominantly smooth or subopaque, with a granular appearance. Mesosternum shelf (surrounded by epicnemial carina) with short, filiform setae along its length. Anterior portion of mesopleuron punctuate-rugose. Side of propodeum with sparse punctuations. Surface of propodeal declivity smooth. Petiolar peduncle irregularly rugulose. Gaster densely

^{*} Intercastes

punctuate; tergite surface of abdominal segments V, VI, and VII finely and densely punctuate, slightly opaque, tergal margins smooth and shiny; sculpture of first gastral sternite slightly more sparse, anterior portion of this sclerite sometimes subopaque to shiny. Antennal scapes smooth or finely rugose, usually shiny. Funiculi densely and finely punctuate, usually opaque. Legs mostly smooth or rugose; procoxae smooth, lateroposterior portion rugose; dorsum of meso- and metacoxae transversely rugose, short and irregular rugae forming foveae of different sizes.

Head disc-shaped, convex posteriorly; sides bordered by a raised margin that extends from the height of compound eyes to posterolateral region and behind the head, forming a crest. Face with central tumosity from the frontoclypeal portion to the posterior portion of head. Frontal sulcus present above the tumosity, separating it from the vertex crest. Vertex margin with convex corners, slightly projected backwards; vertexal crest conspicuous and continuous. Cervical margin carinate. Palp formula 2,2; palps strongly fused, giving the impression of being unsegmented. Stipes subrectangular. Labrum cuneiform; distal margin bilobed, lobes separated by cleft. Mandibles triangular; in full-face view, lateral margins slightly concave; masticatory margin with 10–14 triangular teeth; in lateral view mandibular apex slightly curved ventrally. Clypeus heavily lamellated anteriorly; anterolateral portion gently convex; anterior margin delicately concave on its median portion, hiding the basal angle of mandibles. Scapes with a slightly obtuse basal angle and straight/slightly convex limit before the lamellar crenulate portion. Antennal fossa deep and tapered.

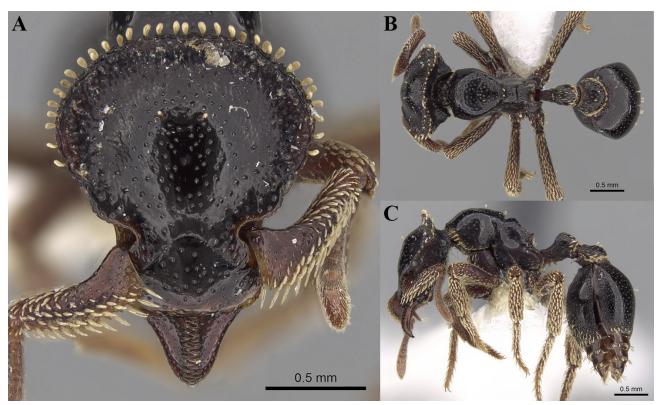


FIGURE 17. *Basiceros militaris*, worker (CASENT0280778, Ecuador: Tiputini); A. full-face view, B. lateral view, C. dorsal view. Image by Estella Ortega (CAS), edited.

Mesosomal profile with bulging promesonotal complex, slightly curving in its posterior portion; promesonotal suture practically imperceptible in dorsal view. Metanotal flange present, slightly oblique to its posterior portion; metanotal suture broad and strongly impressed, longitudinally costulate. Propodeum oblique, anterior margin raised and abruptly followed by the sloping face. In dorsal view, dorsum of propodeum anteriorly narrowed, slightly triangular. Propodeal slope laterally carinate, transverse costulae connecting to short projections, triangular and apically lamellar. Opening of propodeal spiracle round. Metapleural gland bulla protruding, prominent; opening transverse and covered by cuticular lamella. Mesopleuron anteriorly emarginate, interrupted at the epicnemial fossa. In dorsal view, petiolar peduncle longitudinally carinate. In lateral view, petiole claviform; petiolar node with slightly concave anterior surface, dorsal margin domed to convex; postpetiole convex. Subpetiolar process highly variable: from absent to composed of anteroventral projection followed by digitiform protuberances and lamellar region. In dorsal view, petiolar node longitudinally trapezoid, anterior margin narrower and rounded, posterior margin

straight; postpetiole slightly wider than long; anterior margin emarginate; posterior margin convex and widely inserted into anterior concavity of gaster. Gaster anteriorly emarginate; longitudinal gastral sulcus present on median portion, shallow and extending over the entire dorsum of first tergite, slightly narrower posteriorly. Calcar of strigil pectinate. Tarsal claws simple.

Gyne (first description) (n=3): HL 1.48–1.56, HL2 1.47–1.53, HW1 1.38–1.50, MdL 0.63–0.72, SL1 0.81–0.90, SL2 0.75–0.95, PDL 0.10–.12, A3L 0.03–0.04, AFL 0.33–0.38, FuL 0.85–0.91, EL 0.20–0.25, EW 0.17–0.20, LOD 0.03–0.06, MOD 0.03–0.06, OOD 0.3–0.56, ML 1.73–1.86, MSL 0.76–0.88, MSW 0.82–0.88, MLL 0.28–0.30, MLW 0.46–0.50, MfL 1.11–1.19, MtL 0.84–1.00, PH 0.38–0.43, PL 0.65–0.79, PW 0.35–0.40, PPL 0.48–0.53, PPW 0.55–0.62, GL 1.63–1.95, GW 1.28–1.40, TL 6.61–7.40, CI 93–96 CS 1.43–1.53, MCI 41–46, SI 63–64, ESI 26–27, SAI2 240–290, EII 0.27–0.28, MTI 100–108, MLI 132–168, MFI 120–127, PTI 173–178.



FIGURE 18. *Basiceros militaris*, gyne (MCZ, Trinidad & Tobago: Arima Valley) and male (MCZ, Trinidad & Tobago: St. Andrew); A and D. full-face view, B and E. dorsal view, C and F. lateral view. Scale bars: A, D = 0.5 mm, B, C, E, F = 1 mm.

Size and coloration similar to conspecific workers; mesosomal sculpture more developed. Cephalic dorsum with three ocelli: median ocelli inserted slightly below and lateral ocelli inserted just above a pair of clavate and erect hairs. Head pilosity as in workers. Pilosity of anterolateral margin of pronotum denser and longer than on workers. Clavate and erect hairs on mesosoma in the following conformation: three pairs close to the humeral angles and surrounding the posterior limit of pronotum; around four pairs on the dorsum of mesoscutum, one near the center of the scutoscutellar suture; two pairs on the parascutal flange; one pair on each parapside; one pair on the lateral axillar region; two pairs on the dorsum of mesoscutellum; a pair on the metanotal flange, suberect. One pair of erect hairs on the posterodorsal region of petiolar node, other pilosity on petiole same as on workers; pilosity of the postpetiolar dorsum more abundant; postpetiolar sternite with four pairs of curved and subdecumbent clavate hairs. Hairs on the gaster same as on workers. Dorsum of mesoscutum with coarse and irregular longitudinal rugae, forming fovea of different sizes. In lateral view, pronotum and propodeum with coarse and/or foveal punctuations, both sparse. Surface of metepisternum and metakatepisternum either smooth or slightly grainy, subopaque; dorsum of propodeal declivitous face covered by transversal rugae. In dorsal view, mesoscutum anteriorly rounded, slightly cuneiform and with smooth and shiny median carina; posterior margin slightly convex medially at the meeting with the scutoscutellar suture; notauli indistinct; parapsidal lines narrow, slightly curved; distinct (located in a slight

depression surrounded by rugae); parapsides shallow; tegulae subrectangular and apically rounded. Pre-scutellum narrow; axillae short, projected posteriorly, rounded and slightly depressed. Scutoscutellar sulcus well-marked, semicircular; broad and relatively shallow. Mesoscutellum transversely subrectangular, projected posteriorly, anterior limit concave. Dorsal face of propodeum strongly inclined; in lateral view, declivitous margin emarginate; projection as in the workers. In lateral view, anapleural sulcus anteriorly broad, smooth or subopaque, with a submedian transverse carina. Gaster with shiny band on the anterior portion of the sternite of first segment. Forewings type 2; hindwing with five submedian hamuli.

Intercastes: *Holotype*. Weber#140. Ocelli present, fully developed. In dorsal view, mesoscutum clearly delimited, although shorter than on conspecific gynes. Subalar area vestigial, residual tegula and axillary sclerite partially covered by the integument. Wing fossae present. Metanotal suture broad, carinate. Metanotal strip present, scutellum rudimentary.

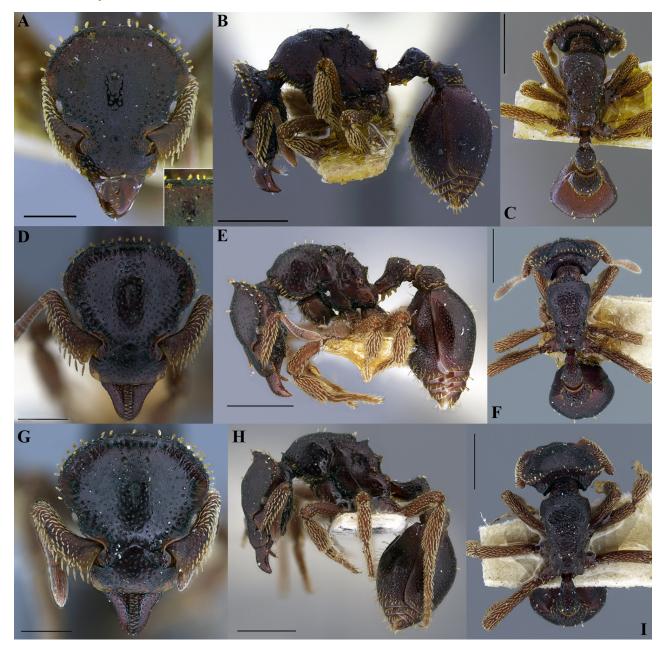


FIGURE 19. *Basiceros militaris*, type-series (all intercastes)—holotype (AMNH, Trinidad & Tobago: Nariva Swamp) and paratypes (MCZ 28746, same locality as holotype); A, D, G. full-face view, B, E, H. lateral view, C, F, I. dorsal view. Inset on A highlights ocelli. Scale bars: A, D, G = 0.5 mm, others = 1 mm.

Paratype Weber#139, MCZ 28746. Lateral ocelli present, fully developed, median ocellus slightly covered by integument. In dorsal view, mesoscutum vestigial; although fairly delimited, shorter than on conspecific gynes. Subalar area vestigial, almost imperceptible, presenting residual tegula partially covered by the integument. Directly below the tegular residue, slightly spiniform projection present, with globular setae on its apex. This same structure is not present on true gynes, although gynes have a prominence bearing setae under their tegulae. Simple setae over the tegulae can be observed in this paratype, same type of pilosity present on the anterior wing fossae of gynes. Metanotal suture extremely broad. In profile view, epicnemial fossa broad, triangle-shaped, pointing posteriorly. Anterolateral region of propodeum, where it meets the metanotal suture, with flap, apparently a metanotal strip. Midportion of mesonotum slightly concave, due to the presence of a vestigial scutum.

Paratype Weber#140.1, MCZ 28746. Head with complete and developed ocellar triangle. Left ocellus appears to be slightly cover by the integument. In dorsal view, mesoscutum clearly delimited, although shorter than on conspecific gynes. Transscutal articulation present. Scutoscutellar sulcus not integrally developed, but presenting a medial carina and irregular foveae typically found on true gynes. Parascutal flange vestigial. Prescutellum indistinct, only recognizable by margin lines. Specimen was probably brachypterous, as the whole wing apparatus is somewhat present, including tegular rudiments. On the right side, pair of specialized hair found on the parapsides of gyne, in the same position. On the left side, only one hair present. Hair on the right side of the specimen on what would be the axilla, the latter undeveloped. Scutellum present, although smaller than on conspecific gynes. Wing fossa developed, with setae similarly as on gynes. The spiniform projection of Weber#139 also present, near the anterior tegula. Hindwing on right side of this specimen glued to specimen's body, short and rudimentary. Propodeal projection more developed than on Weber#139, narrow metanotal arc present.

Other intercaste. Several, from worker-like specimens, with:

- slightly bigger compound eyes;
- presence of only the median ocellus, minute and concealed under the integument;
- vestigial mesoscutum and few other modifications on mesosoma;

to gyne-like specimens, with:

- bigger compound eyes;
- all ocelli developed, especially median;
- mesoscutum present, although undeveloped;
- wing fossae and rudiments (i.e. brachyptery);
- transscutal articulation;
- metanotal suture.

Male (first description) (n=1). HL 0.93, HW1 0.85, HW2 0.95, MdL 0.40, SL2 0.20, PDL 0.10, A3L 0.38, AFL 0.55, EL 0.31, EW 0.25, LOD 0.10, MOD 0.08, OOD 0.34–0.35 ML 1.48, MSL 0.78, MSW 0.75, MLL 0.25, MLW 0.48, MfL 1.21, MtL 0.83, PH 0.25, PL 0.70, PW 0.29, PPL 0.38, PPW 0.40, GL 1.50, GW 1.05, TL 5.38, CI 91, CS 0.89, MCI 43, SI 23, ESI 156, SAI 53, SAI2 36, EI1 0.63, EI2 89, MTI 96, MLI 190, MFI 70, PTI 280.

Size slightly smaller than conspecific gyne. Black coloration; bright portion of mesoanepisternum dark brown; coxae brown, brown to yellowish appendages. Distal portion of mandibles ocher. Wings dark brown. Mandible dorsa with long fine yellow hairs, semierect to subdecumbent, slightly longer on mandibular apex. Head with two main types of hair: medium, yellow and fine, subdecumbent—primarily on the frontal disc of clypeus; long and whitish to yellowish, sometimes with a curved apex and along the genal carina, on vertexal margin and ventral surface. The second hair type is widely present throughout the body: on the dorsum of the mesosoma, waist and gaster, especially long on the ocellar region, on the procoxae and petiolar dorsum. Antennomeres with short yellowish appressed setae. Legs with medium yellowish subdecumbent to decumbent setae. Subdecumbent to decumbent white and short hairs on the anterior half of the mesokatepisternum and procoxae dorsa.

Body uniformly punctuate-reticulate, small changes present on sculpture diameter and degree of impression. Apical portion of mandibles smooth and shiny. Irregular longitudinal rugae present on the neck and faintly on vertexal margin close to the occipital carina. Dorsum of mesoscutellum, metakatepisternum, and propodeum strongly

rugose. Mesoanepisternum slightly darker, smooth and very shiny over a little more than half its length; posteromedian portion of mesokatepisternum smooth and shiny. Dorsolateral rugae present on the anterior portion of petiolar node.

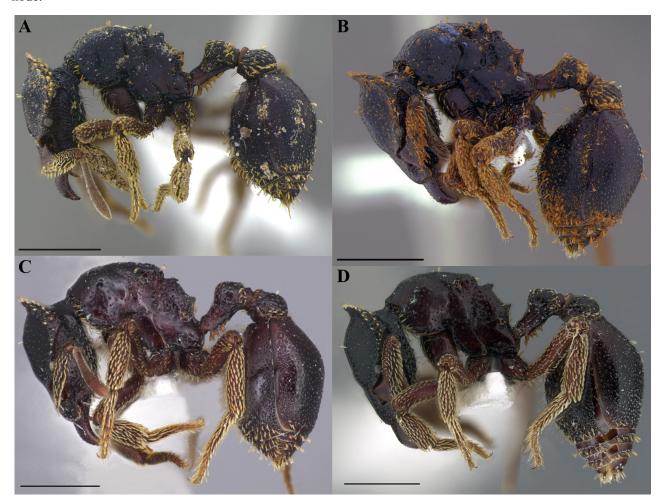


FIGURE 20. *Basiceros militaris*, lateral view of intercastes. A. (MZSP) Brazil: Rondônia, B. (MZSP) Brazil: Pará, C. (MCZ 534522) Trinidad & Tobago: Arima Valley, D. (MCZ) Trinidad & Tobago: St. Andrew, Scale bars: 1 mm.

Head subpiriform; in full-face view, top with median triangular crest just above the ocelli; occipital carina wide and lamellar, medially concave. Palp formula 1,1; palpi slightly intumescent and flattened on its apical half; maxillary palp appearing to be slightly larger and wider than the labial. Mento narrow and triangular. Stipes subrectangular. Labrum elongated; distal margin bilobed; median cleft extensive; approximately ten long and erect setae present. Mandibles triangular, curved towards their apexes; masticatory margin with 11 triangular teeth of similar size. Clypeus with central disc convex, slightly elevated; anterior margin lamellar and slightly concave. Postgenal carina present. Linear longitudinal carina, smooth and shiny; right after the supraclypeal region and extending posteriorly to the median ocellus. Antennal arch expanded as swollen posterolateral lobe, completely hiding the antennal bulb in full-face view. Pedicel longer than wide, third antennomere about three times longer than pedicel. Large globular eyes protruding from cephalic capsule. Ocelli caramel-colored, projected.

In dorsal view, mesoscutum cuneiform, elongated anteriorly. Smooth and shiny carina present on the anteromedial region of mesoscutum, extending near the dorsal margin. Notauli V-shaped, wide and extending to median region of transscutal suture, making it discontinuous. Transscutal suture sloping medially, median portion relatively indistinct. Parapsidal lines smooth and shiny; slightly depressed, curved on the anterior portion, subparallel and slightly sinuous on its median portion; apexes wider. Parapsides oval. Axillae long and projected, strongly curved posteriorly; hook-shaped, with curved posterior margins. Anapleural sulcus broad, strongly impressed—mesoanepisternum significantly elevated to mesokatepisternum; scrobiculate. Scutoscutellar suture smooth and deep, with transversal carina. Mesoscutellum subrectangular; posteromedian depressed; posterior margin strongly concave and depressed. Metanotum with posterior margin lamellar. Propodeal projections short, laminar and obtuse. Propodeal

lobes auricular. Calcar of strigil short and pectinate. Tarsal claws simple; arolia present, short. Petiole claviform; in dorsal view, petiolar node round and petiolar spiracle projected; subpetiolar process with anterior spiniform projection with apex slightly curved forward. Postpetiole approximately half the length of petiole in lateral view. Wings with six submedian hamuli.

Larva (adapted from Wheeler & Wheeler 1955). Body moderately broad; larger diameter on abdominal somite V and VI. Thorax and two first abdominal segments strongly curved ventrally; dorsal profile C-shaped. Anus ventral. Wing and leg trace present. Spiracles minute, mesothoracic slightly wider than the others. Integument of ventral surface of thorax and abdominal somites I and II spinose. Pilosity dense and uniformly distributed, of two types: short (about 0.19 mm), flexuous, denticulate, without alveolus and articular membrane; long (about 0.32 mm), curved or flexuous, denticulate, with alveolus and articular membrane. Cranium vaguely subhexagonal in full-face view; occipital margin weakly impressed in median region; clypeus protruding. Antennae minute, with three sensilla, each with a spinule. Labrum bilobed, twice as wide as long; ventral margin with two continuous sensilla and numerous long spinules. Mandibles heavily sclerotized, somewhat long and narrow, slightly curved medially; apical tooth stout, slightly curved and apically round; two moderately stout teeth projecting inward from the basal margin; short rows of minute spinules present on the basal surface. Maxillae with lateral projection into which the maxillary palp is inserted; apex parabolic and spinose containing the galea, short rows of long spinules; palp digitiform with one lateral sensillum (spinulate) and four apical ones (two encapsulated and two spinulate); galea digitiform with two apical sensilla. Labium large, surface spinose; spinules arranged in short, subtransversal rows; labial palp protruding, with five apical sensilla (three spinulate); sericeous gland with a pair of tiny sensilla on each side; opening transversal. Hypopharynx spinose.

Etymology. From Latin, "militaris", relating to soldiers or war, military service, warrior. Dr. Gustav Mayr probably named this species in reference to the clavate hairs present on the vertexal crest of this taxon, which refers to the top of helmets of some of the Roman legionnaires. An example is the Praetorian Guard (soldiers in charge of protecting the *praetorium*, the central part of the camp of a Roman legion where the officers were installed), whose clothing included a helmet with a crest crowned with horsehair.

Comments. Dietz (2004: 60) mentions that among the gynes he examined, one had alterations in the mesosoma, with flight-associated sclerites reduced, forewing insertion area absent, and an extensive dorsal flange occupied by the pronotum. Based on this, Dietz then conjectured that it could be an ergatoid gyne. During the present study, several intercaste specimens of *B. militaris* were examined, from specimens with minor changes—mesoscutum present as an impression line and slightly larger compound eyes—to specimens with aberrant morphology, presenting a mesoscutum and mesoscutellum, though not fully developed; wing insertions—in general, with thick setae on the bottom of these; and median and/or lateral ocelli.

In his description, Weber (1950) mentions the presence of ocelli in the worker, and although the figure presented by Weber (*op. cit.*, Fig 1) is mostly schematic, it allows the recognition of a median ocellar impression. In the same publication, the outline of the mesosoma in lateral view allows the recognition of mesoscutal rudiments and a metanotal flange, characteristics absent in the "true" workers of this species. In the generic diagnosis of *Aspididris*, Weber (1950) mentions that the worker is "similar to female except for reduced ocelli and thoracic sutures". To the gyne description, Weber adds that it does not have wings and the ocelli are either vestigial or absent, which does not happen with true reproductives of *Basiceros*. Furthermore, flight-associated mesosomal sclerites—integrally present in gynes—are not mentioned in the description. Weber's worker description supports that individual as an intercaste, which was not recognized at that time. The description mentions "ocelli vestigial or absent except for a slight pit marking the anterior ocellus. Thorax with sutures suggesting those of female but in reduced and fused form, especially the promesothoracic sutures" and the examination of the type-series demonstrates that both the holotype and paratypes are intercastes. Interestingly, Brown & Kempf (1960) did not have access to the holotype and only examined one of the paratypes. Although they have described "ergatoids" for other species of the tribe Basicerotini, they do not mention that paratype.

Distribution. Central and South America. Brazil, to Mato Grosso. A picture from Dr. Mark Moffett was found while searching for references linked to *B. militaris* (http://www.mindenpictures.com/cache/pcache/00093908.jpg), with Costa Rica as the location. It would be the first record for this species in Costa Rica, and since there was no way to confirm it, this potential record was not included in this study. That depicted specimen has median and lateral ocelli and a mesosoma lacking fully-developed alar sclerites, undoubtedly features of an intercaste.

Natural history. As mentioned in "Comments", this species has intercaste gynes. A mosaic of intercastes was

uncovered in material examined from Trinidad & Tobago, Guyana, and Brazil (states of Pará and Rondônia) product of different collection events. In some cases, true gynes and intercastes were collected from the same colony (Fig 20), suggesting a high degree of phenotypic plasticity within *B. militaris*. Weber (1950) commented that the holotype was one of "several of the same species that were found slowly stalking over the forest floor", suggesting that intercastes also forage outside of the colony. Additionally, although the reproductive strategy of this species is unknown, examined material revealed potential polygyny, with up to three complete and dealate gynes in the same sample. According to Molet *et al.* (2012) and Peeters (2012), the genetic accommodation (via positive selection) of such morphological mosaic configures an important reproductive strategy for colony maintenance, since intercastes act both as reproductives and workers within the colony, and this modularity might offer an evolutionary advantage to the species. Interestingly, most intercastes for this species were either collected at disturbed (e.g., impacted mining sites) or insular (i.e. Trinidadian areas) environments. Plus, the occurrence of these phenotypes could also be parasite-induced (e.g., by mermithid nematodes) (Laciny 2021), resulting in the mosaic of morphologies observed for the female caste of *B. militaris*.

Material examined. BRAZIL: Acre: Projeto de Assentamento Agroextrativista (PAE) Chico Mendes, -10.883333 -68.35, viii–ix.2010, Miranda et al. cols. (1 worker) [INPA]; Maranhão: São Francisco do Brejão, 05°17'19"S 41°15'1.07'W, 01–09.vi.2005, R. R. Silva & Feitosa R. M. cols. (3 workers, 3 gynes) [MZSP]; Mato Grosso: Alta Floresta, no collector, 24.x.1980 (1 worker); Alta Floresta, 10° 47'S 56°49'W, 24.iv.1999, H. Vasconcelos col. (1 worker) [UFU]; same data, 2 workers [MZSP]; same locality, Frag. 29-C7, 60°33'78"E 89°00'26" (probably GPS mistake), 12.v.2008, Castuera L. O. col. (1 intercaste); Canarana, 13°04'S 52°23W, vi.2013, M. Bicalho & V. Ribeiro cols., UFV-LABECOL 121 (1 worker), UFV-LABECOL 122 (1 gyne) [UFV]; Pará: Carajás, 6°03'10"S 50°15'34"W, 09.ix.2011, C. T. Lopes & R. I. Campos col., (1 worker) [UFU]; Melgaço, Caxiuanã, Estação Científica Ferreira Pena, 1°43'29.42"S 51°25'47.23"W, 26.x.2003, A. Y. Harada e Equip. cols. (1 worker) [MPEG], same data, 1°44'0.96"S 51°30'37.97"W, 29.iv.2005, A. Y. Harada e Equip. cols. (19 workers, 3 gynes, 5 intercastes) [MPEG]; Serra Norte, Est. do Mang., 15.v.1994, (1 gyne) [MPEG]; Serra Norte, Carajás, vii–viii.1985, UNICAMP—Ecol-Campo I, Brandão and Benson col. (3 workers, 1 gyne); Parauapebas, 21.ii.2010. A. A. Matias col. (1 gyne) [INPA]; same locality, 25.iv-02.v.2008, Casa dos Hóspedes, Garagem e Zoobotânico, 06°02'54" a 06°03'4"'S 50°04'55"W, R. R. Silva col. (4 workers, 3 gynes, 4 intercastes) [MZSP]; same locality, 6.03359° a 6.03406°S 50.11623° a 50.11635°W, 666–681m, C. Lopes and/or T. R. Schultz cols. (6 workers) [USNM]; Portel, Rio Acuti Pereira, 2°03'53.5"S 50°39'06.5"W, 22.x.2015 Siqueira, ELS & Eq. col.; (1 worker) [MPEG]; Rondônia: Porto Velho, Área Caiçara, 09°25'39"S 64°46'59"W, 27.ii-11.iii-2010, R. R. Silva & Feitosa R. M. cols. (4 workers, 1 gyne, 5 intercastes) [MZSP]; 09°26'39"S 64°47'46"W, 04–17.i.2011, R. R. Silva & R. S. Probst cols. (2 workers, 3 gynes) [MZSP]; 09°26'30" 64°47'16"W, 27.iii–09.iv.2011, R. R. Silva & Albuquerque E. Z. cols. (4 workers); S 09°26'13"S 64°48'04.4"W, 18–29.vi.2011, E. Z. Albuquerque & L. F. Silva cols. (1 worker) [MZSP]; Área Mutum, metragem 150m, 09°26'30"S 64°47'16"W (Caiçara data?), 09°36'27"S 65°02'55"W, 27.ii–11.iii-2010, R. R. Silva & Feitosa R. M. cols. (1 worker) [MZSP]; 09°36'27"S 65°02'55W, 04-17.i.2011, R. R. Silva & R. S. Probst cols. (4 workers) [MZSP]; 09°35'07"S 65°04'15W, 27.iii-09.iv.2011, R. R. Silva & Albuquerque E. Z. cols. (1 worker) [MZSP]; Área Abunã, 09°35'46"S 65°20'56"W, 27.iii–09.iv.2011, R. R. Silva & Albuquerque E. Z. cols. (3 workers, 1 gyne) [MZSP]; Jaci Paraná, km 3.100, 27.1.2013, no collector (1 worker) [INPA]; UHE de Jirau, 21.x.-02.xi.2010, Sanhudo et al. cols. (1 worker) [MZSP]. ECUADOR: Yasuni National Park: Tiputini Biodiversity Station Lat. -0.638063 Long. -76.149834, xi.2002, K. A. Jackson & D. J. Inward cols. CASENT0280778 (1 worker) [CAS]. FRENCH GUIANA: Saint-Laurent-du-Maroni: Saul, Itoupe. Lat. 3.03326 Long. -53.0962, 11.xi.2014, 577m, J.Orivel & M.Fichaux, ECOFOG-IT14-0437-34 (1 worker) [EcoFog]; Saint-Laurent-du-Maroni: Saul, Itoupe. Lat. 3.022174 Long. -53.10685, 14.xi.2014, 529m, J.Orivel & M.Fichaux, ECOFOG-IT14-0799-43 (1 dealate gyne) [EcoFog]. GUYANA: Dycimbe Forest: 5°17.76'N 54°59.63'W (GPS coordinates fall on Suriname), 06.x.2002, Ted Schultz et al. cols. (2 workers, 1 gyne) [USNM]; between Cuyuni e Maranui Rivers, 08.ix.1935, Weber col., n. NA Weber 358.1 (1 worker) [MCZ]; Iwokrama Forest Reserve: Mabura Hill, camp at end of road from Georgetown to Letham Road, 5°9.313'N 58°41'.982W; 29.X.2012, LaPolla et al. cols. (2 workers) [USNM]; Kanuku Mountains: Moco-Moco Falls, 3°17'297'N 58°38'376'W 224m, Ted Schultz et al. cols. (1 gyne) [USNM]; Rupununi, near Kamoa River, near Kamoa Camp, 1°32.786'N 58°49.929'W, 394m, 22.x.2006, J. Sosa-Calvo col., TRS 061022-LS08 (6 workers) [USNM]. PERU: Madre de Díos: Tambopata Research Center, Lat. -13.14535 Long. -6961483, 276m, x.2000, D. Feener col., TRC-S12-R1C04 (1 worker) [JTL]. TRINIDAD & TOBAGO: no locality, no collector, MCZ 534522 (2 workers, 1 intercaste) [MCZ]; Aripo Village: 1 km SSW, 10.669° -61.232°, 12.ix.2003,

J. Wetterer col., n. 506334 (1 worker) [MCZ]; Mt. San Benedict: 10°69'N 61°40'W, 26.xi.1999, R. R. Snelling col., n. 99.176/LACM 326560 (1 gyne) [LACM]; St. Andrew: Arena Forest Reserve, 06.iii.1992, S.P. Cover col., n. 534386 (2 workers, 1 gyne, 3 intercaste, 1 male) [MCZ]; same data, n. 534385 (1 intercaste, 1 male) [MCZ]; Co. Arena Forest Reserve E San Rafael, 100', 05.iii.1992, S. P. Cover col. (4 workers, 2 gynes) [LACM]; St. George: Arima Valley, co. Aripo Ridge, 18.v.1988, S.P. Cover col., n. (3 workers, 1 gyne, 2 intercastes) [MCZ]; same data (2 workers) [LACM]; Victoria Mayaro Research, 2km N of N gate, 10.157° -61.064° (WGS84), 3.xi.2003, J. Wetterer col., n. 506035 (1 gyne) [MCZ]; Tunapuna-Piarco: Mt. S. Benedict, 10.73145 -61.30609, 620m, 07.vi.1993, S. B. Peck, J. Kukalova-Peck cols. (FMNH 095851) (1 worker) [FMNH], (FMNH 095852) (1 gyne) [FMNH]. VENEZUELA: Bolívar, talud SSE Amarawaí tepui, 5°54' N 63°03'W, 470m, 2.v.1980, J. Lattke col. (2 workers, 3 gynes) [MZSP].

Basiceros scambognathus (Brown 1949)

(Figs 21–22, 32)

Creightonidris scambognatha Brown 1949: 89 (gyne): Brazil.

Feitosa et al. 2007: 23 (worker, male).

Meranoplus singularis Smith 1858 (in part): 195, Plate 13, Figs 6–7 (probably the gyne of *B. scambognathus*, dorsal view and antenna).

Ceratobasis singularis Smith 1860 (in part): 78, Plate 4, Figs 12–13 (probably the gyne of *B. singularis*, head in full-face view and forewing).

See also Brown, 1949: 91 and Brown & Kempf, 1960: 178

Combination in Basiceros: Feitosa et al. 2007: 19.

Type material. BRAZIL: Goiás: Campinas (current West Zone of Goiânia), x.1935, Schwarzmaier col. (one gyne—holotype) (examined).

Diagnosis. Mandibles bizarre, subtriangular, apical portion strongly curved ventrally, oblique basidorsal sulcus present. Clypeus and head dorsa densely covered with decumbent squamiform hairs. Anapleural sulcus present, mesoanepisternum depressed.

Description. *Worker* (n=2): HL 1.37–1.39, HL2 1.37–1.40, HW1 1.12–1.15, MdL 0.59–0.65, SL1 0.84–0.87, SL2 1.03–1.05, PDL 0.11–0.12, A3L 0.03, AFL 0.36–0.40, FuL 0.97–1.00, EL 0.08–0.13, EW 0.06–0.09, ML 1.62, MfL 1.23–1.27, MtL 1.03–1.05, PH 0.33–0.40, PL 0.72–0.75, PW 0.28–0.34, PPL 0.50–0.56, PPW 0.50–0.59, GL 1.80–1.93, GW 1.00–1.21, TL 6.65–6.87, CI 801–84, CS 1.25–1.26, MCI 42–47, SI 89–93, ESI 7.46–12.12, SAI2 257–287, EI1 0.11–0.17, MFI 88–93, PTI 177–228.

Medium size comparatively. Coloration reddish-brown to dark brown; appendages lighter, chocolate to brown. Mandibles generally lighter than predominant body coloration; dorsa covered by obsolete and sparse piligerous punctuation; basal portion with clavate pilosity suberect to subdecumbent; mandibular apex with medium yellowish setae. Basimandibular seta present, narrow and erect. Clavate suberect hair on the dorsum of each stipe. Anterior margin of labrum with long filiform hairs. Clypeal dorsum densely covered with decumbent squamiform hairs. Head with basal layer of hairs with same morphology as clypeal pilosity, slightly more sparse; erect and lightly clavate pilosity as follows: a pair of isolated hairs on the posterior region of frons, close to the median sulcus of vertexal margin; a pair of hairs present or not in front of eyes, a pair near the posterior limit of eyes; six pairs on vertexal corners and eight pairs starting from the superficial emargination projected above the eyes until the vertexal margin. Mesosoma, petiole, postpetiole, and first gastral sternite with basal pilosity short, appressed to decumbent, formed by squamiform hairs. Erect to suberect pilosity on mesosomal dorsum, posterolateral portion of pronotum and gastral segments II–VII relatively abundant, clavate, from whitish to yellowish; pygidium with short, filiform, suberect hairs. A pair of clavate hairs on the anteroventral margin of the postpetiolar sternite. Antennal scapes with whitish to yellowish decumbent pilosity, squamiform; funiculus covered by short, appressed, and yellowish setae. Legs with decumbent and yellowish pilosity, squamiform, becoming thinner towards the tarsus.

Surface of antennal scrobes rugo-punctuate; head dorsum with irregular rugae forming fovea of different sizes, internally punctuate. Pronotum strongly punctuate-reticulate on the lateral portion; anterior portion rugose, punctuate between rugulae spaces. Surface of meso- and metapleura, petiolar node, postpetiole, and gaster slightly shiny and abundantly punctuate-reticulate. Procoxae punctuate-foveate.

Head oblong; posterolateral corners round; vertexal margin concave medially. Vertexal crest present as a ca-

rina-shaped lateral lift, close to the beginning of lateral convexity of head. Mandibles aberrant and subtriangular; external margin of basal portion subparallel; masticatory margin straight bearing 14–16 teeth, apical tooth slightly broader and longer; apical portion of mandibles strongly curved ventrally to the midpoint of their length; basal angle acute; basal portion of mandibles slightly convex in lateral view; in full-face view, oblique sulcus present on basal portion, extending from the masticatory margin to at least half of the lamina; with mandibles closed, these opposing sulci converge, with the aspect of a circumflex accent, posteriorly directed. Frontoclypeal surface convex; anterior margin concave. Tumosity present in the central portion of the head dorsum, circular-shaped and with deep concavity, giving it a ring-like appearance. Eyes inserted on the dorsal margin of antennal scrobes, these deep and extending posteriorly to the vertexal margin. Scape flattened and with a biangulate basal lobe, margin between angles concave; external margin lamellar and strongly crenulated. Antennal apical segment longer than the sum of four anterior antennomeres.

Mesosoma robust; in lateral view, promesonotal profile slightly convex dorsally; metanotal suture strongly impressed, extending as the anapleural sulcus, transversely rugose-costulate. Mesopleura flange transversely scrobiculate, sculpture short; flange reaching a deep and digitiform epicnemial fossa. Propodeum posteriorly oblique; propodeal projections short, triangular and slightly upwards, connected by strong transverse carina; propodeal spiracle round, spiracle relatively projected laterally side and directed posteriorly. Petiole nodiform, peduncle short and shorter than the petiolar node; node prominent and bulging, curved caudad. Subpetiolar process consisting of series of sharp denticles. In lateral view, postpetiole slightly longer than length of petiolar node; slightly flattened, dorsal face slightly projected on its posterior half, posterior margin bulged at the meeting with gaster. In dorsal view, petiolar node slightly oblong, ogive-shaped; postpetiole subtrapezoidal, as long as wide, lateral margins diverging posteriorly and narrowed so that gaster is widely connected to postpetiole. Gaster oval; anterior margin concave; first gastral sternite visibly longer than tergite. Metabasitarsus conspicuously long, longer than metatibia. Tarsal claws simple.

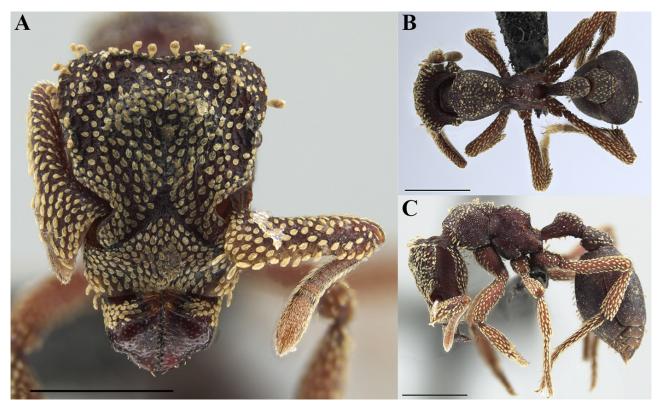


FIGURE 21. *Basiceros scambognathus*, worker (ANTWEB1032521, Brazil: Espírito Santo); A. full-face view, B. lateral view, C. dorsal view. Scale bars: A = 0.7 mm, B–C = 1 mm.

Gyne (n=3). HL 1.34; HL2 1.45–1.47, HW 1.28, MdL 0.66–0.69, SL1 0.91–0.94, SL2 1.09–1.13, PDL 0.13, A3L 0.03, AFL 0.38, FuL 1.03–1.06, EL 0.28, EW 0.25–0.27, LOD 0.08–0.09, MOD 0.08, OOD 0.38–0.39, ML 1.94–2.03, MSL 0.94–1.06, MSW 1.00–1.06, MLL 0.34–0.38, MLW 0.50–0.59, MfL 1.31–1.38, MtL 1.06–1.13, PH 0.47–0.50, PL 0.84, PW 0.38–0.41, PPL 0.59–0.63, PPW 0.61–0.69, GL **2.63–2.66**, GW 1.50–1.53, TL 8.06–8.13,

CI 95, CS 1.31, MCI 48–51, SI 85–87, ESI 25–25, SAI2 280–300, EII 0.40–0.42, MTI 100–106, MLI 145–158, MFI 93–97, PTI 168–180. (In bold: gaster dilated on all measured gynes; measurement was corrected by subtracting pleura range from measured value).

Coloration similar or slightly darker than conspecific worker; slightly larger size; mesosomal sculpture more developed. Ocelli present; median ocellus inserted at the posterior limit of the circular concavity on frons; median ocelli inserted close to the median vertexal sulcus. Head pilosity as on conspecific workers; more abundant on frons. Mesosomal pilosity as follows: basal pilosity on pronotum as in the workers and present in the same way, only slightly sparser on mesoscutum and mesoscutellum dorsa; erect and clavate hairs present in the following configuration: two clavate hairs on the central portion of pronotum; 20–22 hairs arranged on the dorsum of mesoscutum; two hairs on each parascutal flange; 4–6 hairs on mesoscutellum dorsum, 2–4 hairs on metanotum. Other pilosity as presented in the conspecific workers. Sculpture very similar to conspecific workers, only stronger marked on some portions, such as the petiole and postpetiole. Mesoanepisternum, meso- and metakatepisternum with smooth and shiny or matt portion, variably (sometimes only part of mesoanepisternum, only the posterolateral corner of the mesokatepisternum or the entire portion of metakatepisternum; never all these portions are smooth and shiny or matt at the same time. Forewing type 2; hindwing with five submedian hamuli.



FIGURE 22. *Basiceros scambognathus*, gyne (MZSP, Brazil: Minas Gerais); male (CASENT0914889, Brazil: Rondônia; images by Michele Esposito [CAS], edited); A and D. full-face view, B and E. dorsal view, C and F. lateral view. Scale bars: A = 0.5 mm, B–C = 1 mm, D = 0.2 mm, E–F = 0.5 mm.

Male (n=2). HL 0.94–1.12, HW1 0.90–1.00, HW2 1.13–1.19, MdL 0.42–0.47, SL2 0.25–0.28, PDL 0.09–0.12, A3L 0.34–0.37, AFL 0.59–0.65, EL 0.38–0.41, EW 0.34–0.37, LOD 0.09, MOD 0.09, OOD 0.34, ML 1.67–1.90, MSL 0.92–1.03, MSW 0.86–1.09, MLL 0.28–0.31, MLW 0.50–0.59, MfL 1.25–1.38, MtL 0.97–1.00, PH 0.31–0.36, PL 0.69–0.78, PW 0.31–0.36, PPL 0.43–0.48, PPW 0.53, GL 1.50–1.59, GW 1.15–1.31, TL 5.65–6.35, CI 88–96, CS 0.92–1.06, MCI 41–45.00, SI 25–31, ESI 133–162, SAI 66–81, SAI2 38–47, EI1 0.73–0.78, EI2 80–84, MTI 93–106, MLI 177–190, MFI 72–72, PTI 217–220.

Coloration dark brown, with areas slightly ferruginous (e.g., propodeal lobes, lateral of postpetiole, and first gastral tergite and sternite). Appendages yellowish to light brown. Pilosity primarily composed of long filiform whitish hairs densely covering the body, mainly head, dorsum of promesonotum, and gaster.

Body sculpture mainly punctuate-rugose, exception to the mesoanepisternum and metakatepisternum, with portions that are variably smooth and shiny or subopaque; head covered with irregular rugae; mesosoma with irregular rugae on dorsal surface of promesonotum, in the lower portion of the mesopleuron, lateral of propodeum and petiolar peduncle; other integument covered by coarse reticulate punctuations, mainly on the lateral surfaces of the mesosoma, petiole and postpetiole. Gaster densely punctuate-reticulate, punctuations fine.

Mandibles subtriangular, as long as wide. Masticatory margin with 10 conical teeth, third and fourth teeth from the base slightly broader than others; apical tooth acute, conspicuously separated from the subapical and projected; external margins of mandibles strongly convex on the basal portion and apically straight, apex almost concave. Head ovoid. Ocelli large and positioned on cephalic crest close to occipital margin; median ocellus inserted before a transversely rugose cleft; lateral ocelli with interocellar rugae. As for other Basiceros males, a deep concave sulcus is present along the frontoclypeal region. Central disc of clypeus convex, central portion raised forming a distinct circular area; anterior margin and lateral portions slightly depressed. Anterior clypeal margin smooth and slightly concave. Eyes globular, large. Antennal fossa shallow. In dorsal view, mesoscutum slightly cuneiform anteriorly, as wide as long; anterior margin with smooth and shiny median carina, extending along dorsum of mesoscutum to the point of convergence of notauli, these lightly impressed. Scutoscutellar suture broadly concave. Parapsides oval, slightly deep. Parapsidal lines smooth and shiny. Scutoscutellar sulcus broad and deep, transversally costulate. In dorsal view, mesoscutellum transversely rectangular, longitudinally divided by a median sulcus. Propodeal projections round, propodeal lobes auricular and slightly narrow. Petiole and gaster as in conspecific females. Subpetiolar projection consisting of only a small triangular lamella, inserted just before the beginning of node, or by this lamella followed by 1–2 denticles; petiolar spiracle projected laterally. Forewing type 2; hindwing with five submedian hamuli.

Larva. Unknown.

Etymology. From Greek, "skambos", curved, arched + "gnathos", mandible. Dr. William Brown Jr. must have named this species based on the aberrant shape of its mandibles, whose apical region is conspicuously facing the ventral region.

Comments. Basiceros scambognathus has undergone several taxonomic changes since its description. Smith (1858) describes the species Meranoplus singularis based on the study of a worker and a winged gyne. In 1860, Smith recognized that M. singularis corresponded to another genus and described Ceratobasis to include this taxon based on its peculiar morphology. However, the gyne described two years prior was not compared with the gyne described by Smith in 1858 (Brown 1949) and continued to be considered to belong to B. singularis, a situation corrected through the establishment of the genus Creightonidris by Brown (1949). In their review of Basicerotini, Brown & Kempf (1960) consider Creightonidris as a valid genus, based primarily on its mandibular morphology, although they recognize the close relationship of this genus to Basiceros. Dietz (2004) suggests the combination of Creightonidris in Basiceros based on the comparison of males of this first taxon, unknown until that moment. This combination is formally presented by Feitosa et al. (2007), whose worker description corroborated Dietz's proposal. It is interesting to mention that Dr. Thomas Borgmeier placed a label on the specimen designated as holotype before its description, classifying it as "Basiceros n. sp."

In the description of the holotype gyne, the measured value for TL is 7.4 mm; Brown & Kempf (1960) add an amendment to this measure, stating that this specimen presents the gaster dilated, adding around 0.4 mm to the total length. Examined workers varied on coloration, pilosity, and body size.

The phylogenetic reconstruction by Probst *et al.* (2019) suggests that *B. scambognathus* could be a cluster of putative species hardly differentiated based on the morphological information available at that time. That molecular reconstruction recovered males from three different locations in South America were clustered together, apart from two workers from the state of Rondônia, in Brazil. Additional collections highlight that subtle difference, and those two workers are here identified as *B. tumucumaquensis* **sp. nov.** Considering the known *Basiceros* males, the males of *B. scambognathus* have unique mandibular morphology, with the apical tooth narrow and projected, isolated from the other teeth on the masticatory margin; this tooth can vary in size, width, and be variably close to the subapical tooth. Additionally, they present the maximum degree of antennal torsion among all known *Basiceros* males.

Distribution. Brown (1949: 91) discusses the locality of the gyne erroneously associated to *B. singularis*, in the passage reproduced below:

"It was noted above that I consider this to be the same form Frederik Smith described 89 years ago as the female of *Ceratobasis singularis*, the only doubt stemming from certain differences in Smith's figures, which are

often inaccurate and vague. I do not know whether Ega [currently Tefé] is the proper locality for Smith's specimen, but seemingly it was taken somewhere in the Amazon Basin by the famous naturalist Henry Bates. Although Smith cautioned Bates, as he says, to keep good records and proper associations of the castes of one species, it appeared that Smith himself had a perverse genius for mixing up these same records and associations as few have ever done. Most of Smith's locality records bear little examination, and it is not safe to accept them too specifically for types. Many previous authors have flayed the same hide while themselves committing errors as grievous, so it is perhaps best to let Mr. Smith rest in peace while his detractors have their well-deserved turn."

However, later collections show that perhaps Smith was not mistaken. *Basiceros scambognathus* has a wide geographic distribution and there are scattered records in the Brazilian territory, from Minas Gerais (new records) to the Central and Northern States, in addition to French Guiana, Peru, and Venezuela. This species probably occurs in Suriname. New records for the present study are represented mainly by males collected in Malaise traps. Feitosa *et al.* (2007) mentions that the apparent discontinuity of distribution—in the form of scattered records—may reflect the use of inappropriate techniques for collecting this taxon, as aspects of its natural history are entirely unknown. This taxon was probably collected in southern Colombia (Dr. Benoit Guénard, University of Hong Kong, pers. comm.), but it was impossible to examine such material in the present work, so that record is not confirmed.

Souza & Delabie's (2013) geographic distribution model for *B. scambognathus* not only validated the previously known distribution for this taxon but also estimated new areas where the species could be found according to a probabilistic model (see Souza & Delabie 2013, Fig 1). According to the authors, it is unlikely for *B. scambognathus* to be found in areas where the model indicates a lower than 30% chance of occurrence. However, the model shows that the suitable ecological niche for *B. scambognathus* extends to the biogeographic provinces (*sensu* Morrone 2006) of Maracaibo, Magdalena, Ecuador and arid West, Choco, the western region of the Isthmus of Panama, the Gulf of Mexico, east of Central America, and the Lesser Antilles, and even to Trinidad & Tobago. Nevertheless, to date, there are no records for this last round of biogeographic provinces. Besides, the distribution model was not sensitive enough to predict the occurrence of *B. scambognathus* in Salvador (state of Bahia, Brazil) (Castilho *et al.* 2007) and showed a low probability of occurrence for SE areas of the state of Minas Gerais—for the present study, specimens from the municipality of Marliéria were examined. Souza & Delabie (2013) point out that the results obtained with potential geographic distribution models restricted to fundamental niches cannot be considered definitive since knowledge of the distribution of a given taxon must also include nesting information (including potential interspecific interactions), dispersal ability, and historical factors.

Natural history. *Basiceros scambognathus* is one of the most obscure taxa in terms of natural history. The aberrant mandibles of *B. scambognathus* likely reflect specific predatory behavior. Feitosa *et al.* (2007) mention that the first dealate gyne was collected in Uruaçu, State of Goiás, Brazil in 1995 (by CRFB) and kept in artificial conditions for a few weeks, with the only behavioral record mentioning the gyne having accepted termites as food. Unfortunately, most records for this species are of males or alate gynes, usually collected with flight-intercept traps, thus preventing inferences about nesting and foraging behaviors and potential interactions with other species.

Although workers recorded so far have been found in litter samples, it is important to mention that the laboratory-maintained gyne (see above) escaped its terrarium and was eventually found dead inside the fungus garden of an artificial leaf-cutter nest of *Atta sexdens* (Linnaeus, 1758) kept in the same laboratory. Feitosa *et al.* (2007) conjecture the possibility of *B. scambognathus* nesting inside *Atta* (or another fungus-growing ant) nests, partially explaining the difficulty of finding this species in nature.

Material examined. BRAZIL: Amapá: Amapari, Tucano 2, 08–10.xi.1993, A. Pena col. (1 male); same data, F. F. Ramos col. (2 males); same data, N. Bittencourt (1 male); same data, W. França col. (1 male) [MZSP]; Alagoas: Coruripe, 2.x.1978, F.M. Oliveira (1 headless male) [MPEG]; Amazonas: 30km W de Itaquatiara (Itacoatiara), Rio Urubu, 13.i.1981, Ginter Ekis col. (1 gyne) [MPEG]; same locality and data, Ekis & Davidson cols., MPEG03005219 and MPEG03005220 (2 males) [MPEG]; Estirão do Equador, Rio Javari, ix.1979, Alvarenga col. (1 gyne, 1 male) [MZSP]; N de Manaus, Reserva Florestal Adolfo Ducke, 22–26.xi.1966, no collector (4 males) [MZSP]; Reserva Florestal Adolfo Ducke, 28.xi.1981, J. A. Rafael (1 male) [MZSP]; same locality, 14.viii.1981, G. B. Farchild & J. A. Rafael (1 male) [INPA]; same locality, no collector, 08–13.vi.2005 (3 males) [MZSP]; Bahia: Maracás, Fazenda Maria Inácia, 24–29.xi.1990, Brandão, Diniz & Oliveira cols. (1 male) [MZSP]; Salvador, 11.viii.2001, J. R. Maia (2 workers) [MZSP]; same data (3 workers) [CEPEC]; same locality, i.1995, J. H. C. Delabie col. (1 gyne) [CEPEC]; Espírito Santo, near ReBio Córrego Grande, -18 201288 -39,881503, 21.iv–10.v.2017, 73m, JMC#0259, Safar N., Aquila C, Guimarães C. cols., ANTWEB1032518 (2 workers) [JTL]. Goiás: Campinas

(current Goiânia, West zone) Serra da Mesa, Colinas do Sul, 14°01'S 48°12'W, Silvestre, Dietz & Campaner cols. (1 male) [MZSP]; Jataí, xii.1972, F. M. Oliveira, n. 8911 (1 gyne) [MZSP]; Maranhão: Estreito, Fazenda Itaueras, 06°31'54"S 47°22'16"W, 12-22.iv.2006, Silva R. R. & Feitosa R. M. cols. (1 worker) [MZSP]; Mato Grosso: Sinop, 12°31'S 55°37'W, x.1974, Alvarenga & Roppa, n. 12551 (1 headless gyne); same data, n. 12552 (4 malesgold coated); same locality, M. Alvarenga col., n. 12517 (1 male), same data, n. 12307 (6 males), same data, n. 12306 (1 gyne—gold coated) [MZSP]; Vera ("Vila Vera"), x. 1973, M. Alvarenga col. N. 10253 (13 males) [MZSP]; same locality and data, CASENT0633289 (1 male) [JTL]; Minas Gerais: Marliéria, P. E. do Rio Doce, Trilha do Gambá, 19°46'75"S 42°35'38"W, 31.x-05.xi.2010, J. C. Almeida & G. Ide cols. (2 gynes, 1 male) [MZSP]; Pará: Belém, 26.ix.1987, Henry Harada (1 dealate gyne) [INPA]; Belém, Outeiro E. Bosque, 30.iv-03.v.1993, J. Dias & F. Ramos cols. (1 male) [MPEG], Igarape-Açú, i. 1949, Gonçalves col., CASENT0172825 (1 gyne) [MCZ]; Juruti, Alcoa, 13-18.xii.2007, 02°29'32.10"S 56°09'20.04"W, E. Monteiro-Santos, R.L. Trindade, Domingos Guimarães, L.A. Quaresma cols. (1 male) [MPEG]; Museu Paraense Emílio Goeldi, xii.1966, S. N. de Oliveira col. (2 males) [MZSP]; Paragominas, Faz. Cachoeira do Rio Vermelho, 18–21.i.1991, B. Mascarenhas col. (4 males) [MPEG]; same data, same locality, J. Dias col. (1 male) [MPEG]; same data, same locality, P. Tadeu col. (1 male) [MPEG]; Santarém Novo, Fazenda Jaburu, 07–09.i.1993, J. Dias col. (1 male) [MPEG]; Senador José Porfírio, right margino f Xingu River, 23–25.ii.2001, R. Santos & J. Dias cols. (5 males) [MPEG]; Vitória do Xingu, right margin of Xingu River, Ilha Taboca, 18–20.xii.2010, R. Santos & J. Dias cols. (17 males) [MPEG]; same locality, 22–24.xii.2010, same collectors (1 male) [MPEG]; same locality, primary forest, same date, same collectors (5 males) [MPEG]; Rondônia: 62 km S of Ariquemes, Fazenda Rancho Grande, 10°32'S 62°48'W, 12-22.XI.1991, E. M. Fisher col., CASENT0914889 (1 male) [UCDC]; 09°35'07"S 65°04'15"W, 04-17.i.2011, R. R. Silva & R. Probst cols. (1 worker) [MZSP]; M5—Metragem 400m, 27.ii–11.iii.2010, R. R. Silva & Feitosa, R. M. cols. (1 gyne) [MZSP]; Área Abunã, 09°35'07"S 65°03'13"W, 27.iii-09.iv.2011, R. R. Silva & Albuquerque, E. Z. cols. (1 worker) [MZSP]; 09°38'07"S 65°27'13"W, 27.iii-09.iv.2011, R. R. Silva & Albuquerque, E. Z. cols. (1 worker) [MZSP]; Roraima: Ilha de Maracá, Rio Uraricoera 18–29.vii.1987, J. S. Rafael, L. S. Aquino, J. F. Vidal & Elias Binda cols. (1 male) [INPA]; Tocantins: Paraña, Rio Ouro Fino, Serra Contenda, 12°56'03"S 47°57'42"W, 11.x.2004, R. R. Silva & B. H. Dietz cols. (1 gyne) [MZSP]. FRENCH GUIANA: Saül: Belvedere de Saül, 03°37'22"N 53°12'57"W, 27.x.2010, Vitrees C. A. A. P. & S. E. A. G. team col. (1 gyne) [DZUP]; Saül: Belvedere de Saül, alt. 326m, 03°37'22"N 53°12'57"W, 22.iii.2011 S.E.A.G. team leg. VPVO2 (2 gynes, 1 dealate and 1 with right forewing attached) [DZUP]. PERU: Loreto, Estación Jenaro Herrera, 04°53'55"S 73°39'00.4"W, 13–23.i.2011, Hymenoptera Course (1 male) [MZSP]. No data, no collector, gift from Barry Bolton, NHM 5974/CASENT0172317 (1 gyne) [ANIC].

Basiceros singularis (Smith 1858)

(Figs 23–25, 30)

Meranoplus singularis Smith 1858 (*in part*): 195, Plate 13, Figs 8–10 (worker; gyne probably of *Basiceros scambognathus*, see Brown & Kempf 1960: 175): Brazil.

Combination in *Ceratobasis*: Smith 1860: 78. Combination in *Basiceros*: Wheeler 1916: 9.

Wheeler 1916: 9 (gyne);

Kugler 1978: 438, Figs 43–49 (sting apparatus)

Brown 1974: 140 (male diagnosis).

Wheeler & Wheeler 1977: 599, Fig 9 (Basiceros sp. larva = B. singularis)

Wheeler & Wheeler 1980: 537, Fig 4 (larva).

Type material. BRAZIL: Amazonas: Ega (=Tefé): no data, no collector (*Meranoplus singularis*, one worker—lectotype) [MNH] (examined).

Diagnosis. Very similar to *B. manni*. Comparatively large; coloration light brown to brown. Double layer of specialized pilosity distributed as a basal layer of subdecumbent plumose hairs and a layer of fine erect and clavate hairs. In general, specimens densely covered with soil and/or litter particles. Clypeomandibular space ample; anterodorsal region of mandibles and clypeus dorsum usually with squamiform pilosity. Petiole claviform, elongate and with a depressed node. Anterior margin of first gastral sternite medially elevated, with a longitudinal projection in the form of a carina or prominence.

Description. Worker (n=5). HL 1.29–1.31, HL2 1.43–1.56, HW1 1.09–1.43, MdL 0.90–0.95, SL1 1.18–1.22,

SL2 1.19–1.25, PDL 0.12–0.15, A3L 0.03–0.06, AFL 0.47–0.50, FuL 1.19–1.31, EL 0.19–0.25, EW 0.15–0.21, ML 2.05–2.37, MfL 1.72–1.89, MtL 1.37–1.56, PH 0.40, PL 1.06–1.15, PW 0.243–0.47, PPL 0.53–0.64, PPW 0.59–0.67, GL 1.81–1.97, GW 1.25–1.44, TL 7.65–8.40, CI 84–109, CS 1.19–1.37, MCI 69–72, SI 87–108, ESI 15–20, SAI2 253–250, EII 0.29–0.34, MFI 63–76, PTI 261–282.

Large size compared to other *Basiceros*. Coloration (when integument is visible, not densely covered with particles) brown to light brown; appendices slightly lighter. Mandibles with same coloration as appendages, slightly reddish-brown; dorsum with tiny piligerous punctuations close to the masticatory margin, remaining surface either covered by coarse piligerous punctuations with squamiform, slightly whitish decumbent or irregularly and superficially rugose; mandibular apex with short yellowish setae; interdental setae present, yellowish and brush-shaped, slightly longer than teeth. Basimandibular seta present, narrow and erect, located at the anteroventral limit of mandibular peduncle. Stipes covered by fine, medium and subdecumbent pilosity; suberect clavate hair on its dorsum close to anterior margin. Labrum densely covered with piligerous punctuations: short, decumbent and squamiform setae. Dorsal surface of clypeus covered by coarse piligerous punctuations, with decumbent, short and squamiform yellowish hairs. Head dorsum predominantly covered by piligerous fovea, pilosity squamiform or with plumose aspect, subdecumbent; long erect to suberect hairs sparse on the anterior portion of head and more abundant near the posterolateral region and vertexal margin. Ventral surface of head covered by piligerous punctuations; hairs long and erect close to head sides and as line on head center, and by squamiform hairs marginating the ventral limit of antennal scrobes. Pilosity on meso- and metasoma as a double layer of specialized hairs. Basal layer composed of yellowish and subdecumbent plumose hairs, more abundantly than on B. manni, as follows: dense, surrounding the anterior margin of pronotum; a little more sparse on pronotum and mesonotum dorsa, on dorsum and lateral of propodeum, on mesopleuron flange near the epicnemial fossa, on the upper portion of mesopleuron, on dorsal surface of petiolar and postpetiolar nodes; petiolar peduncle with plumose hairs on its side; densely covering the postpetiole sternite; gaster pilosity with hairs with plumose aspect and squamiform hairs, relatively sparse; on anterior face and anterolateral portion of procoxae and on the dorsum and anteroventral margin of all coxae. The second layer is composed of erect to suberect hairs, distributed slightly more sparsely than on B. manni, long and slightly apically, present on the meso- and metasoma as follows: dense on the dorsal surface of pronotum, petiolar node, postpetiole and gaster (on the ventral portion, relatively sparse on the anterior region of first segment); one pair present on the metanotal suture; three pairs on the dorsum and sides of propodeum; slightly thinner and sparse on petiolar peduncle; two pairs on each side of the anterior margin of postpetiole sternite; present on the anterior face and anterolateral portion of procoxae; two to three pairs on the dorsum of meso- and metacoxae. Femora and tibiae covered by short subdecumbent hairs, with a flattened aspect on tibiae. Appressed and clavate minute hairs also present on these segments, more easily recognized on the ventral surface of femora, tibiae and basitarsi of all legs. Antennal pilosity unique: subdecumbent squamiform hairs on the basal lobe of scape, dense hairs, erect to suberect on scape dorsum; external margin with long erect hairs and slightly swollen medially, distributed along the crenulation; short and apically curved hairs also following the external margin; ventral face with short, subdecumbent setae; funiculus densely covered with short, decumbent setae.

When it is possible to observe the integument, it is mostly smooth and shiny on glabrous regions. Dorsum of mandibles and clypeus covered by punctuations or rugae. Anteroventral portion of mandibles slightly alveolate. Dorsal surface of labrum finely reticulate. Head irregularly rugose, rugae forming foveae of different sizes; antennal fossa reticulate; antennal scrobe surface punctuate-foveate on its posterior half; ventral face of head granulose-punctuate, punctuations coarse and slightly overlapping. Anterior and lateral margins of pronotum foveate. Mesonotum with lateral costulae, extending to the anterolateral surface of propodeum, the latter with coarse punctures. Petiolar peduncle finely reticulate-punctuate. Gaster densely punctuate-reticulate; tergite of abdominal segments V, VI and VII finely and densely punctuate, slightly opaque, tergal margins smooth and shiny, slightly yellowish; sculpture slightly sparser on first gastral sternite, especially anteromedially. Antennal scapes finely rugo-reticulate. Coxae punctuate-foveate, other leg segments superficially rugo-reticulate.

Head oblong, lateral emarginate from eye height to posterolateral region and behind the head; posterior portion of head slightly depressed, projected posteriorly; vertexal margin with rounded corners, less divergent in the posterior portion than observed for *B. manni*, median portion largely concave. Occipital margin narrower than that of *B. manni*, cervical margin wide, lamelliform and conspicuously transversely carinate. Palp formula 2,2; palps strongly fused; maxillary palp slightly larger and wider than labial, with a sensillum; labial palp apically clavate, with two sensilla. Stipes subrectangular. Labrum lunate, arched laterally; round, anterior margin continuous. Man-

dibles triangular; in full-face view, lateral margins slightly concave; basal margin conspicuously concave leaving a wide clypeomandibular space; basal angle round, followed by about 18 denticles, slightly serrated and gradually decreasing in size along the masticatory margin; in lateral view, mandibular apex slightly curved ventrally. Clypeus lamellated laterally and on anterolateral portion; anterior margin medially concave. Compound eyes developed. Coarse ruga in front of eyes, projecting from the middle of antennal fossa limit and extending to head side like an arc. Antennal scape with slightly rounded lamellar basal angle, outer margin crenulate and lamellar. Antennal fossa deep. Antennal scrobe deep on anterior half, posterior and ventral limit weakly distinct.

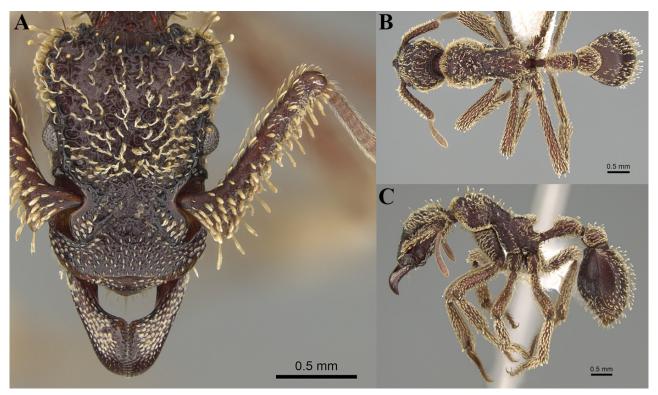


FIGURE 23. Basiceros singularis, worker (CASENT0914890, Ecuador: Napo); A. full-face view, B. lateral view, C. dorsal view. Images by Michele Esposito (CAS), edited.

Mesosoma slender; lateral profile of promesonotal complex continuously convex, strongly sloping caudad; metanotal suture wide. Mesopleuron anteriorly bordered, interrupted at the meeting with a narrow epicnemial fossa. In lateral view, anterior portion of propodeum short and slightly oblique posteriorly, dorsal surface of propodeum slightly sloping posteriorly. Propodeal declivity laterally carinate and with strong transverse lamellar carina connecting the short, sharp and tapered propodeal projections. Opening of propodeal spiracle round. Metapleural gland bulla protruding, prominent; opening transverse and covered by cuticular lamella. Petiolar peduncle longitudinally carinate on its dorsal surface. In lateral view, petiole claviform, petiolar node obsolete, conspicuously low; dorsal margin bulging; postpetiole subcircular, subequal to petiolar node. Subpetiolar process extremely variable: from short anterior spiniform process followed or not by short spines to the most diverse combinations of bifid processes, lamella, simple spines and vestigial processes of different sizes. In dorsal view, petiolar node ogive-shaped; posterior margin of postpetiole convex, widely inserted to anterior concavity of gaster. Postpetiolar sternite conspicuously carinate anteromedially, prora present, lamellar and slightly darkened. Gaster with yellowish lamellar anterodorsal margin; anteroventral margin of the sternite keeled or carinate medially (this character is sometimes hindered by particle covering). Although it is not possible to notice a gastral sulcus like the one found on B. manni, the central longitudinal band of the first gastral tergite is entirely glabrous. Calcar of strigil pectinate. Meso- and metabasitarsi conspicuously long, about ³/₄ of tibial length. Tarsal claws simple. Sting apparatus (after Kugler, 1978): wide, spiracular plate ovoid, anterior apodeme subtriangular. Body shortly extended to medial connection. Spiracle small, near center of plate. Quadrate plate: apodeme and body narrow and reduced; anterodorsal corner with digitiform process, well sclerotized; plate gradually reduced ventrad, especially apodeme. Oblong plate not divided into preincision and post-incision; dorsal crest as wide as length of posterior arm; arm not on midline; transversely broad,

anterior apodeme spatulate; ventral arm short and broad; fulcral arm narrow, continuously tapering from base; vertical. Gonostylus: sclerites well-defined; only trichoid and chaetoid sensilla present; proximal segment tapering from base. Triangular plate: elongated; prominent apicoventral process. Lancet: sword-shaped; single valve relatively large, but not very developed; sulcus converging to ventral crest. Sting: blade slightly longer than the sum of the lengths of the bulb and the valve chamber, gently curved upwards and moderately sclerotized; valve chamber slightly shorter than the sting bulb; sting base moderately arched and obliquely truncated in lateral view. Basal notch short and heavily arched; articular processes short and slightly directed to ventral margin. Sting bulb large; sides straight and gently converging. Furcula: T-shaped, extremities of lateral arms extending slightly over sting bulb.

Gyne (n=3). HL 1.35–1.40, HL2 1.0–1.44, HW1 1.06–1.14, MdL 0.90–0.91, SL1 1.15–1.18, SL2 1.13–1.18, PDL 0.14–0.15, A3L 0.05, AFL 0.45–0.48, FuL 1.16–1.26, EL 0.25, EW 0.23–0.24, LOD 0.08, MOD 0.06, OOD 0.37–0.38, ML 2.13–2.15, MSL 1.00–1.05, MSW 0.8–0.82, MLL 0.25–0.3, MLW 0.4–0.42, MfL 1.70–1.71, MtL 1.38, PH **0.32–0.42**, PL **1.00–1.07**, PW **0.3–0.42**, PPW **0.52–0.57**, GL 1.92–1.95, GW 1.32–1.35, TL 7.93–8.00, CI 77–84, CS 1.22–1.25, MCI 65–66, SI 103–105, ESI 21–22, SAI2 250–257, EI1 0.38–0.40, MTI 76–82, MLI 141–160, MFI 62–66, PTI 235–330. (In bold measurements influenced by accumulation of litter and soil particles on the integument).

Coloration and sculpture similar to conspecific workers; slightly larger size. Cephalic dorsum with three ocelli: median ocellus inserted at the height of posterior limit of compound eyes and lateral ocelli inserted slightly above. Head pilosity as in conspecific workers. Double layer of specialized pilosity on pronotum denser than in workers. Basal pilosity more sparsely present on the mesoscutum and mesoscutellum. Median portion of metanotum with a pair of long, clavate and suberect hairs, and four hairs on the basal layer with a plumose appearance.

Basal pilosity present on posterior corner of mesoanepisternum, just below forewing insertion. Ventral and posterior limits of mesokatepisternum with basal pilosity, as well as ventral portion of metakatepisternum. Pilosity on rest of body with shape and configuration similar to conspecific workers. Mesoscutum with irregular longitudinal rugae, interposed with rugulae forming foveae of different sizes. Mesoscutellum irregularly rugo-foveate. Mesopleuron irregularly rugose, sparse punctuation within foveae formed by these rugae. Anapleural sulcus granular, submedian transverse carina present. Anterior portion of petiolar peduncle finely reticulate. Lateral of mesoscutellum striate-reticulate. Metanotum finely reticulate. Gastral sculpture stronger impressed than on workers. Sculpture of other regions as in conspecific workers. In dorsal view, humeral angles strongly projected, dividing the pronotum into two regions. Mesoscutum slightly cuneiform, anteriorly round, with a short, smooth and subopaque longitudinal carina on its anteromedial portion; slightly cuneiform; posterior margin broadly convex at the meeting with the scutoscutellar suture. Notauli and parapsidal lines indistinct; parapsides slightly deep, subreniform; tegulae narrow, elongated and somewhat translucent, apical margin round. Pre-scutellum narrow; axillae projected posteriorly, round and slightly depressed. Sulcus scutoscutellar well-marked, with transverse costulae. Mesoscutellum trapezoidal, posterior limit concave; in lateral view, one the same level as or just below the scutum. Anapleural sulcus wide, matte, and transversal to body axis. Sting developed. Forewing type 1; hindwing with 5–8 submedian hamuli.

Intercastes. Several individuals, ranging from worker-like specimens bearing:

- slightly bigger compound eyes;
- minute ocelli;
- vestigial mesoscutum and few other modifications on mesosoma;
- mesoscutum and mesoscutellum present, although undeveloped;
- scutoscutellar sulcus not impressed.
- wing fossae and rudiments (i.e. brachyptery);
- transscutal articulation inconspicuous, covered by integumental sculpture;
- axillae vestigial, seen as very short lamellae;
- tegulae vestigial;
- metanotal suture more impressed than in the regular conspecific workers;
- metanotum, as transversal arch with indistinct posterior limit, delimited by strongly marked longitudinal carina from the metanotal suture;



FIGURE 24. *Basiceros singularis*, gyne (MCZ 534402/T2-56, Trinidad & Tobago: St. Andrew) and male (MCZ, Trinidad & Tobago: St. Andrew); A and D. full-face view, B and E. dorsal view, C and F. lateral view. Scale bars: A, D = 0.5 mm, B, C, E, F = 1 mm.

to gyne-like individuals, with:

- rudiments of forewing articulation and pteralia;
- vestigial wing buds;
- fully-developed wing fossae, less impressed than on conspecific gynes;
- vestigial parapsides, shorter than on true gynes;
- transscutal suture, somewhat flat;
- scutoscutellar sulcus, slightly narrower than in the conspecific gynes;
- axillar carina, axillae slightly shorter than on true gynes and with specialized pilosity on the posterolateral corner;
- scutellum, depressed as in the conspecific gynes but shorter;
- metanotum like in the conspecific gynes, although slightly shorter, carinate dorsomedially;
- dorsal subplumose pilosity similar to conspecific gynes
- tegulae present, although shorter than the conspecific gynes;
- metanotal suture deeply impressed, presenting broad longitudinal carina;
- axillary sclerites;
- rudimentary forewings, hindwings sometimes still attached to body.

Male (n=2). HL 0.91–1.00, HW1 0.90–0.93, HW2 1.04–1.08, MdL 0.55–0.56, SL2 0.20–0.23, PDL 0.13–0.15, A3L 0.58–0.63, AFL 0.55–0.63, EL 0.34, EW 0.30, LOD 0.09–0.1, MOD 0.09, OOD 0.31–0.33 ML 1.88–1.93, MSL 1.03–1.04, MSW 0.72–0.75, MLL 0.3, MLW 0.42–0.45, MfL 1.8, MtL 1.38, PH 0.28–0.29, PL 0.90–0.95, PW 0.31–0.33, PPL0.39–0.43, PPW 0.39–0.44, GL 1.58–1.60, GW 1.15–1.18, TL 6.21–6.45, CI 92–98, CS 0.91–0.96, MCI 55–61 SI 22–24, ESI 150–168, SAI 34–36, SAI2 32–40, EI1 0.66–0.70, EI2 86–86, MTI 69–73, MLI 141–150, MFI 48–50, PTI 327–330.



FIGURE 25. *Basiceros singularis* intercastes from Trinidad & Tobago: St. Andrew; A–D: MCZ534402/T2-56); A. lateral view of mesosoma, white arrow pointing to wing fossa and wing trace, B. lateral view, C. dorsal view highlighting mesoscutum line (white arrow) and wing trace (black arrow), D. dorsal view; E–H: (MCZ/T2-56); E. oblique view of mesosoma, white arrow pointing to vestigial hindwing, F. lateral view, G. dorsal view highlighting rudiments of a mesoscutum (left white arrow), mesoscutellum (right white arrow), and forewing trace (black arrow), H. dorsal view. Scale bars: 1 mm.

Slightly smaller than conspecific gyne. Coloration dark brown to black; propodeal lobes and disc of first gastral tergite sometimes testaceous; appendages light brown to yellowish. Wigs yellowish, amber or brown. Dorsum and apex of mandibles with long, fine yellow hairs, semierect to subdecumbent, longer on the latter. Head with two main types of hair: medium, yellow and fine, subdecumbent; primarily on frontal disc of clypeus; and long yellowish or brown, sometimes apically curved and primarily on frons, along the genal carina, on the vertexal margin, and ventral surface. The latter type is widely present throughout the body: on mesosomal dorsum, waist and gaster, coxae and mesokatepisternal suture; especially long on the lateral margin of pronotum and dorsum of petiole. Antennomeres with short yellowish appressed setae. Legs with semierect setae sparsely distributed between short decumbent to decumbent setae.

Body uniformly punctuate-reticulate, minor changfes in diameter and degree of impression. Apical portion of mandibles smooth and shiny. Irregular longitudinal rugae present on neck to faintly on the vertex margin, close to occipital carina. Irregular transverse rugae on dorsum of mesoscutellum; on the side of pronotum and propodeum. Mesokatepisternum irregularly carinate-rugose.

Head piriform; occipital margin wide and lamellar. Palp formula 1,1, palps apically subclavate and subequal in size; maxillary palp slightly wider than labial; apexes of palpi with long, filiform sensilla. Stipes subrectangular. Labrum trapezoidal; basal region transversely striated; distal margin weakly concave; sides angled; approximately 10 long and erect setae present. Mandibles triangular, about twice as long as wide and gently curved apically; masticatory margin with 11–12 conical teeth, basal tooth biffid or subquadrate, apical tooth slightly falcate. Clypeus with convex central disc, slightly elevated; lateral regions depressed; anterior margin lamellar and slightly convex. Genal carina present, extending posteriorly almost to upper margin of compound eyes. Longitudinal carina on frons, with or without anteroposterior sulcus; keeled medially and extending posteriorly as a line to median ocellus. Antennal arch expanded medially in posterolateral lobe, hiding the antennal bulb in full-face view. Pedicel longer than wide, third antennomere about six times longer than pedicel. Eyes large and globular, protruding from cephalic capsule; posterior margin emarginate. Ocelli pearl-like and projected.

In dorsal view, mesoscutum keel-shaped, cuneiform; in lateral view pronotum with triangular side flaps. Shiny subtriangular carina present on the anteromedial region of mesoscutum, extending as a line until near the dorsal region, where it continues as a carina until meeting the notauli. Anterior region of mesoscutum narrow and slightly higher and obliquely convex in profile. Parapsidal lines shiny; curved anteriorly, subparallel and directed anterolaterally to the parascutal flange. Parapsides broad, deep and oval. Transscutal suture slightly convex. Axillae protruding, strongly curved posteriorly and downwards; spear-shaped. Anapleural sulcus broad, strongly imprinted (mesoanepisternum strongly elevated to mesokatepisternum); scrobiculate. Scutoscutellar sulcus broad, about half the length of mesoscutellum; longitudinally carinate and with posteromedial transverse carina. Mesoscutellum subrectangular; posteromedially depressed; posterior margin strongly concave and depressed. In dorsal view, metanotum distinct, posterior margin projected; lateral margins lamellar. Propodeum armed with triangular projections; carinate as in conspecific females. Propodeal lobes auricular. Calcar of strigil pectinate. Tarsal claws simple (see comments); arolia present, short. Petiole long, similar to conspecific females; in lateral view, claviform; in dorsal view, petiolar spiracle projected; subpetiolar projections absent. Postpetiole short; in lateral view, dorsally convex; spiracle projected; sternite with transverse lamellar prora close to anterior margin; in dorsal view, only slightly wider than the petiole. Forewing type 1, hindwings with five submedian hamuli.

Larva (description updated and modified from Wheeler & Wheeler 1977, 1980). Length through spiracles 5.0 mm; profile pogonomyrmecoid: larger diameter near the middle of the abdominal region, thorax slender than abdominal region; curved ventrally. Anus ventral, opening weakly convex, anal flap present. Spiracles small. Integument of ventral region densely covered by spinules arranged in transverse rows. Pilosity moderate, hairs short to long; usually flexuous and denticulate. Cranium slightly subcordiform, occipital margin with median impression; antennae minute, with 3 spinulate sensilla. Clypeus protruding. Labrum bilobed; ventral surface densely spinose; anteroventral margin of each lobe with ca. 6 spinose sensilla. Mandibles ectatommoid, long and narrow, medially curved; subapical tooth slightly anterior to the plane of a large apical tooth; anteroventral margin densely covered by spinules in short, arcuate subtransverse rows. Maxillae parabolic, dorsum with 5 setae, apex densely spinose; maxillary palps galeae digitiform, subequal in size and diameter; maxillary palp with 5 sensilla: two apical, encapsulate, two lateral with one spinule, and a subapical, spinulose; galeae with two spinulose apical sensilla. Labium densely spinulose; spinules arranged in short arcuate rows; labial palp papillary, with five apical sensilla (two encapsulated and three spinulate); a short, isolated sensillum on each side of the opening of sericeous gland; opening transversal. Hypopharynx densely spinulose; long spinules arranged in numerous subparallel rows.

Etymology. From Latin, "singularis", different, rare, unusual. Smith possibly named this taxon—the first described for the genus—based on its peculiar morphology.

Comments. Some specimens collected in Peru and Colombia examined for the present study do not have the combination of squamiform hairs on the clypeal dorsum and anterodorsal region of mandibles. However, they also do not have piligerous punctuations in these regions as observed in *B. manni* specimens, but a combination of irregular and subopaque rugulae. Furthermore, these specimens have the head shape and anteroventral projection of the first gastral sternite exclusive to *B. singularis*. This peculiarity of Peruvian and Colombian specimens highlights the possibility of hybridization between populations of *B. manni* and *B. singularis* in these regions. However, more fieldwork is necessary to fill gaps in the distribution of both species to make this assumption more credible. The current distribution of *Basiceros singularis* in Colombia is many kilometers away from the southernmost distribution of *Basiceros manni*, which makes the possibility of hybridization between these species difficult (Dr. Roberto Guerrero, pers. comm.). Dietz (2004) identified two specimens of *B. singularis* from Colombia and one from Peru as *B. manni*, which emphasizes the difficulty of identifying specimens from these locations. In addition, a worker collected in Colombia was considerably smaller than other workers of *B. singularis* analyzed in the present work (with that size variation reflected in the smallest values obtained for the measurements).

One of the eight males examined in this study presents a basal lobe along the ventral margin of metatarsal claws. Since all specimens were from the same collection series or at least came from nearby collection points (Trinidad: St. Andrew), that basal lobe might be the result of some error during development.

In addition to the general morphological similarity, the unique pronotal division present on *B. manni* males also occurs in the male of *B. singularis*, which reinforces the phylogenetic relatedness between these species (Probst *et al.* 2019).

Some specimens from Trinidad & Tobago examined in the present study were covered by oribatid mites. It is not possible to confirm whether such arachnids are phoretic, commensal myrmecophiles, or parasites.

Brown (1974) mentions that he dissected workers to determine the number of Malpighian tubules present, recognizing five.

As mentioned for *B. disciger* and *B. militaris*, *B. singularis* displays intercastes (Fig 25). The examined morphological mosaic for this species has gynes virtually identical to conspecific workers, differing only by the presence of a median and/or lateral ocelli and a slight scutellar impression, and the most aberrant case of ergatoidism within the genus, in which a gyne presented alar rudiments, even without showing complete development of the mesosomal sclerites associated with flight (Fig 25E). Obviously, this brachypterous gyne could not fly. Similar to *B. militaris*, intercastes and true gynes co-occur in the same colony. Together with a general morphology analogous to conspecific workers, it reinforces a scenario similar to that found by Molet *et al.* (2009) for *Mystrium* gynes in Madagascar, with ergatoids having functional ovaries, spermatheca, and alar rudiments, acting as a "multitasking" caste within the colony. Almost all specimens of *B. singularis* are collected covered by a thick layer of particles that prevents the visualization of morphological changes on the mesosoma and head. The intercaste mosaicism was revealed after the cleaning of several specimens; therefore, the presence of intercastes in this species is probably underestimated.

Distribution. Brazil: Amazonas, Mato Grosso, Pará, and Rondônia; Colombia; Ecuador; Guyana; French Guiana, Peru; Trinidad and Tobago; and Venezuela.

Natural history. Weber (1950) mentions that he found a worker in Trinidad foraging during the day (at 1pm). Brown (1974) collected a colony in the north of the state of Mato Grosso in July 1973, at Fazenda Junqueira Vilela; the colony was nesting on rotting trunks in the shade, and Brown found headless termite bodies with ant workers and reproductives (alate males and gyne) in what looked like grossly-built chambers. Adults presented thanatosis when disturbed and, according to Brown "are exceedingly hard to distinguish by eye". The author discusses the incrustation presented by this species and conjectures that it could be a product of secretions of nasute termite soldiers (Termitidae: Nasutitermitinae) or even that the ants themselves produced it. Brown ends up commenting that newly hatched adults and alate forms of both sexes did not present particle covering or secretion.

In Dr. Mark Moffett's photographic exhibition—"Farmers, Warriors, Builders: The Hidden Life of Ants"—organized at the USNM in 2009, one of the photographs (see Probst *et al.* 2019, Fig 1C) depicted a *B. singularis* worker (identified as *B. conjugans*) probably preying on a Subulinidae mollusk with a spiral and pointed shell from genus *Beckianum* or *Allopeas*, recognized for being litter predators (Dr. Jaime Jardim pers. comm.). This information was already reported for this species—also by Dr. Moffett—in the August 2008 issue of the National Geo-

graphic magazine, with a photo recording the moment a *B. singularis* larva preys on a gastropod with a shell similar to that recorded by Dr. Michael Branstetter inside *B. manni* nests in Nicaragua (see comments under *B. manni*). Transcribed below is the report associated with the photograph:

"One species of ant that will never win a prize for cleanliness is *Basiceros singularis* of Ecuador. Once thought to be rare, they are in fact fairly common ants that are uncommonly dirty, camouflaging themselves with mud held in place on their bodies by feathery hairs. Workers move at a snail's pace—not a problem if your favorite prey is, in fact, snail. The chase ends—finally—with a strike. The ant then drags her booty home to a nest in the rain forest leaf litter composed of only a dozen or so workers and their queen. Stooped over a little colony I'd captured in a petri dish, I photographed a worker feeding a snail to a larva, which gobbled it up from its shell with the enthusiasm of a child lapping ice cream from a cone".

The fact that *B. singularis* and *B. manni* potentially use terrestrial mollusks as prey reinforces the idea of phylogenetic relatedness between these species (see Probst *et al.* 2019).

Material examined. BRAZIL: Amazonas: Reserva Dimona, PDBFF, 2°22'S 59°50'W, 27–29.xi.2004, C.E. Sanhudo col. (1 worker) [MZSP]; Mato Grosso: Fazenda Junqueira Vilela, município Diamantino, 3 km E from house, 17–18.vii.1973, W.L. Brown col. (2 workers) [MCZ]; Pará: Melgaço, Caxiuanã, Estação Científica Ferreira Pena, 1°45'15.95"S 51°31'20.66", 3.v.2004, C.E. Sanhudo col. (1 worker) [MZSP]; same data, 1°43'29.42"S 51°25'47.23"W, 26.x.2003, A. Y. Harada e Equip. cols. (1 worker) [INPA]; same data, 1°44'0.96"S 51°30'37.97"W, 29.iv.2005, A. Y. Harada e Equip. cols. (1 worker) [MPEG]; Rondônia: Porto Velho, Área Abunã, 09°37'34.1"S 65°26'39.3"W, 08–21.IX.2010, R. M. Feitosa & R. R. Silva cols. (1 worker) [MZSP]. COLOMBIA: Amazonas: Araracuara, no data, no collector (1 worker) [IAVH]; Guaviare: San Jose del Guaviare, Insp. de Tomachipán, Rio Irinida, i.1996, F. Fernández col. (1 gyne) [IAVH]. GUYANA: no locality, no data (1 worker) [AMNH]; Kaieteur: 14.viii.1911, F. Lutz col., W.M. Mann 1954 [USNM]; Kurupung: Cuyuni-Mazaruni, xi.1922, Herbert O. Lang col., MCZ 546475 (1 worker) [MCZ]; Oronoque River, 2°42', 3.viii.1936, N.A. Weber col., MCZ 546476 (1 worker.) [MCZ]; no data, Herbert O. Lang col., MCZ 546474 (2 workers) [MCZ]; same data (3 workers) [MZSP]; same data (1 worker) [IFML]; Rupununi, near Kamoa River, near Kamoa Camp, 1°32.786'N 58°49.929'W, 394m, 22.x.2006, J. Sosa-Calvo col., TRS 061022-LS01 (1 worker) [USNM]; Tukeit: 17.viii.1911, F. Lutz col. [AMNH]. FRENCH GUIANA: Cayenne: Itoupe, 9.xi.2014, Lat. 3.026391 Long -53.07616, 762m, J.Orivel & M.Fichaux cols., ECOFOG-IT14-0106-61 (1 worker) [EcoFog]; UMR Korou: Near Petit-Saut, 02-28.xi.2011, S. Lacau & B. Fleck (5 workers, 1 male) [MZSP]; same data (1 worker, 1 male) [CEPEC]. PERU: Loreto: Camping San Jacinto, 06.vii.1993, Richard Leschen col., n. 546477 (2 workers), n. 546478 (1 worker), n. 546479 (2 workers) [MCZ]; Jenaro Herera, 04°53'55"S 73°39'00"W, 121 m, 20.xi.2011, R. Silvestre col. (1 worker) [MuBio]; Madre de Díos: Estación Ecológica Villa Carmen, -1286371° -71.400528° ±300m, 1175m, 05–15.vii.2013, AntCourse, INC087730 (1 worker) [ICNC]; same data, Trail 14, -12902437° -71407672°, 590m, 06.viii.2013, CSM2987, C. S. Moreau col. (1 worker) [FMNH]; Puerto Maldonado, Sachavacayoc Center, 12°49'36.5"S 69°22'14.4"W, Alt. 209m, 19-31.vii.2012, R. Feitosa & R. Probst cols. (1 worker, 1 gyne) [MZSP]; Puerto Maldonado, Sachavacayoc Center (Castanhal), 12°51'21"S 69°21'43"S, R. Feitosa col., n. UFV—LABECOL63 (1 worker) [UFV]; Tambopata Research Center, Lat. -13.14535 Long. -6961483, 276m, vii.2011, D. Feener col, TRC-S12-R2CO1. VENEZUELA: Bolívar Talud: W. Amarowai Tepui, 5°55'N 62°15'W, 500m, J. T. Lattke col., J.Lattke 778/LACM 326548 (2 workers) [LACM]; same data, ICN 015366 (2 workers) [ICNC]. TRINIDAD & TOBAGO: Sul de Sangre Grande: Saint Andrew County, right after 9_{3/4} mileage marker of Southern Road (current Cunapo Southern Road), 07.iii.1992, S. P. Cover col., MCZ 534400 (1 worker, 1 male) [MCZ]; same data, MCZ 534402 (1 intercaste, 1 gyne); same data, MCZ 534403 (1 worker, 1 male); same data (4 workers, 2 intercastes, 2 gynes, 4 males) [MCZ]; St. Andrew: Co. Arena Forest Reserve E San Rafael, 100', 05.iii.1992, S. P. Cover col., LACM 326552 (1 worker, 1 male); same data, LACM 326553 (1 worker, 1 gyne) [LACM]; same data., (3 workers, 1 male) [MCZ]; same data, MCZ 534392 (1 worker, 1 male) [MCZ]; same data, MCZ 534393 (1 worker, 1 gyne) [MCZ]; Verdant ("Verdent") Vale: 05.vi.1950, 1400', T. S. Schneirla col., LACM 326549 (2 workers; and 1 worker probably of Mayaponera constricta [Forel, 1886] headless, glued to pin); same data, LACM 326550 (2 workers, 1 gyne) [LACM]; same data, LACM 326551 (3 workers) [LACM].

Basiceros tumucumaquensis Probst & Brandão sp. nov. (Figs 26–28, 32)

Type material. *Holotype worker*: BRAZIL: Amapá, PNMT, 1.242333 -52.419778 ±10m, 132m, 25.xii.2018, R. Probst & O. Guilherme cols. (*R. S. Probst* #678) [MZSP, CASENT0647157]. *Paratype workers*: Same data as holotype [MZSP, 4 workers, CASENT0647158, CASENT0647159, CASENT0647160, CASENT0647161; MPEG, 2 workers, CASENT0647162, CASENT0647163; DZUP, one worker, CASENT0647164; MCZ, one worker, CASENT0647165; JTL, one worker, CASENT0647166]. *Paratype male*: Same data as holotype [one male, MZSP, CASENT0647167].

Diagnosis. Mandibles bizarre, apical portion strongly curved ventrally, basidorsal sulcus present, slightly transversal to mandibular dorsa, basal angle translucent. Clypeus densely covered with decumbent squamiform hairs. Head dorsum rugulose, with long clavate hairs.

Descriptions. *Worker* (n=5, range downward from size of smallest to biggest individual. Includes holotype, 3 paratypes, and a non-type each from Amapá and Rondônia). HL 1.28–1.44, HL2 1.22–1.47, HW1 1.04–1.24, MdL 0.48–0.58, SL1 0.97–0.99, SL2 1.02–1.08, PDL 0.09–0.11, A3L 0.03–0.04, AFL 0.385–0.409, FuL 0.95–1.02, EL 0.09–0.12, EW 0.09, ML 1.556–1.7, MfL 1.28–1.35, MtL 1.0–1.06, PH 0.32–0.35, PL 0.74–0.76, PW 0.29–0.33, PPL 0.51–0.54, PPW 0.51–0.538, GL 1.54–1.71, GW 1.04–1.12, TL 6.2–6.63, CI 81–85, CS 1.16–1.31, MCI 40–42, SI 84–97, ESI 9–11, SAI2 3011–3347, EII 0.15–0.16, MFI 81–91, PTI 213–234.

Medium size comparatively. Coloration reddish-brown to brown; appendages lighter. Mandible dorsa covered by minute sparse piligerous punctuation, bearing erect to suberect setae; basal portion with clavate pilosity suberect to subdecumbent; mandibular apex with medium yellowish setae. Basimandibular setae present, narrow and erect. Clavate suberect hairs on the dorsum of each stipe. Anterior margin of labrum with long filiform hairs. Clypeal dorsum densely covered with decumbent squamiform hairs. Head with basal layer of hairs with similar morphology as clypeal pilosity (although longer), sparse and located at margin of sculpture; erect and slightly clavate pilosity as follows: one pair on frons, close to the median head depression, one pair on the temple, around the sulcus of vertexal margin, a pair present anterior to and a pair near the posterior limit of eyes; several on vertexal corners and superficial emargination projected above the eyes until the vertexal margin. Mesosoma, petiole, postpetiole, and first gastral sternite with basal pilosity suberect to sudecumbent, slightly clavate to clavate. Erect to suberect pilosity on mesosomal dorsum, petiole and postpetiole, coxae, and gaster; relatively abundant, clavate, yellowish; pygidium with short, filiform, suberect hairs. Antennal scapes mainly with yellowish suberect clavate hairs; funiculus covered by short, appressed, and yellowish setae. Tibiae and femora with abundant subdecumbent clavate pilosity, tarsi with subdecumbent setae.

Surface of antennal scrobes matte, finely strigulate; head dorsum rugulose, median temple punctate. Pronotum laterally punctuate-reticulate; anterior portion rugulose. Surface of mesopleuron and propodeum matte, rugulae sparse. Petiole and postpetiole rugulose. Procoxae areolate-rugulose. Gaster densely areolate-punctate.

Head oblong; posterolateral corners round; vertexal margin slightly raised medially. Vertexal crest present, shallow; sulcus around head visible; temple medially depressed. Mandibles aberrant, trapezoidal; external margin slightly concave; masticatory margin straight bearing 10–11 teeth, apical tooth slightly broader and longer; apical portion of mandibles strongly curved ventrally to the midpoint of their length; basal angle strongly convex, portion translucent; in full-face view, sulcus present on basal portion, extending from the masticatory margin to at least half of the lamina, slightly transversal. Labrum short and triangular, overall shape similar to *B. scambognathus* (see Figs 2E and 3E from Probst *et al.* 2019 and Fig 27B–C); lateral lobes short, distal margin with cleft extending slightly longer and more slit-like than on *B. scambognathus*. Frontoclypeal surface convex; anterior margin medially concave. Tumosity present on frons, circular-shaped and with central concavity. Eyes inserted on the dorsal margin of antennal scrobes, these deep and extending posteriorly to the vertexal margin. Scape flattened and with a biangulate basal lobe, margin between angles concave; external margin lamellar and crenulated. Antennal apical segment slightly longer than the sum of three anterior antennomeres.

Mesosoma robust; in lateral view, promesonotal profile slightly convex dorsally; metanotal suture strongly impressed, extending as the anapleural sulcus, transversely rugulose. Propodeum posteriorly oblique; propodeal projections short, triangular and slightly upwards, connected by strong transverse carina; propodeal spiracle elliptic, spiracle directed posteriorly. Petiole nodiform, peduncle short; node anteriorly oblique and strongly tapered posterad. Subpetiolar process consisting of series of long sharp denticles. In lateral view, postpetiole slightly longer

than length of petiolar node; slightly dorsoventrally flattened, dorsal face slightly projected on its posterior half, posterior margin bulged at the meeting with gaster. In dorsal view, petiolar node slightly oblong, ogive-shaped; anterior margin of postpetiole strongly concave, posterior margin convex. Gaster oval; anterior margin concave; first gastral sternite visibly longer than tergite. Metabasitarsus conspicuously long, longer than metatibia. Tarsal claws simple.



FIGURE 26. *Basiceros tumucumaquensis* **sp. nov.** holotype worker (MZSP, CASENT0647157, Brazil: Amapá); mandibles in A. dorsal view, B. oblique view, C. lateral view, D. ventral view, highlighting ventrolabrum, E. dorsal view, F. lateral view, G. full-face view, H. oblique view of head and pronotum. Scale bars: A–D = 0.2 mm, E–F = 1 mm, G–H = 0.5 mm.

Male. (n=1) HL 1.072, HW1 0.954, HW2 1.113, MdL 0.431, SL2 0.21, PDL 0.118, A3L 0.387, AFL 0.63, EL 0.347, LOD 0.11, MOD 0.083, OOD 0.396, ML 1.78, MSL 1.009, MSW 0.85, MLL 0.32, MLW 0.552, MfL 1.469, MtL 1.023, PH 0.36, PL 0.8, PW 0.317, PPL 0.474, PPW 0.462, GL 1.627, GW 1.17, TL 6.18, CI 88, CS 1.01, MCI 40, SI 22, ESI 165, SAI 54, SAI2 33, EI1 0.63, EI2 85, MTI 84, MLI 172, MFI 64, PTI 222.

Coloration black, with areas slightly ferruginous (e.g., propodeal lobes and scutoscutellar sulcus). Coxae and central portion of femora dark, rest of appendages lighter, yellowish. Pilosity primarily composed of long filiform whitish hairs covering the body, mainly head, dorsum of promesonotum, and sparser on gaster. Wigs brown, microtrichia dense.

Integument matte, with a grainy aspect. Head covered with irregular rugulae, punctuate in between; mesosoma dorsally rugulose. Mesokatepisternum rugulose, mesoanepisternum rugulose-punctate, other integument covered by dense rugulose-punctate sculpture that resemble reticulate punctuations on lower magnification.

Mandibles sinuous, elongated; rugulose. Masticatory margin with 10 short triangular teeth, second and third teeth from the base slightly broader than others; apical tooth falcate; external margins of mandibles convex. Head subpiriform, cervical flange conspicuous. Antennal torsion conspicuous. Ocelli large and positioned on cephalic crest; median ocellus inserted after a transversely rugose cleft. As for other *Basiceros* males, a deep concave sulcus is present along the frontoclypeal region. Central disc of clypeus convex, central portion raised; anterior margin and lateral portions slightly depressed. Anterior clypeal margin slightly concave medially, lateral margin convex. Eyes globular, large, and shiny. Antennal fossa deep. In dorsal view, mesoscutum slightly cuneiform anteriorly, as wide as long; anterior margin with smooth and shiny median carina, extending along dorsum of mesoscutum but not reaching notauli, these lightly impressed. Scutoscutellar suture broadly concave. Parapsides oval, slightly deep. Parapsidal lines smooth and shiny. Scutoscutellar sulcus broad and deep, transversally costulate. In dorsal view,

mesoscutellum transversely rectangular, longitudinally divided by a median posterior sulcus. Propodeal projections round, propodeal lobes auricular and slightly narrow. Petiole and gaster similar to conspecific females. Subpetiolar projection absent, only obsolete spine on peduncle present; petiolar spiracle slightly projected laterally. Forewing type 2; hindwing with five submedian hamuli.

Gyne and larva. unknown.

Etymology. The species name *tumucumaquensis* is masculine and a Latin singular adjective in the Nominative, paying homage to the Tumucumaque Mountains National Park (PNMT), type locality and protection area named after the Tumuc-Humac mountain range in the states of Pará and Amapá. The PNMT is Brazil's largest national park and one of the world's largest protected tropical forests.

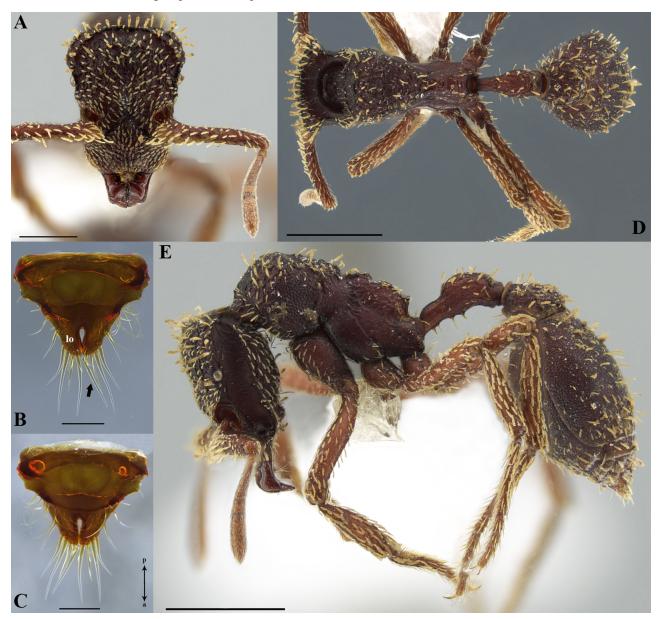


FIGURE 27. *Basiceros tumucumaquensis* **sp. nov.** paratype worker (MZSP, CASENT0647158, Brazil: Amapá); A. full-face view, D. dorsal view, E. lateral view. Labrum from non-type worker (MZSP, Brazil: Rondônia); B. dorsal view and C. ventral view; lo: lateral lobe, black arrow: specialized seta on anterior margin. Crossed arrows give the orientation: a, anterior; p, posterior. Scale bars: A = 0.5 mm, D–E = 1 mm, B–C = 0.1 mm.

Comments. Basiceros tumucumaquensis **sp. nov.** can be separated from other Basiceros by the combination of mandibular and labrum morphologies and general pilosity on the worker, and by head and mandibular morphologies, pilosity, and mesosomal sculpture on the male. This new species is very similar to B. scambognathus, from which the worker caste can be differentiated based on head shape and pilosity, body pilosity, mesosomal and gastral

sculpture, and mandibular shape. The male of this new species looks like a chimera between males of *B. conjugans*, *B. manni*, and *B. scambognathus*. Body coloration is almost uniformly dark; mandibles are sinuous and not subtriangular like in *B. scambognathus*; the apical tooth follows the profile of the masticatory margin, not being projected as in *B. scambognathus*; the head is subpiriform, resembling other males of *Basiceros*—in *B. scambognathus*, it is subhexagonal.

In terms of variation, workers of *B. tumucumaquensis* present slightly variations in integumentary coloration and sculpture, pilosity density, and subpetiolar process, size, and slightly on labrum morphology—the cleft on distal margin can vary on extension and inner margin of lateral lobes can be more or less straight. The holotype and some paratypes had oribatid mites on the ventral face of mandibles. It is not possible to confirm whether such arachnids are phoretic, commensal myrmecophiles or parasites.

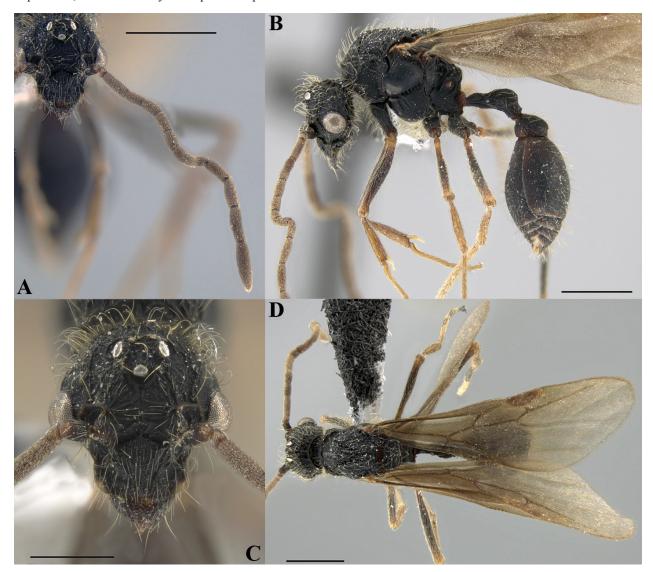


FIGURE 28. Basiceros tumucumaquensis **sp. nov.** paratype male (MZSP, CASENT0647167, Brazil: Amapá); A. head and antenna, B. lateral view, C. full-face view, D. dorsal view. Scale bars: A–B, D =1 mm, C = 0.5 mm.

Distribution. North and NW South America. Currently known from the PNMT, the state of Rondônia, and potentially from a forest fragment close to Manaus, state of Amazonas (Itanna Oliveira, pers. comm., material not examined). This species occurs in sympatry with its sister taxon *B. scambognathus*, and hints of cryptic variation came from two workers collected in Rondônia (included in the phylogenetic analyses from Probst *et al.*, 2019). At that time, those two workers (BSCJ1 and BSCJ2) were considered to be populational variations within *B. scambognathus*—so much that Probst (2015) included photographs of one of those workers under *B. scambognathus*. The boundaries of *B. scambognathus* started to make more sense after the phylogenetic study of *Basiceros* (Probst *et al.* 2019; see Fig 5), which *recovered B. scambognathus* as two sister clades. One clade grouped three male specimens

from Amazonas (North of Brazil), Minas Gerais (Southeast of Brazil), and Peru; the other clade grouped those two workers from Rondônia (west of the Amazonian biome). In the same study, Probst *et al.* (2019) pointed out the unique morphology of these two workers in terms of pilosity patterns, head, and body shape, and suggested that they may correspond to a cryptic species within *B. scambognathus*. Supported by phylogenetic information from Probst *et al.* (2019) and by studying additional specimens, we raise it here as a new species.

Natural history. Virtually nothing is known about the biology of this species. The type-series was collected below surface, close to tree roots, with the nest apparently scattered in indistinct chambers. RSP also collected two workers from a leaf litter sample taken around superficial roots of a Brazil nut tree (*Bertholletia excelsa*, Lecythidaceae). Those two workers were kept alive in laboratory conditions for three days, in which sparse interactions between specimens were observed. Workers moved slowly through the terrarium, with occasionally slow-paced antennation and showing thanatosis when disturbed. Unfortunately, all the conducted "cafeteria" experiments failed and specimens did not accept any items offered. Similarly, part of the type-series was kept alive in laboratory conditions for several weeks, consistently ignoring live prey dropped inside the terrarium, but sometimes accepting freshly-killed adult fruit flies.

Material examined. BRAZIL: Amapá, PNMT, 1.242333 -52.419778±10m, 132m, 25.xii.2018, R. Probst & O. Guilherme cols. (additional 20 non-type workers, several broken and/or dissected) [RSPPC]; Rondônia: Porto Velho, Área Mutum 09°34′49"S 65°03′13"W, 15–30.vii.2013, R.S. Probst & G.R. Mazão cols. (2 workers) [MZSP].

Names excluded from Basiceros

Basiceros redux (Donisthorpe 1939) = Octostruma reducta comb. nov. (Fig 29)

Type-material: holotype (male), Donisthorpe 1939: 152, GUYANA.

Type-locality: Guyana ("British Guiana"): Kaieteur Savannah, 5.ix.1937 (O.W. Richards) (MNH1014339) (examined).

Incertae sedis in Rhopalothrix: Brown & Kempf, 1960: 164.

Combination in Basiceros: Bolton 1995: 80.

Status as species: Kempf 1972: 227; Bolton 1995: 80.

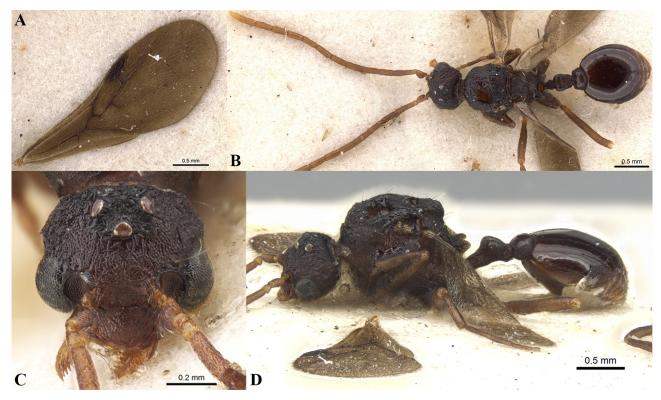


FIGURE 29. *Basiceros redux = Octostruma reducta* **comb. nov.**, holotype (CASENT0900942, Guyana: Kaieteur); A. forewing, B. dorsal view, C. full-face view, D. lateral view. Original images by Will Ericson (CAS), edited.

Comments. Brown & Kempf (1960), while mentioning the taxonomic uncertainty regarding *Basiceros*-genus group males, added that *Rhopalothrix redux* could be placed in *Eurhopalothrix*, *Rhopalothrix*, *Octostruma*, or *Talaridris*. Few are the species from the *Basiceros*-genus group in which the males are known, making it hard to address intraspecific variation. Despite the holotype conditions, a detailed examination revealed unique features present of *Basiceros redux* when compared to other "basicerotine" males:

- 1. Mandibles—shape and dentition: most *Basiceros* males have mandibles somewhat elongate, with the external margin apically curved and 9-14 teeth on the masticatory margin. In *Basiceros redux*, the mandibles are triangular, having seven or eight teeth;
- 2. Head shape: *Basiceros* males have an anteriorly elongated head (the overall head shape has a piriform to subpiriform aspect) and the occipital margin projected and carinate, forming a neck. In *B. redux* the head is rounded and the occipital margin lacks a neck;
- 3. Antennae: antennomeres of *B. redux* are subequal from A3 to the apical segment, a condition not observed in any *Basiceros* male examined for this study;
- 4. Ocelli: in general, *Basiceros* males have the ocelli arranged on the top of the head, surrounded by a conspicuous cephalic crest. In *B. redux*, although the ocelli are located on the top of the head, the crest is absent;
- 5. Mesosoma: in *B. redux* the posterior face of mesoscutellum is strongly truncated and the metanotal band is extremely reduced, giving the mesoscutum + mesoscutellum set an aspect of plateau. In *Basiceros* males, the posterior margin of mesoscutellum is rounded and the metanotum, although reduced, is detached from the mesoscutellum:
- 6. Petiolar node in dorsal view: for *Basiceros* males is elongated, longitudinally rectangular. In *B. redux* and the known males of *Octostruma*, *Rhopalothrix*, and *Eurhopalothrix*, the node is transversally rectangular;
- 7. Postpetiolar node in dorsal view: in *Basiceros* males is nodiform and subglobular, conditions not observed for *B. redux*;
- 8. Gastral integument: in opposition to the shiny integument and the sparse pilosity found in *B. redux*, males of *Basiceros* possess finely punctuate to reticulate integument and a more abundant pilosity;
- 9. Propodeal projections: *Basiceros* males have short projections, sometimes angled. In *B. redux* the propodeum is armed with a well-developed triangular and lamelliform projection, similar to observed for *Octostruma* males;
- 10. Forewing venation: in *B. redux* the vein M+Cu has a spectral basal portion, similarly to observed for *Octostruma* males, whereas in *Basiceros* males that vein is invariably complete. *Eurhopalothrix* males tend to have M+Cu completely spectral;
- 11. Forewing venation II: submarginal cell 1: known *Rhopalothrix* males have the submarginal cell 1 open (for *Eurhopalothrix* males, the Rs+M vein is in general spectral or slightly tubular, and a close observation shows that it closes the submarginal cell 1) and the veins Rs, M, Cu, and A nebular or spectral in their basal half (similar condition observed for examined *Eurhopalothrix* males). This set of characteristics are absent in *B. redux*, with the male having a submarginal cell 1 closed, feature shared by *Basiceros* and *Octostruma* males. Additionally, *B. redux* presents another configuration for other veins above cited;
- 12. Pterostigma: *Eurhopalothrix* males lack the pterostigma or it is poorly developed. Both *Basiceros* and *Octostruma* share a conspicuous pterostigma (for the latter, in some males it can be slightly narrower and not greatly developed);
- 13. Tegula: in *B. redux* the tegulae are round, contrasting with other *Basiceros* males, where they are subrectangular and with the posterior margin convex;

Dietz (2004: 151) also proposed transferring *B. redux* to *Octostruma* based on wing features. In addition, Dietz suggested that *B. redux* could be a male of *O. iheringi*, based on the pilosities of the petiolar peduncle and ventral face of the postpetiole. However, the current knowledge of *Octostruma* males is considerably scarce, therefore preventing a correct association of *Basiceros redux* to a valid *Octostruma* taxon.

4. Conclusion

The dirt ants remain a mysterious (and intriguing) group in terms of general biology (especially regarding dietary preferences) and behavior. The combination of peculiar pilosity and mouthparts are worth investigating. The presence of a complex intercaste mosaic makes the genus a potential model for the study of reproductive development in ants. Furthermore, additional phylogenetic information might change species boundaries within *B. disciger*. We hope that this study will contribute (and stimulate) future taxonomic and phylogenetic endeavors on the former Basicerotini.

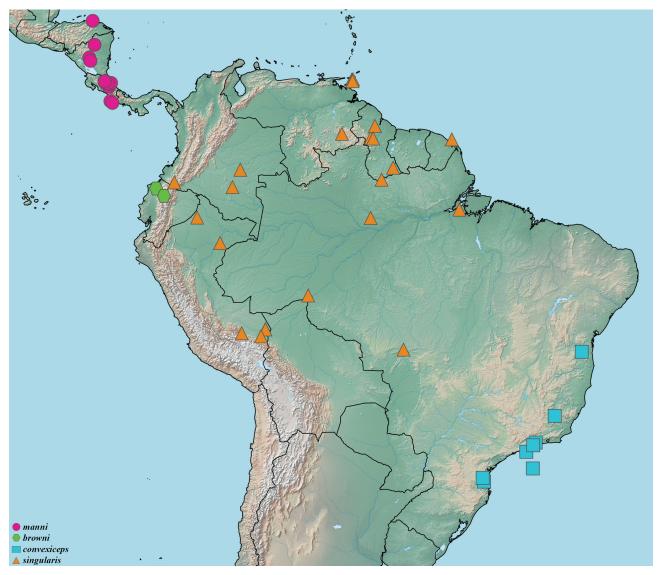


FIGURE 30. Distribution map of Basiceros species from the singularis clade.

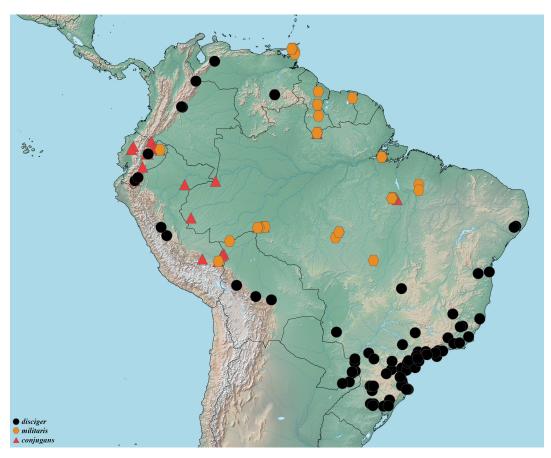


FIGURE 31. Distribution map of Basiceros species from the disciger clade (in part).

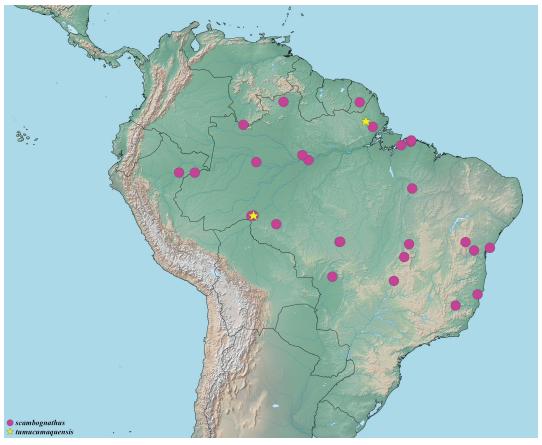


FIGURE 32. Distribution map of Basiceros scambognathus and B. tumucumaquensis sp. nov.

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